

**#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

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**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 eCO<sub>2</sub> 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 eCO<sub>2</sub> (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 [CO<sub>2</sub>] was not beneficial for model outputs: growth and photosynthesis would have been lower had we used constant [CO<sub>2</sub>] 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**

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#### **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 it's 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 CO<sub>2</sub> 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  $R_d$  as a direct function of  $A_n$  can include important bias in the model.  $R_d$  changes with temperature following an exponential function with a change in the sensitivity of parameters as  $Q_{10}$  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  $A_n$ . Maybe, modifying exponential response to temperature of  $R_d$ , according to water stress, would improve the models in a more realistic way than a mere linear dependence of  $R_d$  with  $A_n$ . On the other hand the linear dependence of  $R_d$ - $A_n$  assumes implicitly a constancy in the  $A_n/R_d$  that is well known from ecophysiology not true. A similar shortcoming arises from the linear dependence of  $J_{max}$  with  $V_{cmax}$  (line 22, page 2752). It's true both are highly coupled, but it's unclear how the  $J_{coef}$  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  $J_{max}/V_{cmax}$ , we tried also several formulations as from De Pury and Farquhar 1997 and Maseyk 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  $A_n$  to  $A_c$  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  $A_n=A_c-R_d$ , and that  $R_d=f(A_c)$ .**

**We prefer 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  $C_c$  instead of  $C_i$  in the model of Farquhar in order to take into account effect of some functional parameters as mesophyll conductance to  $CO_2$ . 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  $C_i$  instead of  $C_c$  in the Farquhar model.

**Yes, this is also true. Please, see new lines 208-213 and 245-248 where we further explain how this is addressed 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 coefficient of extinction is used to model in continuous LAI through 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 LAI<sub>sunny</sub> (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 considered 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 right. 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 does not seem 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 mismatch 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  $g_s$ ,  $E$ +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**

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### **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: [CO<sub>2</sub>] should be defined properly the first time it is used, presumably as atmospheric CO<sub>2</sub> 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: "CO<sub>2</sub>" 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 C<sub>s</sub> 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 K<sub>b</sub> used. C917

**Line 254**

pg. 2758, l20, l25 and Fig. 2: I think the units of stem biomass increment should be g m<sup>-2</sup> year<sup>-1</sup> ("-" 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 CO<sub>2</sub> effect on g<sub>s</sub>, from the effect of [CO<sub>2</sub>] on temperature? But it would be easy to make such a separation using factorial experiments (e.g. fixed [CO<sub>2</sub>] 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 K<sub>o</sub> in this equation should in fact be K<sub>c</sub>?

**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 CO<sub>2</sub> 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 processes..."

**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**

1 **Modelling the climatic drivers determining photosynthesis and carbon allocation**  
2 **in evergreen Mediterranean forests using multiproxy long time series**

3 <sup>1,\*</sup>Gea-Izquierdo G, <sup>2</sup>Guibal F, <sup>3</sup>Joffre R, <sup>3</sup>Ourcival JM, <sup>4</sup>Simioni G, <sup>1</sup>Guiot J

4 <sup>1</sup>CEREGE UMR 7330, CNRS/Aix-Marseille Université. Europole de l'Arbois BP 80  
5 13545 Aix-en-Provence cedex 4, France. <sup>2</sup>IMBE, CNRS /Aix-Marseille Université  
6 UMR 7263 Europole de l'Arbois BP 8013545 Aix-en-Provence cedex 4, France. <sup>3</sup>Centre  
7 d'Ecologie Fonctionnelle et Evolutive CEFE, UMR 5175, CNRS - Université de  
8 Montpellier - Université Paul-Valéry Montpellier – EPHE, 1919 Route de Mende,  
9 34293 Montpellier Cedex 5, FRANCE. <sup>4</sup>Ecologie des Forêts Méditerranéennes, INRA  
10 UR 629, Domaine Saint Paul, 84914 Avignon Cedex 9, France.

11 \* Author for correspondence: [gea-izquierdo@cerege.fr](mailto:gea-izquierdo@cerege.fr)

12

13 **Abstract**

14 Climatic drivers limit several important physiological processes involved in  
15 ecosystem carbon dynamics including gross primary productivity (GPP) and carbon  
16 allocation in vegetation. Climatic variability limits these two processes differently. We  
17 developed an existing mechanistic model to analyse photosynthesis and variability in  
18 carbon allocation in two evergreen species at two Mediterranean forests. The model was  
19 calibrated using a combination of eddy covariance CO<sub>2</sub> flux data, dendrochronological  
20 time series of secondary growth and forest inventory data. The model was modified to  
21 be climate explicit in the key processes addressing acclimation of photosynthesis and  
22 [the pattern of C allocation, particularly to water stress](#). It succeeded to fit both the high-  
23 and the low-frequency response of stand GPP and carbon allocation to [stem growth](#).  
24 This would support its capability to address both [C-source](#) and [C-sink](#) limitations.  
25 Simulations suggest a decrease in mean stomatal conductance in response to [recent](#)

Guillermo Gea Izquierdo 3/4/y 13:28

**Supprimé:** the

Guillermo Gea Izquierdo 10/4/y 13:37

**Supprimé:** carbon

Guillermo Gea Izquierdo 3/4/y 14:10

**Supprimé:** environmental changes

29 | [enhancement in water stress](#) and an increase in mean annual intrinsic water use  
30 | efficiency (iWUE) in both species during the last 50 years. However, this was not  
31 | translated [into](#) a parallel increase in ecosystem water use efficiency (WUE). [Interannual](#)  
32 | [variability of WUE followed closely that of iWUE at both sites. Nevertheless, long-term](#)  
33 | [decadal variability of WUE followed the](#) long-term decrease in annual GPP [matching](#)  
34 | the local trend in [annual](#) precipitation [observed](#) since the 1970s [at one site](#). In contrast,  
35 | [at the site where long-term precipitation remained stable](#) GPP and WUE did not show a  
36 | negative trend and the trees buffered the climatic variability. In our simulations these  
37 | temporal changes would be [related to acclimation processes to climate at the canopy](#)  
38 | [level including modifications in LAI and stomatal conductance, but also](#) partly related  
39 | to increasing [CO<sub>2</sub>] because the model includes biochemical equations where  
40 | photosynthesis is directly linked to [CO<sub>2</sub>]. Long-term trends in GPP did not match those  
41 | in growth, in agreement with the C-sink hypothesis. There is a great potential to use the  
42 | model with abundant dendrochronological data and analyse forest performance under  
43 | climate change. This would help to understand how different interfering environmental  
44 | factors produce instability in [the pattern of carbon allocation, hence](#) the climatic signal  
45 | expressed in tree-rings.

46

47 | **Keywords:** *Pinus halepensis*, *Quercus ilex*, process-based model, dendrochronology,  
48 | eddy covariance; global change.

Guillermo Gea Izquierdo 7/4/y 14:53

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Supprimé: observed at the site where long-term precipitation remained stable.

56

## Introduction

57 Global change challenges forest performance because it can enhance forest  
58 vulnerability (IPCC 2013). Trees modify multiple mechanisms at different scales to  
59 tackle with environmental stress, including changes in photosynthesis and carbon  
60 allocation within plants (Breda et al. 2006; Niinemets 2007; Chen et al. 2013). Many  
61 factors affect the different physiological processes driving forest performance. Among  
62 them, the net effect of rising [CO<sub>2</sub> mixing ratio](#) ([CO<sub>2</sub>]) and climate change is  
63 meaningful to determine the forests' capacity of acclimation to enhanced xericity  
64 (Peñuelas et al. 2011; Keenan et al. 2011; Fatichi et al. 2014). Forest process-based  
65 models have been developed to mimic these mechanisms. They can include different  
66 levels of complexity but generally implement calculations of leaf photosynthesis up-  
67 scaled to the canopy and carbon allocated to different plant compartments (Le Roux et  
68 al. 2001; Schaefer et al. 2012; De Kauwe et al. 2013). Although there is evidence that  
69 the tree performance depends to some extent on stored carbohydrates (Breda et al. 2006;  
70 McDowell et al. 2013; Dickman et al. 2014), these models have received some criticism  
71 when used to understand plant performance in response to climate change. This is in  
72 part because they are C-source oriented, therefore can exhibit certain limitations to  
73 represent the C-sink hypothesis ([i.e. that growth rates are limited by environmental](#)  
74 [factors such as water stress, minimum temperature or nutrient availability rather than by](#)  
75 [carbohydrate availability](#)) and address dysfunctions related to the tree hydraulics  
76 ([Millard et al. 2007](#); [Breshears et al. 2009](#); [Sala et al 2012](#); [Körner et al. 2013](#);  
77 [McDowell et al. 2013](#); [Fatichi et al. 2014](#)).

78 Complex process-based models profit from multiproxy calibration, particularly  
79 when such data [are applied](#) at different spatio-temporal scales (Peng et al. 2011). The  
80 temporal scale can be approached using time growth series of dendrochronological data.

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82 However the analysis of the past always adds uncertainties related to the influence of  
83 unknown stand conditions to properly scale productivity. Flux data including stand  
84 productivity can be estimated using the eddy covariance technique (Baldocchi 2003).  
85 These data overcome many of the limitations of dendroecological data (e.g. intra-annual  
86 resolution, control of stand conditions and scaling of net productivity) but they lack  
87 their spatial and temporal coverage. Thus, CO<sub>2</sub> [flux](#) data can be used to implement  
88 unbiased models of [canopy](#) photosynthesis, and then combined with dendroecological  
89 data to study how carbon is allocated [to stem growth](#) as a function of environmental  
90 forcing (Friedlingstein et al. 1999; Chen et al. 2013, McMurtrie & Dewar 2013).

91 Mechanistic models can be also used to analyse the environmental factors  
92 determining instability in the climate-growth response (D'Arrigo et al. 2008). Different  
93 process-based models have been applied with dendroecological data used either in  
94 forward or inverse mode (see Guiot et al. 2014 for a review). Among these models, the  
95 process-based model MAIDEN (Misson 2004) was originally developed using  
96 dendroecological data. The model explicitly includes [CO<sub>2</sub>] to calculate photosynthesis  
97 (hence its influence on carbon allocation) and includes a carbohydrate storage reservoir.  
98 The latter being one of its strengths compared to other models (Vaganov et al. 2006;  
99 Sala et al. 2012; Guiot et al. 2014). It has been previously employed to analyse growth  
100 variability in one temperate and two Mediterranean species (Misson et al. 2004;  
101 Gaucherel et al. 2008) and recently on inverse mode (also including C and O stable  
102 isotopes) to reconstruct past climate (Boucher et al. 2014). However, it requires further  
103 development to [ensure that it provides](#) unbiased estimates of forest productivity and  
104 [assesses](#) uncertainties in the response of trees to climatic variability at a greater [spatial](#)  
105 scale [at the regional level](#). Particularly, its parameterization would need improvement [if](#)

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108 | the model is applied to assess how climate modulates forest performance and the pattern  
109 | of C allocation within plants (Niinemets & Valladares 2004; Fatichi et al. 2014).

110 | In this study we use multiproxy data to develop a process-based model and  
111 | investigate how evergreen Mediterranean forests have modified stand photosynthesis  
112 | and carbon allocation in response to interacting climatic factors and enhanced [CO<sub>2</sub>] in  
113 | the recent past. The first objective was to develop a process-based model based on  
114 | MAIDEN (Misson 2004). Within the new version of the model, photosynthesis, carbon  
115 | allocation, canopy turnover and phenology are now calculated using climate explicit  
116 | functions with a mechanistic basis. The model is adapted to give unbiased estimates of  
117 | canopy photosynthesis and stem growth using instrumental data. Specifically, within the  
118 | new model formulation: (1) photosynthesis is penalized by prolonged water stress  
119 | conditions through reductions in leaf area index (LAI) and maximum photosynthetic  
120 | capacity; (2) the pattern of carbon allocation is directly determined by soil water content  
121 | (i.e. water stress) and temperature through nonlinear relationships; (3) these  
122 | relationships can be contrasting for different phenophases and affect independently  
123 | photosynthesis and the pattern of C allocation. Once the model was developed, a second  
124 | objective was to analyse how [CO<sub>2</sub>] and climatic variability affect the temporal  
125 | instability in annual forest productivity, water use efficiency and carbon allocation. We  
126 | hypothesise that they will exhibit differences in their long-term variability in relation to  
127 | recent climate change driven by different functional acclimation processes within trees.

## 129 | **Material and methods**

### 130 | *Study sites and climatic data*

131 | The study sites were two evergreen Mediterranean monitored forests in Southern  
132 | France where CO<sub>2</sub>, water vapour and energy fluxes are measured using the Eddy

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141 covariance technique (Baldocchi 2003). Both sites are included in FLUXNET  
142 (<http://fluxnet.ornl.gov/>). The first site Fontblanche (43.2° N, 5.7° E, 420 m) is a mixed  
143 stand where *Pinus halepensis* Mill. dominates the open top canopy layer reaching about  
144 12 m, *Quercus ilex* L. forms a lower canopy layer reaching about 6 m and there is a  
145 sparse shrub understory including *Quercus coccifera* L. (Simioni et al. 2013). The  
146 second site, Puechabon (43.4°N, 3.4° E, 270 m), is a dense coppice in which overstory is  
147 dominated by *Q. ilex* with density around 6,000 stems/ha (Rambal et al. 2004; Limousin  
148 et al. 2012). Both forests grow on rocky and shallow soils with low retention capacity  
149 and of Jurassic limestone origin. The climate is Mediterranean, with a water stress  
150 period in summer, cold or mild winters and most precipitation occurring between  
151 September and May. Meteorological data were obtained from the neighbouring stations  
152 of St. Martin de Londres (for Puechabon) and Aubagne (for Fontblanche). According to  
153 those data Puechabon is colder and receives more precipitation than Fontblanche (Table  
154 1). Meteorological data showed a decrease in total rainfall since the 1960s in Puechabon  
155 but no trend in Fontblanche. Both sites exhibit a positive trend in temperatures more  
156 evident for the maximum values (Figure A1).

157 We assumed that GPP is driven by the top pine and/or oak layers and that the  
158 percentage of LAI related to the understory shrub layer will behave like that of the oak  
159 species (evergreen, shrubby). For Fontblanche we considered a maximum leaf area  
160 index ( $LAI_{max}$ ) of  $2.2 \text{ m}^2 \cdot \text{m}^{-2}$  ( $3 \text{ m}^2 \cdot \text{m}^{-2}$  plant area index, PAI), composed by a 70% of  
161 pine and 30% of oak (Simioni et al. 2013). For Puechabon we considered a  $LAI_{max}$  of  
162  $2.0 \text{ m}^2 \cdot \text{m}^{-2}$  ( $2.8 \text{ m}^2 \cdot \text{m}^{-2}$  PAI) monospecific of *Q. ilex* (Baldocchi et al. 2010; Limousin et  
163 al. 2012). Specific leaf area ( $SLA$ ) considered was  $0.0045 \text{ m}^2 \cdot \text{g}^{-1}$  for *Q. ilex* and  $0.0037$   
164  $\text{m}^2 \cdot \text{g}^{-1}$  for *P. halepensis*, respectively (Hoff & Rambal 2003; Maseyk et al. 2008).

165

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167 *The model*

168 We used MAIDEN (Misson 2004), a stand productivity mechanistic model driven  
169 by a number of functions and parameters representing different processes. The model  
170 inputs are precipitation, maximum and minimum temperature and CO<sub>2</sub> with a daily time  
171 step. This model has been previously implemented for monospecific forests including  
172 two oaks and one pine species using dendroecological chronologies of growth and,  
173 when available, stand transpiration estimates from sap-flow sensors (Misson et al. 2004;  
174 Gaucherel et al. 2008). However, the model has never been compared to actual CO<sub>2</sub>  
175 data to ensure that it provides unbiased estimates of [forest](#) productivity. In this study,  
176 the model was further developed to match ground-based observations and generalize  
177 model use by modifying the photosynthesis and allocation modules (including the  
178 different phenophases) in relation to climatic drivers. To properly scale model outputs  
179 and get unbiased estimates of stand productivity we used CO<sub>2</sub> eddy covariance [fluxes](#)  
180 (Baldocchi 2003). Different parameters were calibrated to different data sources,  
181 including some species-dependent and some site-dependent parameters, as follows. [The](#)  
182 [transpiration rate \(E\) of day j is calculated using a conductance approach as](#)  
183 [E\(i\)=g<sub>s</sub>\(i\)·VPD\(i\)/P<sub>atm</sub>\(i\), where P<sub>atm</sub> is atmospheric pressure and g<sub>s</sub> and VPD are](#)  
184 [stomatal conductance and vapour pressure deficit, respectively, as described below](#)  
185 [\(Misson 2004\).](#) Those [other](#) equations used to calculate micrometeorological  
186 covariates, soil humidity and photosynthetic active radiation, as well as those functions  
187 describing the water cycle (including soil evaporation and plant transpiration) are  
188 explained in the original model formulation from Misson (2004). Therefore they won't  
189 be described here. The rest of the model was modified as follows.

190  
191 *Modelling the effect of climatic forcing on photosynthesis*

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195 Leaf photosynthesis ( $A_n$ ) is calculated based on the biochemical model of Farquhar  
 196 et al. (1980).  $A_n$  is a function of the carboxylation ( $V_c$ ), oxygenation ( $V_o$ ) and dark  
 197 respiration rates ( $R_d$ ):  $A_n(i) = V_c - 0.5V_o - R_d$ , where photosynthesis at day  $i$  is limited by  
 198 either the rate of carboxylation when Rubisco is saturated ( $W_c$ ) or when it is limited by  
 199 electron transport ( $W_j$ ), i.e.  $A_c = V_c - 0.5V_o = \min\{W_c, W_j\}$ .  $R_d$  was considered a fixed  
 200 function of  $A_c$  ( $0.006 \cdot A_c$ ), because it performed better in our daily model than  
 201 exponential formulations as a function of temperature (Sala & Tenhunen 1996; De Pury  
 202 & Farquhar 1997; Bernacchi et al. 2001). Following De Pury & Farquhar (1997):

$$W_c(i) = \frac{V_{cmax}(i) \cdot (C_i(i) - \Gamma(i))}{C_i(i) + K_c(i) \left(1 + \frac{[O_2]}{K_o(i)}\right)} \quad [E1],$$

$$W_j(i) = \frac{J_{max}(i) \cdot (C_i(i) - \Gamma(i))}{4C_i(i) + 8\Gamma(i)} \quad [E2];$$

203 where  $C_i$  is the CO<sub>2</sub> intercellular concentration,  $\Gamma$  is the [CO<sub>2</sub>] compensation point for  
 204 photosynthesis in the absence of dark respiration, and  $K_c$  and  $K_o$  are the kinetic  
 205 Michaelis-Menten constants for carboxylation and oxygenation, respectively.  $V_{cmax}$  and  
 206  $J_{max}$  are temperature dependent parameters as follows. [Photosynthesis is known to  
 207 respond to the carbon concentration within chloroplasts  \$C\_c\$  rather than to  \$C\_i\$ . We keep  
 208 through the paper the notation presented here in \[E1\] and \[E2\] but discuss below how  
 209 mesophyll conductance is taken into account empirically in relation to water stress  
 210 when calculating  \$g\_s\$  and acknowledge the possible limitations of our approach  
 211 \(Reichstein et al. 2002; Grassi & Magnani 2005; Flexas et al. 2006; Sun et al. 2014\).](#)

212 Climate influences leaf photosynthesis calculations through the temperature  
 213 dependence of different parameters (Bernacchi et al. 2001; Nobel 2009).  $\Gamma$ ,  $K_c$  and  $K_o$   
 214 were modelled using Arrhenius functions of daily mean temperature ( $T_{day}$ , in °C) with  
 215 parameters as in De Pury & Farquhar (1997). We modelled  $J_{max}$  as a fixed rate of  $V_{cmax}$   
 216 ( $J_{max}(i) = J_{coef} \cdot V_{cmax}(i)$ ) after comparing with different temperature dependent

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219 formulations (De Pury & Farquhar 1997; Maseyk et al. 2008). The [model behaviour](#)  
 220 [was better when the](#) temperature dependence of  $V_{cmax}$  [was](#) modelled using a logistic  
 221 function (Gea-Izquierdo et al. 2010) rather than an exponential function as in Misson  
 222 (2004):

$$V_{cmax}(i) = \frac{V_{max}}{(1 + \exp(V_b \cdot ((T_{day}(i) + 273) - V_{ip})))} \cdot \theta_p \quad [E3];$$

223  $V_{max}$ ,  $V_b$  and  $V_{ip}$  are parameters to be estimated, with  $V_{max}$  being the asymptote and  $V_{ip}$   
 224 the inflection point.  $\theta_p$  is a soil water stress function dependent on soil moisture  
 225 conditions of the previous year. It takes into account [down-regulation of photosynthesis](#)  
 226 [in response to](#) protracted drought [through its impact](#) on the photosynthetic capacity of  
 227 active LAI in evergreen species caused by constraints in  $V_{cmax}$  produced by irreversible  
 228 photoinhibition, modifications in [leaf](#) stoichiometry and/or aging of standing foliage  
 229 through lower [leaf](#) replacement rates in response to long-term water stress (Sala &  
 230 Tenhunen 1996; Niinemets & Valladares 2004; Niinemets 2007; Vaz et al. 2010).  
 231  $\theta_p = 1 - \exp(p_{str} \cdot SWC_{180})$  [E4], where  $p_{str}$  is a parameter to be estimated and  
 232  $SWC_{180}$  is the mean soil water content (mm) from July to December of the previous  
 233 year.

234 Photosynthesis is coupled to stomatal conductance calculation, which is estimated  
 235 using a modified version of the Leuning (1995) equation:

$$g_s(i) = \frac{g_1 \cdot A_n(i)}{(C_s(i) - \Gamma(i)) \cdot (1 + VPD(i)/VPD_0)} \cdot \theta_g(i) \quad [E5],$$

236  $g_1$  and  $VPD_0$  are parameters,  $VPD(i)$  is daily vapour pressure deficit,  $C_s$  is the [leaf](#)  
 237 surface [ $CO_2$ ];  $\theta_g$  is a non-linear soil water stress function as:

$$\theta_g(i) = \frac{1}{1 + \exp(soil_b \cdot (SWC(i) - soil_{ip}))} \quad [E6],$$

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242  $soil_b$  and  $soil_{ip}$  are parameters and  $SWC(i)$  is daily soil water content (mm).  $\theta_g$  accounts  
 243 for variability in gas exchange under drought conditions which cannot be taken into  
 244 account only through stomatal control, e.g. related to mesophyll conductance or  
 245 stomatal patchiness. [Therefore, with this empirical expression, we partly represent the](#)  
 246 [effect of CO<sub>2</sub> fractionation during mesophyll conductance under water stress,](#)  
 247 [acknowledging that this will be likely more complex under environmental stress](#)  
 248 [\(Reichstein et al. 2002; Grassi & Magnani 2005; Flexas et al. 2006; Sun et al. 2014\).](#)  
 249 The coupled photosynthesis-stomatal conductance system of equations was estimated  
 250 separately for sun and shade leaves. Canopy photosynthesis was integrated using LAI  
 251 divided into its sunlit and shaded fractions (De Pury & Farquhar 1997). Transmission  
 252 and absorption of irradiance was calculated following the Beer-Lambert law as a  
 253 function of LAI, with  $LAI_{sun}=(1-\exp(-LAI))\cdot K_b$  ( $K_b$  is the beam light extinction  
 254 coefficient, [which was set to 0.8](#)) and  $LAI_{shade}=LAI-LAI_{sun}$  (Misson 2004). In the mixed  
 255 stand (Fontblanche), photosynthesis was calculated separately for *Q. ilex* and *P.*  
 256 *halepensis*, and then integrated to get stand estimates [of forest productivity](#).

257

### 258 *Modelling the effect of climatic forcing on carbon allocation*

259 The model allocates daily carbon assimilated either to the canopy, stem, roots or  
 260 storage of non-structural carbohydrates (NSC) to mimic intra-annual carbohydrate  
 261 dynamics (Misson 2004; Dickman et al. 2014). [Although trees can store carbon within](#)  
 262 [different above-ground and below-ground compartments \(Millard et al. 2007\), carbon](#)  
 263 [storage is treated as a single pool within the model.](#) Tree autotrophic respiration ( $R_a$ ) is  
 264 modelled as a function  $f(i)$  of daily photosynthesis and maximum daily temperature  
 265 ( $T_{max}$ ) (Sala & Tenhunen 1996; Nobel 2009) as:

266 
$$R_a(i)=\max\{0.3, f(i)\}, \text{ with } f(i) = 0.47 \cdot A_n(i) \cdot (1 - \exp(p_{respi} \cdot T_{max}(i))) \quad [E7];$$

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274 where  $p_{respi}$  is a parameter. Net photosynthesis is calculated for day  $i$  as  $A_N(i)=A_n(i)-$   
 275  $R_d(i)$ . The model simulates several phenological phases [during](#) the year (see Figure 1):  
 276 [P1] winter period where all photosynthates assimilated daily  $A_N(i)$  are allocated to the  
 277 storage reservoir (NSCs) but there is no accumulation of growing degree days (GDD).  
 278 [P2] winter period where all  $A_N(i)$  are allocated to storage (i.e. the same as in [P1]) but  
 279 in opposition to [P1] there is active accumulation of GDD which define the threshold  
 280  $GDD_I$  to trigger the next phenophase [P3] (budburst, leaf-flush).  
 281 [P3] budburst, where carbon available  $C_T(i)=A_N(i)+C_{bud}$  ( $C_{bud}$  is daily C storage utilized  
 282 from buds, a parameter) is either allocated to the canopy, to roots or to the stem.  
 283 [P4] once the canopy has been completed in [P3], [the next phenophase \[P4\] starts: in](#)  
 284 [this period](#) daily photosynthates  $A_N(i)$  are allocated either to the stem or to storage;  
 285 [P5] the last phenophase [P5] starts when the photoperiod (parameter) crosses a  
 286 minimum threshold in fall. In this phase root mortality occurs. Otherwise [P5] is similar  
 287 to [P1] and [P2], in the sense that all  $A_N(i)$  is used for storage until next year [P3] starts.  
 288 Allocation of carbon to different plant compartments is complex because it can be  
 289 decoupled from photosynthetic production depending on different factors, some of them  
 290 climatic, acting at different temporal scales (Friedlingstein et al. 1999; Sala et al. 2012;  
 291 Chen et al. 2013; McMurtrie & Dewar 2013). In this new version of the model we set  
 292 the different allocation relationships as nonlinear functions of temperature and soil  
 293 water content,  $h(i)=f_1(T_{max}):f_2(SWC)$ , in [P3] and [P4] [following the functional](#)  
 294 [relationships described in Gea-Izquierdo et al. \(2013\)](#). This means that now we take into  
 295 account homeostatic acclimation processes at the canopy level related to LAI  
 296 dependence on water availability (Hoff & Rambal 1993; Sala & Tenhunen 1996;  
 297 Reichstein et al. 2003). LAI is negatively related to long-term drought because litterfall  
 298 is negatively linked to water stress (Limousin et al. 2009; Misson et al. 2011) and bud

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301 size depends on climate influencing the period of bud formation (Montserrat-Marti et al  
 302 2009). Therefore the actual carbon that can be allocated to the canopy in [P3] of year j  
 303 ( $AlloC_{canopy}(j)$ ) was set as a function of previous year moisture conditions ( $\theta_{LAI}(j)$ ), and  
 304 maximum carbon that can be allocated to the canopy ( $MaxC_{canopy}$ ).  $MaxC_{canopy}$  is  
 305 calculated from  $LAI_{max}$  and  $SLA$ , and  $AlloC_{canopy}(j)=\theta_{LAI}(j)\cdot MaxC_{canopy}$ , where:

$$306 \theta_{LAI}(j) = \left(1 - 2 \cdot \frac{p_{LAI} - SWC_{250}}{p_{LAI}}\right), \text{ constrained to } \theta_{LAI}(j) \in [0.7, 1.0] \quad [E8]$$

307  $p_{LAI}$  is a parameter to be calibrated [representing the threshold over which  \$\theta\_{LAI}\(j\) = 1\$](#)   
 308 [and](#)  $SWC_{250}$  is mean soil water content [for May-December of previous year.](#)

309 Leaf turnover is variable within years and partly related to water availability  
 310 (Limousin et al. 2009, 2012). We considered a mean [leaf](#) turnover rate of 3 years for  
 311 pines and 2 for oaks. To model within year variability in [leaf](#) phenology (i.e. leaf  
 312 growth and litterfall) we followed Maseyk et al. (2008) and Limousin et al. (2009)  
 313 (Figure 1). [C](#) allocation to the canopy (i.e. including primary growth) in [P3] is  
 314 calculated as:  $C_{canopy}(i)=C_T(i)\cdot(1-0.2\cdot h_{3\_1}(i))\cdot Ratio_{root/leaf}$ ,  $Ratio_{root/leaf}$  was fixed to 1.5  
 315 for both species (Misson et al. 2004; Ourcival, unpublished data), and:

$$316 h_{3\_1}(i) = \left(1 - \exp(p_{3moist} \cdot SWC(i)) \cdot \left(\exp\left(-0.5 \cdot \left(\frac{T_{max}(i) - p_{3temp}}{p_{3sd}}\right)^2\right)\right)\right) \quad [E9],$$

316  $p_{3moist}$ ,  $p_{3temp}$  and  $p_{3sd}$  are parameters [representing the scale of the  \$SWC\$  and the optimum](#)  
 317 [and dispersion of the  \$T\_{max}\$  functions respectively.](#) The carbon allocated to the stem  
 318 ( $C_{stem}$ ) in [P3] is  $C_{stem}(i)=C_T(i)\cdot 0.2\cdot h_{3\_1}(i)\cdot h_{3\_2}(i)$ , where:

$$319 h_{3\_2}(i) = \left(1 - \exp(st_{3moist} \cdot SWC(i)) \cdot \left(\exp\left(-0.5 \cdot \left(\frac{T_{max}(i) - st_{3temp}}{st_{3sd\_temp}}\right)^2\right)\right)\right) \quad [E10];$$

320 with  $h_{3\_1}(i)$  as in [E9];  $st_{3moist}$ ,  $st_{3temp}$  and  $st_{3sd\_temp}$  are parameters [as in  \$h\_{3\\_1}\(i\)\$](#) . The  
 321 carbon allocated to roots in [P3] is set complementary to that of the other compartments  
 322 to close the carbon budget within the tree, i.e.:  $C_{roots}(i)=C_T(i)-C_{stem}(i)-C_{canopy}(i)$ .

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329 | Finally, in [P4] carbon assimilated daily  $A_N(i)$  is allocated either to [stem growth](#) or  
330 | to storage until changing to [P5]. There since in [P1] and [P2] again all  $A_N(i)$  is only  
331 | allocated to storage until [P3] next year (Misson 2004). In [P4], the amount of carbon to  
332 | be allocated to [stem growth](#) is now also set as a function of climatic forcing:

333 |  $C_{stem}(i) = A_N(i) \cdot (1 - h_4(i))$  and  $C_{stor}(i) = A_N(i) \cdot h_4(i)$ , with:

334 | 
$$h_4(i) = \left(1 - \exp(st_{4temp} \cdot T_{max}(i))\right) \cdot \left(\exp\left(-0.5 \cdot \left(\frac{SWC(i)}{st_{4sd\_moist}}\right)^2\right)\right) \quad [E11];$$

335 |  $st_{4temp}$  and  $st_{4sd\_temp}$  are parameters [as from \[E10\]](#).

336 |

### 337 | *Eddy covariance CO<sub>2</sub> flux and dendrochronological data*

338 | The process-based model was calibrated using daily gross primary productivity  
339 | (GPP), dendrochronological data and inventory data. To develop the model, in a first  
340 | step those functions used to model daily stand photosynthesis (i.e. [E1] to [E9]) were  
341 | calibrated against GPP values. GPP estimates were obtained from half-hourly net CO<sub>2</sub>  
342 | [flux measurements](#) (NEP). GPP was obtained as the difference between measured net  
343 | ecosystem productivity and calculated ecosystem respiration (Reichstein et al. 2005).  
344 | Negative GPP values were corrected following Schaefer et al. (2012). Half-hourly GPP  
345 | data were integrated to obtain daily estimates for the period 2001-2013 (Puechabon,  
346 | methods detailed in Allard et al. (2008)) and 2008-2012 (Fontblanche) (Table 1).

347 | [In](#) a second step, those functions used to model how carbon assimilated and/or  
348 | storage is allocated to [growth of](#) the tree stem (i.e. [E10] and [E11]) were developed  
349 | using calculated annual stem biomass increment time series. Stem biomass increment  
350 | chronologies were built combining dendroecological data and forest inventory data  
351 | collected at each site. We built one chronology for *Q. ilex* in Puechabon, a second for *Q.*  
352 | *ilex* in Fontblanche and a third one for *P. halepensis* at Fontblanche (Figure 2). For  
353 | pines, two perpendicular cores were extracted using an increment borer from 25 trees in

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359 fall 2013 whereas for oaks we used crosssections. In Fontblanche, 15 oak stems were  
360 felled and basal sections collected in spring 2014. A total of 17 oak stems from  
361 Puechabon were logged in 2005 and 2008. The age and diameter distributions of the  
362 studied forests are depicted in [Figure A2](#).

363 All samples were processed using standard dendrochronological methods (Fritts  
364 1976). Annual growth (RW) was measured using a stereomicroscope and a moving  
365 table switched to a computer. RW crossdating was visually and statistically verified.  
366 RW estimates were transformed to basal area increments (BAI,  $\text{cm}^2 \cdot \text{year}^{-1}$ ). Mean BAI  
367 chronologies were obtained by averaging individual tree BAI time series. In  
368 Fontblanche BAI during the period 1987-1995 was standardized relative to the mean  
369 calculated after excluding that period (Figure 2). BAI data were standardized because  
370 we did not find a climatic explanation for the abrupt growth peak observed in  
371 Fontblanche during that period (Figure 2). Therefore we assumed that it had been  
372 caused by a release event (i.e. reduction in competition) produced by the death of  
373 neighbours as a consequence of winter frost during 1985 and 1987 (Vennetier, pers.  
374 comm., 2014). These two frosts were reflected by the presence of characteristic frost  
375 rings in most individuals from Fontblanche.

376 To scale BAI chronologies to the same units as annual stem biomass (which is an  
377 output of the model) we used plot inventory data collected around the flux towers at the  
378 two sites. Inventory data included stem diameter for all trees and tree height collected  
379 for a subsample every two years during 2007-2011 in Fontblanche, and annual diameter  
380 estimates for the period 1986-2011 for Puechabon. Individual annual biomass  
381 increments were estimated by subtracting stem biomass at consecutive years and then  
382 stand stem biomass increment (SBI,  $\text{g C m}^{-2} \cdot \text{year}^{-1}$ ) built integrating plot data. Stem  
383 biomass was calculated using allometric functions. For pines, we calculated stem

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385 biomass using diameter and estimated stem height assuming that the tree bole follows a  
386 paraboloid shape (Li et al. 2014). For oaks, stem biomass was calculated following  
387 Rambal et al. (2004). Once SBI had been estimated for the years [when](#) we had available  
388 inventory data, BAI chronologies were correlatively scaled to SBI units ( $\text{g C m}^{-2}\cdot\text{year}^{-1}$ ).  
389 <sup>1</sup>). We built two mean stand SBI chronologies, one for each site, meaning that we  
390 analysed carbon allocation within stands, not differentiating between species in  
391 Fontblanche. These two SBI chronologies were used to calibrate sitewise [E10] and  
392 [E11].

393

#### 394 *Model development and analyses*

395 Parameters were selected according to the ecological characteristics of the species,  
396 exploring the model using comprehensive sensitivity analysis to sequentially optimize  
397 groups of parameters. In a first step, a group of common parameters (those included in  
398 [E2] to [E8]) was selected using GPP data from Fontblanche (Table 2). The species-  
399 dependent parameters selected for *Q. ilex* in this first step were independently validated  
400 when applied in Puechabon (those in Table 2 common for the two sites). In a second  
401 step, a subset of site-dependent parameters was calibrated against GPP and SBI data.  
402 Four from [E6] and [E9] were calibrated using GPP data, and five parameters in [E10]  
403 and [E11] were calibrated using stem biomass increment data (Table 2). The local  
404 parameters were calibrated constrained to an ecologically realistic range using a global  
405 optimization algorithm and maximum likelihood principles (Gaucherel et al. 2008).

406 To compare model output with stem biomass chronologies as estimated from  
407 dendroecological data we used only the period where we had available daily  
408 meteorological data (1960-2013), which was also a period that did not include juvenile  
409 years with increasing BAI (BAIs reached an asymptote after increasing the first 15-20

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410 juvenile years, Figure 2). The model does not take into account how size differences in  
411 allometry or ontogeny affect carbon allocation (Chen et al. 2013). We tried to keep the  
412 model as simple as possible also because we had no such data to calibrate ontogenic  
413 effects. Hence the model is designed for non-juvenile stands with canopies that reached  
414 a steady state with asymptotic  $LAI_{max}$ . For the same reasons it does not take into  
415 account how changes in management affect carbon allocation. The model was analysed  
416 in terms of goodness of fit. Additionally, for the period where we had available daily  
417 meteorological data we simulated time series of GPP, ecosystem water use efficiency  
418 ( $WUE = GPP/ET$ , with  $ET$ =actual evapotranspiration) and intrinsic water use  
419 efficiency of sun leaves ( $iWUE = A_N/g_s$ ) calculated following Beer et al. (2009).

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## Results

422 The studied evergreen forests exhibit a bimodal pattern in GPP with maxima in  
423 spring and autumn (Figure 3) as often observed in Mediterranean ecosystems (e.g.  
424 Baldocchi et al. 2010). GPP was above zero almost every day of the year, including  
425 winter, particularly in the milder site, Fontblanche (Table 1). This means that there is  
426 active photosynthesis all year round in these evergreen forests, including both periods of  
427 climatic stress with low temperature and short photoperiod in winter, and with low  
428 moisture availability in summer (Figure 3). Mean annual GPP was  $1431.4 \pm 305.4 \text{ g C m}^{-2}$   
429  $\text{year}^{-1}$  and precipitation  $642.7 \pm 169.7 \text{ mm}$  in Fontblanche; whereas it was  $1207.3 \pm 206.7$   
430  $\text{g C m}^{-2} \text{ year}^{-1}$  and  $1002.6 \pm 328.2 \text{ mm}$  in Puechabon (see Table 1 for more details). Mean  
431 GPP was higher at Fontblanche because carbon assimilation was greater in the low  
432 temperature winter period but similar the rest of the year (Figure 3). Stem growth did  
433 not show any long-term (decadal) growth trend for any of the species studied (Figure 2).

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439 The model accurately represented the low frequency response of GPP: both the  
440 seasonal variability in GPP within years and variability in GPP among years (Figure 4).  
441 The model explained over 50% of the annual biomass growth variance, and 46% and  
442 59% of daily GPP in Fontblanche and Puechabon, respectively (Figure 4). This means  
443 that we were able to mimic the daily seasonal and long-term trends in stand  
444 productivity with unbiased estimates but also to model how carbon is allocated to stem  
445 growth along the year at the different phenophases described. The model assumed  
446 species-specific carbon allocation responses set to the different plant compartments as  
447 nonlinear functions of temperature and soil moisture. These relationships were  
448 biologically meaningful in the sense that photosynthesis and carbon allocation could be  
449 decoupled to some extent as a function of climatic variability. Once the canopy has been  
450 formed in spring, the model allocated more carbon to the stem and less to storage when  
451 less severe stress occurs, i.e. with decreasing temperatures and more humid conditions  
452 (Figure 5).

453 Both sites exhibited an increase in temperature particularly evident in the maximum  
454 values but only Puechabon suffered a decrease in annual precipitation between 1960 and  
455 2012 (Figure A1). In the model, the studied forests acclimated to changing climatic  
456 conditions in the last decades coupling different physiological traits and simulated  
457 annual GPP greatly followed the overall trends in precipitation observed. In  
458 Fontblanche, which is milder and receives less precipitation, GPP remained stable since  
459 the 1960s and presented no apparent long-term trend (Figure 6). In contrast, in the  
460 coldest and rainiest site (Puechabon) the model simulated a decrease in GPP (Figure 6),  
461 which was driven by the prevailing decrease in precipitation observed since the 1960s  
462 (Figure A1). This reduction of GPP was partly a consequence of decreased LAI in  
463 response to enhanced long-term water stress (Figure A3; Limousin et al. 2009; Misson

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472 et al. 2011). Simulated long-term decadal trends in mean annual stomatal conductance  
473 were similar and decreasing at the two sites [with greater water stress](#), as a consequence  
474 of enhanced temperatures (Figure 6). The two species studied showed a long-term  
475 increase in simulated iWUE ([Figure 7](#)) following the decrease in simulated  $g_s$  ([Figure](#)  
476 [6](#)). The interannual variability of WUE and iWUE were highly and positively correlated  
477 ([Figure 7](#)). However, in the long-term they followed a different pattern particularly in  
478 [Puechabon](#) where there was a recent decline in WUE (not observed in iWUE) forced by  
479 [trends in ET and GPP \(Figure 7\)](#). This means that the recent reduction in simulated GPP  
480 [was proportionally greater than that of simulated ET \(Figure 6; Figure A3\)](#).

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## 482 Discussion

### 483 *Linking photosynthetic production to carbon allocation as a function of climate*

484 The model calculates stand productivity and carbon allocation to stem growth in  
485 response to climate and [CO<sub>2</sub>] with realism. It is particularly well suited to mimic the  
486 effect of water stress in plant performance by the explicit assessment of different  
487 acclimation processes [at the canopy level](#) including changes in stomatal conductance  
488 and [photosynthetic capacity](#) (Sala & Tenhunen 1996; Reichstein et al. 2003; Limousin  
489 et al. 2010; Misson et al. 2011). Additionally, the model simulates carbohydrate storage  
490 dynamically as a function of environmental variability. Climate [can](#) affect differently  
491 the carbon dynamics and [pattern of C-allocation](#) to different tree compartments at  
492 different phenophases. In the model the storage reservoir is an active sink for  
493 assimilated carbon during some periods of the year and a source in spring to be used in  
494 primary and secondary growth ([Figure A5](#)). [Additionally stem growth is limited by](#)  
495 [climatic constraints \(in \[P3\] and \[P4\]\) rather than just by the amount of available](#)  
496 [carbohydrates \(Millard et al. 2007\)](#). This means that water stress and optimum

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502 temperature directly affect the modelled processes assuming that cell-wall expansion in  
503 the xylem can relate to climatic variability differently than photosynthetic production  
504 (Sala et al. 2012). The model showed C-limitation (for primary growth) the years when  
505  $LAI_{max}$  was not achieved (i.e. a limitation in LAI is driven by limitations in the C supply  
506 in spring), e.g. all years in Puechabon for the period shown in Figure A5 (1995-2012)  
507 but only those years in Fontblanche when the minimum value considered as a threshold  
508 was reached. Therefore both C-source (photosynthesis) and C-sink (just related to  
509 growth, other sinks such as volatile organic compounds or root exudates are not  
510 explicitly included in the model) limitations can be assessed at different years within  
511 one site and even at different periods within the same year (Millard et al. 2007; Sala et  
512 al. 2012; Chen et al. 2013; Fatichi et al. 2014). This hypothesis seems plausible as  
513 drought stress affects both C-source (e.g. through reduced stomatal conductance) and C-  
514 sink limitations (e.g. cell water turgor, hydraulic performance) (McDowell et al. 2013).  
515 Whether the pattern of C-storage simulated is realistic is something that needs to be  
516 validated against actual data. However, the flexible way in which stored C is modelled  
517 has much potentiality to improve ecosystem models that only view a carbon-source  
518 limitation (Sala et al. 2012; Friend et al. 2014).

519 Water stress is generally considered the greatest limitation for Mediterranean  
520 ecosystems, driving an intimate relation between precipitation and both growth and  
521 photosynthesis (Breda et al. 2006; Pereira et al. 2007; Baldocchi et al. 2010; Gea-  
522 Izquierdo & Cañellas 2014). Our results show that a long-term decrease in precipitation  
523 triggered a decrease in simulated GPP at the more rainy and continental site. However,  
524 this decline was not expressed in the growth-trends. This means that long-term  
525 productivity and allocation of C to secondary growth were decoupled and did not match  
526 (Sala et al. 2012; Chen et al. 2013; Fatichi et al. 2014). The existence of trade-offs

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534 between carbon assimilation and allocation in relation to environmental variability  
535 suggests caution when using growth as a direct proxy to investigate stand productivity  
536 dynamics (e.g. Piovesan et al. 2008; Peñuelas et al. 2008; Gea-Izquierdo & Cañellas  
537 2014). GPP was greater in the site receiving less precipitation, which could be related to  
538 differences in soil retention capacity. However both soils are calcareous, shallow and  
539 stony and differences in GPP were greatly explained by less limitation for carbon  
540 assimilation of low winter temperatures at the warmest site (Fontblanche). They can  
541 also be a result of different species composition (oak vs. pine-oak). LAI is greater at the  
542 site yielding higher annual GPP. Nonetheless, had this factor been responsible for the  
543 observed differences in winter photosynthesis, there would have also been differences  
544 in spring photosynthesis, which was not the case (Figure 3).

545 A better understanding of the underlying processes determining carbon allocation  
546 will benefit process-based models (Sala et al. 2012; Fatichi et al. 2014). Model  
547 parameters were within the range found in the literature, bearing in mind that using a  
548 daily time step to study differential processes or not distinguishing between leaf ages  
549 will affect the scaling of parameters such as  $J_{max}/V_{cmax}$  or  $R_d$  (De Pury & Farquhar 1997;  
550 Grassi & Magnani 2005; Masseyk et al. 2008; Vaz et al. 2010). Daily climatic data are  
551 readily available at a greater spatial scale than data with a higher temporal resolution,  
552 which increases applicability of daily models. Model performance could be improved  
553 by addressing respiration changes related to ontogeny and allometry, nutrient limitations  
554 (e.g. N/P) on photosynthesis, or including more complex up-scaling of leaf-level  
555 photosynthesis (Niinemets et al. 1999; Niinemets 2007; Chen et al. 2013; McMurtrie &  
556 Dewar 2013). However, it is difficult to find suitable data to calibrate such processes.  
557 Similarly, it would be challenging to include allocation to reproductive effort in the  
558 carbon budget. This is because, even if it is influenced by water stress in the studied

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562 forests (Pérez-Ramos et al. 2010), there is still great uncertainty in the causal factors  
563 driving multi-annual variability in fruit production (Koenig and Knops 2000).  
564 Addressing stand dynamics would also help to generalize model applicability. Stand  
565 disturbances modifying stand competition can leave an imprint in growth for more than  
566 a decade whereas they do not seem to affect stand GPP over more than one or two years  
567 if the disturbance is moderate (Misson et al. 2005; Granier et al. 2008). In response to  
568 changes in competition the trees modify carbon allocation or keep the root:shoot ratio  
569 constant to enhance productivity on a per-tree basis but up to an asymptotic stand GPP.  
570 Still, the model behaviour was good compared with other studies that addressed  
571 ontogenic changes in the carbon-allocation response to photosynthesis (Li et al. 2014),  
572 [and](#) similar or better than that of other mechanistic approaches calibrated to  
573 standardized dendroecological data (Misson et al. 2004; Evans et al. 2006; Gauchere et  
574 al. 2008; Tolwinski-Ward et al. 2011; Touchan et al. 2012).

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#### 576 *Forest performance in response to recent climate change and [CO<sub>2</sub>] enhancement*

577 Few studies under natural conditions observed a net increase of growth rates in  
578 response to enhanced CO<sub>2</sub> levels since the late 1800s, meaning that other factors such as  
579 water stress and/or N/P were more limiting for photosynthesis and/or allocation to  
580 growth than [CO<sub>2</sub>] (Niinemets et al. 1999; Peñuelas et al. 2011; McMurtrie & Dewar  
581 2013; Lévesque et al. 2014). Yet the forests have increased their iWUE. This can be  
582 partly a passive consequence of enhanced [CO<sub>2</sub>] but higher iWUE observed in more  
583 water stressed sites suggests that climate is co-responsible [for an](#) active acclimation [of](#)  
584 physiological plant processes (Keenan et al. 2013; Leonardi et al. 2013; Saurer et al.  
585 2014). These processes would include a higher stomatal control like in our results where  
586 in turn we did not observe any increase in long-term carbon assimilation. The mean

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591 annual stomatal conductance simulated was driven by climate but also decreased  
592 | simultaneously in time with increasing [CO<sub>2</sub>] (Appendix [A4](#)). Furthermore, there is  
593 | debate on whether there has been an increase in ecosystem WUE in response to recent  
594 | changes in [CO<sub>2</sub>] under a warming climate (Beer et al. 2009; Reichstein et al. 2002;  
595 | Keenan et al. 2013). [In our results the high-frequency of WUE followed that of iWUE,](#)  
596 | [but there was some mismatch between the two traits in the low-frequency.](#) We observed  
597 | an increase in simulated annual WUE for the period 1980-2000 at the site where  
598 | precipitation remained stable, whereas [there was a decrease in WUE following that in](#)  
599 | [GPP particularly evident in the site experiencing a drier climate in recent years. This](#)  
600 | [trend was not observed in iWUE, which means that reductions in GPP and g<sub>s</sub> were](#)  
601 | [proportionally greater than those in ET \(Figure 6, Figure 7, Appendix A3\).](#)  
602 | Higher CO<sub>2</sub> concentrations enhance photosynthesis with the equations used to  
603 | calculate leaf photosynthesis in biochemical models (e.g. Gaucherel et al. 2008; Keenan  
604 | et al. 2011; Leonardi et al. 2013; Boucher et al. 2014). Thus, the absence of a long-term  
605 | increase in GPP and growth would not mean that enhanced [CO<sub>2</sub>] was not beneficial for  
606 | model outputs [\(particularly in the case of C-source limitation\) but that the net control](#)  
607 | [exerted by other factors such as climatically driven stress was more limiting than that of](#)  
608 | [\[CO<sub>2</sub>\] availability: growth and photosynthesis would have been lower had we used](#)  
609 | constant [CO<sub>2</sub>] with the same model parameters. The absence of any [modification in the](#)  
610 | [growth trends,](#) even if there [is](#) changes in WUE, [would](#) express sink limitation [mostly](#)  
611 | related to hydraulic constraints (Peñuelas et al. 2011; Sala et al. 2012; Keenan et al.  
612 | 2013). Often, the trees express a growth decline at those sites where there is an  
613 | enhancement in long-term water stress that dominates species performance (e.g. Bigler  
614 | et al. 2006; Piovesan et al. 2008; [Gea-Izquierdo et al. 2014](#)). In contrast, it has been  
615 | observed under certain conditions that trees have increased growth with warming since

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623 | the 1850s (Salzer et al. 2009; Gea-Izquierdo & Cañellas 2014). These studies suggest  
624 | the existence of a positive effect of warming rather than that of [CO<sub>2</sub>] fertilization upon  
625 | growth in forests where water stress is not the most limiting factor. Our study sites are  
626 | located within the Northern limit of the Mediterranean Region, meaning that the two  
627 | species studied occupy drier and warmer areas more to the South. [The two species have](#)  
628 | [different functional characteristics, e.g. oaks are anisohydric whereas pines tend to be](#)  
629 | [isohydric. This confers them different capacities of adaptation to climate change, which](#)  
630 | [means that they should play different roles in future stand dynamics.](#) Our results express  
631 | the existence of trade-offs in response to climate at different phenological periods. This  
632 | is important since synergistic environmental stresses acting at different periods can  
633 | trigger tree mortality (McDowell et al. 2013; Voltas et al. 2013). Model sensitivity  
634 | analysis could be performed to discuss the influence of specific factors such as climate  
635 | or [CO<sub>2</sub>] causing instability in the climate-growth response (D'Arrigo et al. 2008;  
636 | [Boucher](#) et al. 2014). However [CO<sub>2</sub>] enhancement and climate warming are mixed in  
637 | analysis performed using data from field studies, which can make the isolation of their  
638 | effect problematic. The model can be applied using abundant dendrochronological data  
639 | used to determine the site-dependent parameters. This would give much flexibility to  
640 | investigate growth trends and forest performance in response to global change at a  
641 | larger scale.

642

### 643 **Conclusions**

644 | By developing an original process-based model with carbon allocation relationships  
645 | [explicitly expressed as functions of climate](#) we accurately simulated gross primary  
646 | productivity and [allocation of carbon to secondary](#) growth in evergreen Mediterranean  
647 | forests. Different processes were modelled as functions of environmental variability,

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653 including CO<sub>2</sub> and climate. The studied forests expressed trade-offs in carbon allocation  
654 to different plant compartments in response to stress in different seasons, namely [with](#)  
655 [low temperatures and a short photoperiod in winter](#), and [with moisture shortage in](#)  
656 [summer](#). We modelled a decreasing time trend in stomatal conductance, which would  
657 suggest a partly active increase of iWUE in the forests studied. [Interannual variability in](#)  
658 [WUE followed closely that of iWUE](#). However, WUE [exhibited a decreasing trend at](#)  
659 [the site where we simulated a decrease in LAI and GPP in response to a decrease in](#)  
660 [annual precipitation since the 1980s](#). Long-term GPP remained at similar levels in the  
661 last 50 years just in one stand whereas it declined in the forest suffering a reduction in  
662 precipitation. This suggests different acclimation processes [at the canopy level and in](#)  
663 [the pattern of allocation in response](#) to enhanced xericity and increasing CO<sub>2</sub> levels,  
664 which could not counterbalance the [negative](#) effect of warming just in one site. Tree  
665 growth was partly decoupled from stand productivity, highlighting that it can be risky to  
666 accept growth as a direct proxy to GPP. [The model is flexible enough to assess both C-](#)  
667 [source and C-sink limitations and includes a dynamic estimation of stored C. These](#)  
668 [features would improve ecosystem models with a fixed C-source formulation](#). By  
669 calibrating a limited number of parameters related to carbon allocation the model has  
670 great potential to be used with abundant dendroecological data to characterise past  
671 instability in the growth response in relation to environmental variability and simulate  
672 future forest response under different climatic scenarios.

673

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**Supprimé:** winter

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684

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951 **Table 1.** Characteristics of mean annual gross primary productivity, climatic (annual  
952 means) and growth data. Standard deviations are shown between parentheses.  
953 Precipitation=mean annual precipitation; Tmax=annual mean of mean daily maximum  
954 temperature; Tmin= annual mean of mean daily minimum temperature.  
955 Length=chronology year replicated with more than 5 radii; RW=mean annual ring-  
956 width; Rbs = mean correlation between series; AR = mean autocorrelation of raw series;  
957 MS = mean sensitivity; EPS = mean expressed population signal Rbs, AR, MS and EPS  
958 are classical statistics to characterise growth chronologies, and follow Fritts (1976).  
959

		Fontblanche		Puechabon
Flux Data	Period	2008-2012		2001-2013
	GPP annual (g C m <sup>-2</sup> year <sup>-1</sup> )	1431.4 (305.4)		1207.3 (206.7)
Climate	Period	1964-2012		1954-2013
	Precipitation (mm)	642.7 (169.7)		1002.6 (328.2)
	Tmax (°C)	20.6 (0.9)		17.8 (1.26)
	Tmin (°C)	8.8 (0.5)		8.1 (0.8)
Growth Data	Species	<i>P. halepensis</i>	<i>Q. ilex</i>	<i>Q. ilex</i>
	# Trees/Radii	25/47	15/30	17/32
	Length	1910-2013	1941-2013	1941-2005
	RW (mm)	2.19 (1.1)	1.25 (0.7)	1.13 (0.7)
	MS	0.308	0.372	0.443
	AR	0.684	0.591	0.436
	Rbs	0.541	0.281	0.457
EPS	0.963	0.884	0.949	

960

961 **Table 2.** Model parameters. Those parameter differing between sites were optimized  
962 either with GPP data (photosynthesis and allocation module) or with growth-based  
963 biomass increment chronologies (allocation module). The rest were common parameters  
964 for both sites and selected while developing the model in the first step for Fontblanche  
965 using GPP data (represented in ‘Cal’ with a ‘-’). Meaning of parameters, equation  
966 number (E#) and phenophase [P#] are as in the text in Material and Methods.  
967 Fontb=Fontblanche; Puech=Puechabon; Cal=local parameters to be calibrated with GPP  
968 or stem biomass increment data (SBI).

969

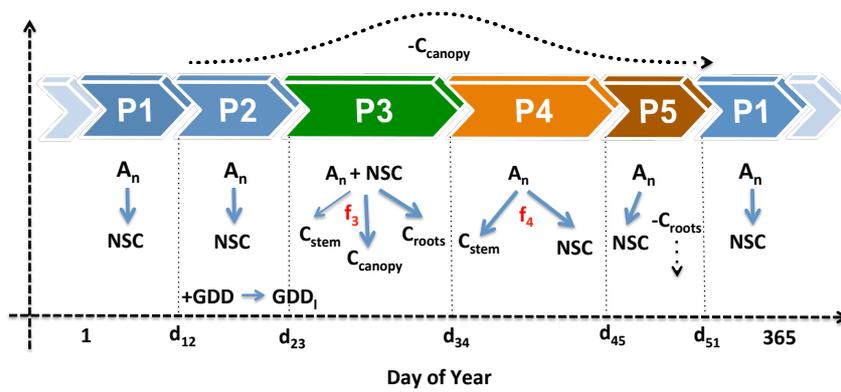
Process	Process/Equation #	Parameter	Fontb	Puech	Units	Cal	
Photosynthesis	Leaf photosynthesis [E2]	$J_{coef}$	QUIL	1.59		$\mu\text{mol C m}^{-2} \text{s}^{-1}$	-
		PIHA	1.44	-			
	Leaf photosynthesis [E3]	$V_{max}$	QUIL	32.3		$\mu\text{mol C m}^{-2} \text{s}^{-1}$	-
			PIHA	46.0	-		
		$V_b$	QUIL	-0.106		$^{\circ}\text{C}^{-1}$	-
			PIHA	-0.180	-		
	$V_{ip}$	QUIL	13.7		$^{\circ}\text{C}$	-	
		PIHA	20.0	-			
	Stress $V_{cmax}$ [E4]	$p_{str}$	-0.05		$\text{mm}^{-1}$	-	
	Stomatal conductance [E5]	$g_l$	QUIL	7.5		-	-
			PIHA	6.1	-		
	Water stress [E6]	$VPD_0$	30000		Pa	-	
$Soil_b$		-0.054		$\text{mm}^{-1}$	-		
$Soil_{ip}$		22.2	81.8		mm	GPP	
Allocation	Respiration [E7]	$p_{respi}$	-0.225		$^{\circ}\text{C}^{-1}$	-	
	Stress LAI [E8]	$p_{LAI}$	65.5		mm	-	
	[P2]	$GDD_l$	203.3		$^{\circ}\text{C}$	-	
	Stored carbon buds [P3]	$C_{bud}$	7		$\text{g C day}^{-1}$	-	
	[P5]	Photoperiod	9.5		hours	-	
	Allocation canopy [P3], [E9]	$st_{4moist}$	-0.089	-0.173	$\text{mm}^{-1}$	GPP	
		$st_{4temp}$	53.3	75	$^{\circ}\text{C}$	GPP	
		$st_{4sd}$	26.9	26.1	$^{\circ}\text{C}$	GPP	
	Allocation stem [P3], [E10]	$st_{3moist}$	-0.045	-0.117	$\text{mm}^{-1}$	SBI	
		$st_{3temp}$	32.9	6.3	$^{\circ}\text{C}$	SBI	
		$st_{3sd}$	38.0	3.0	$^{\circ}\text{C}$	SBI	
	Allocation stor/stem [P4], [E11]	$st_{4moist}$	200.8	119.3	mm	SBI	
$st_{4temp}$		0.060	-0.097	$^{\circ}\text{C}^{-1}$	SBI		

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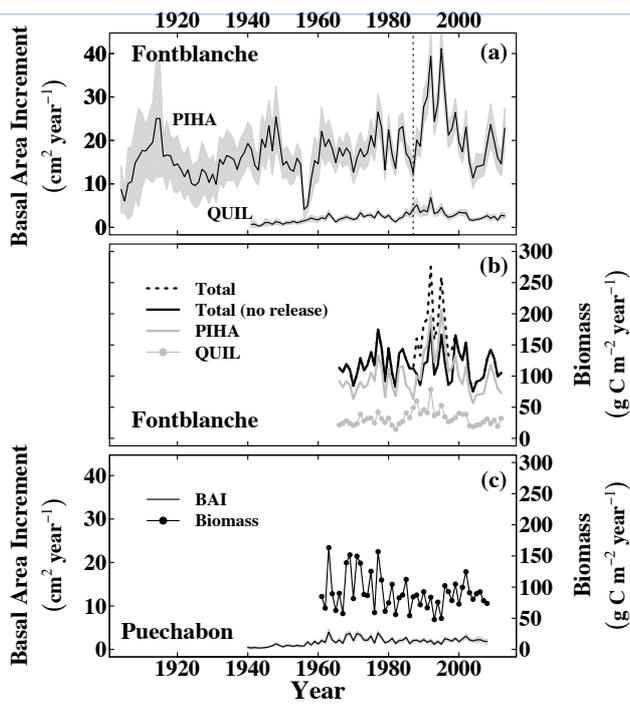
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971 **Figure 1.** Outline of the different phenological phases (P1 to P5) and carbon allocation  
 972 in the model within a given year.  $A_n$ =net daily carbon assimilation; NSC=storage (non-  
 973 structural carbohydrates); GDD=growing degree days,  $GDD_i$ =parameter determining  
 974 shift from P2 to P3 (see text);  $C$ =carbon allocated either to the stem, canopy or roots;  
 975  $d$ =day of year. Solid arrows correspond to allocation within the plant whereas dashed  
 976 arrows correspond to litterfall (canopy or roots).  $f_3$  and  $f_4$  are nonlinear functions of  
 977 soil water content and temperature determining carbon allocation to different  
 978 compartments (see text for more details).

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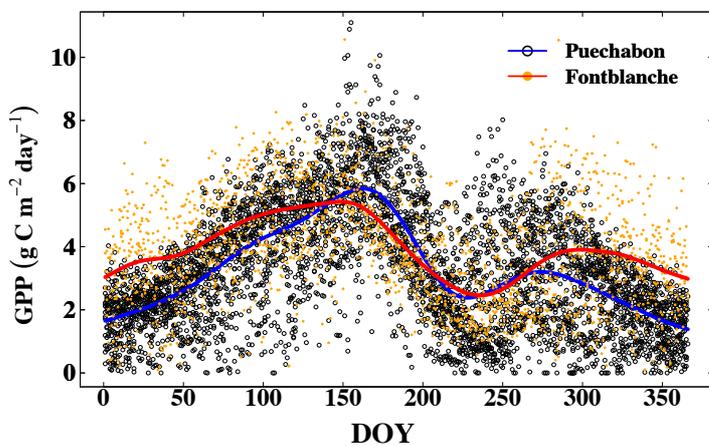


980 **Figure 2.** Growth (basal area increment, BAI,  $\text{cm}^2 \cdot \text{year}^{-1}$ ) and biomass allocated to the  
 981 tree stem ( $\text{g C} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$ ) of *Q. ilex* and *P. halepensis* at Fontblanche (growth shown in  
 982 (a), biomass in (b)) and *Q. ilex* at Puechabon (growth and stem biomass shown in (c)).  
 983 A vertical dashed line marks the release event in Fontblanche produced by the enhanced  
 984 winter mortality in 1985 in (a). Dark lines for BAI correspond to yearly means while  
 985 grey polygons show confidence intervals (at 95%) on the standard errors of the mean.



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**Figure 3.** Daily gross primary productivity (GPP) at Puechabon (2001-2013, black dots, blue line) and Fontblanche (2008-2012, orange dots, red line). DOY=day of year. Thick lines correspond to smoothers fitted to the mean to highlight seasonal trends at the two sites.



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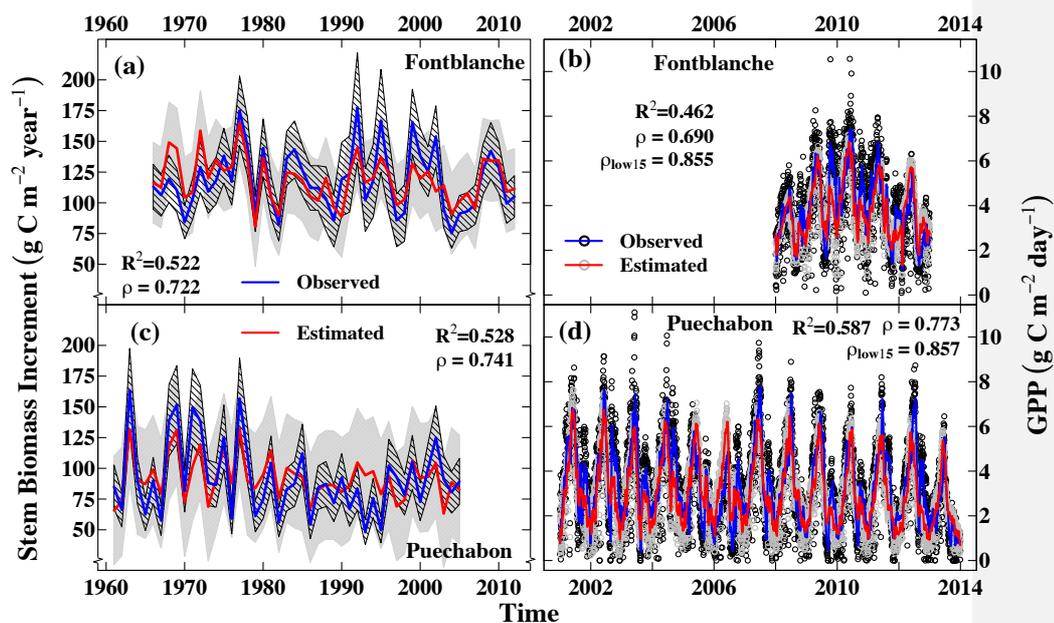
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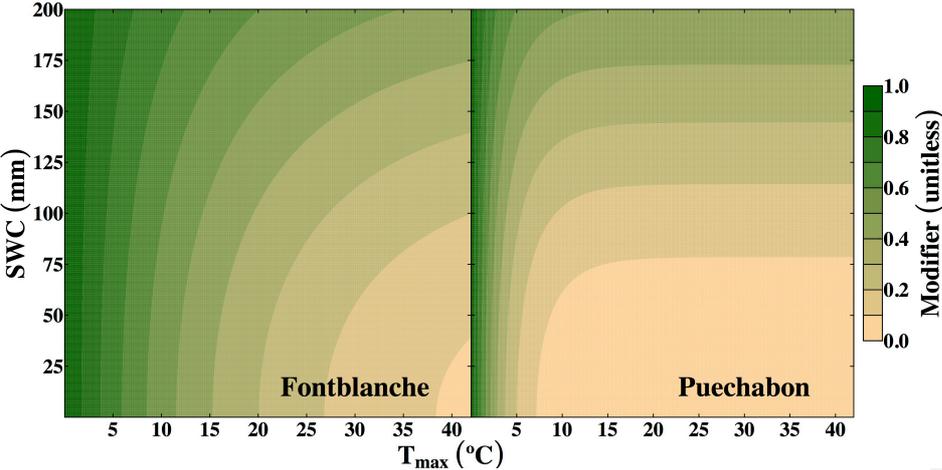
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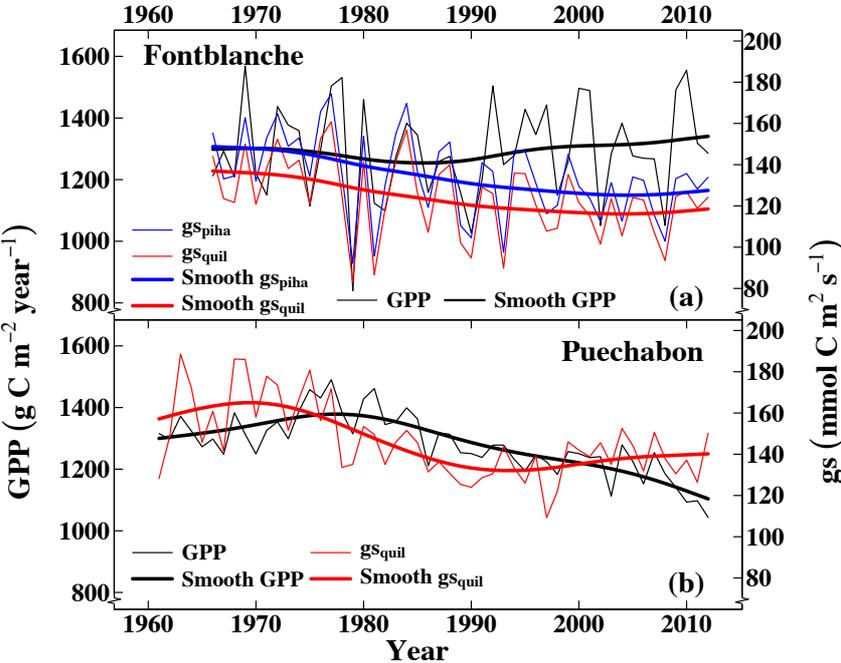
**Figure 4.** Model fit to stem biomass increment (a) and GPP (b) in Fontblanche; and stem biomass increment (c) and GPP (d) in Puechabon.  $R^2$ =coefficient of determination;  $\rho$ =linear correlation between estimated and observed data,  $\rho_{low15}$ =linear correlation between estimated and observed data smoothed with a 15 year low-pass filter (blue and red lines in (b) and (c)). Polygons behind the estimated values in (a) and (c) correspond to confidence intervals of the mean: solid grey polygons for estimated values and dashed polygons for observed stem biomass increment values.



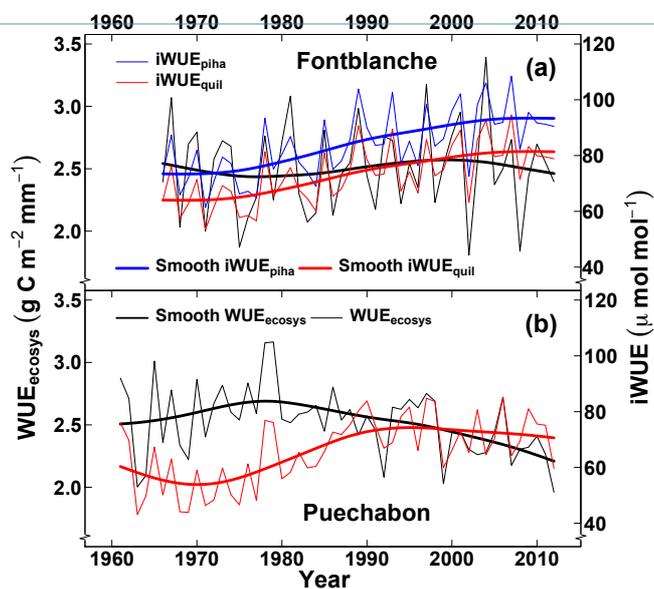
**Figure 5.** Modelled carbon allocation trajectory to the stem when leaf flush has finished in phenological period [P4]. We show the unitless modifier  $1-h_4(i)$  (i.e.  $h_4(i)$  is the portion of allocated carbon to storage) from  $C_{stem}(i) = A_N(i) \cdot [(1-h_4(i))]$  as from [E11]. The modifier [0,1] is a function of soil water content (SWC) and maximum temperature ( $T_{max}$ ) and multiplies available daily carbon to distribute daily carbon allocated between secondary growth and storage.



**Figure 6.** Modelled total annual stand gross primary productivity (GPP) and mean stomatal conductance of sunny leaves (gs) for Fontblanche (a) and Puechabon (b) for the period where meteorological data were available.



**Figure 7.** Ecosystem WUE (integral annual) and iWUE for sun leaves (mean daily, for PIHA and QUIL separated in Fontblanche) for (a) Fontblanche and (b) Puechabon for the period where we had available meteorological data.



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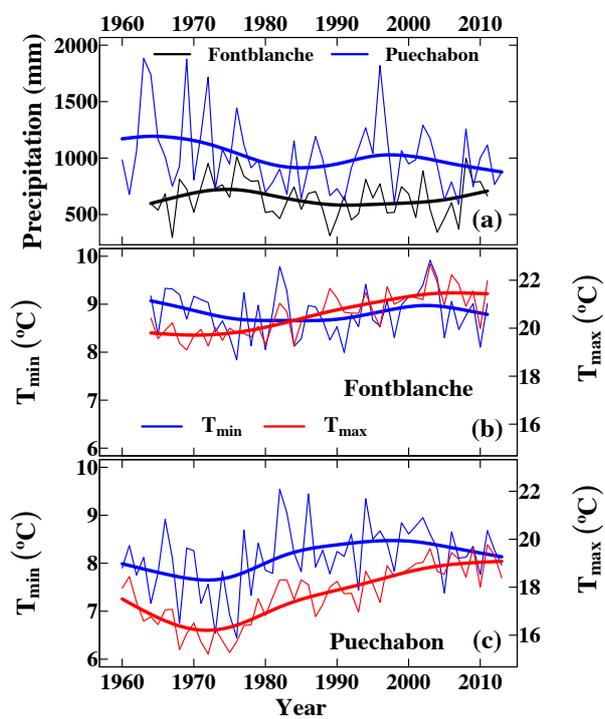
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**Figure A1.** Mean climatic time series in the last 50 years. (a) annual precipitation; (b) and (c) annual maximum ( $T_{max}$ ) and minimum ( $T_{min}$ ) temperatures for Fontblanche (b) and Puechabon (c).



**Figure A2.** Diameter (dbh, cm) and age (years) distribution of trees included in the chronologies. Frequencies are calculated separately by species and site.

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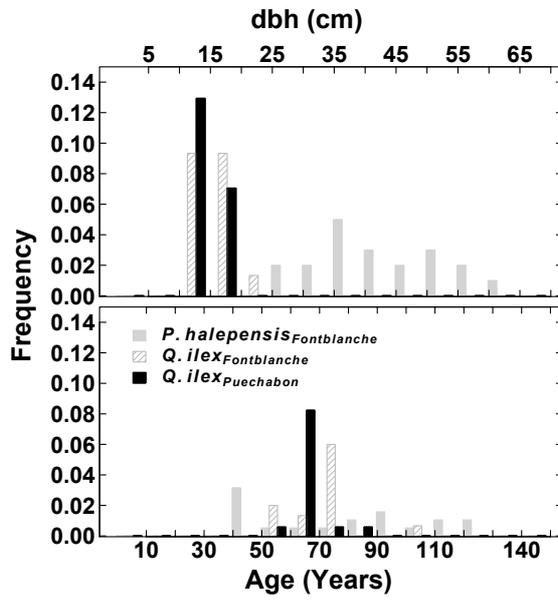
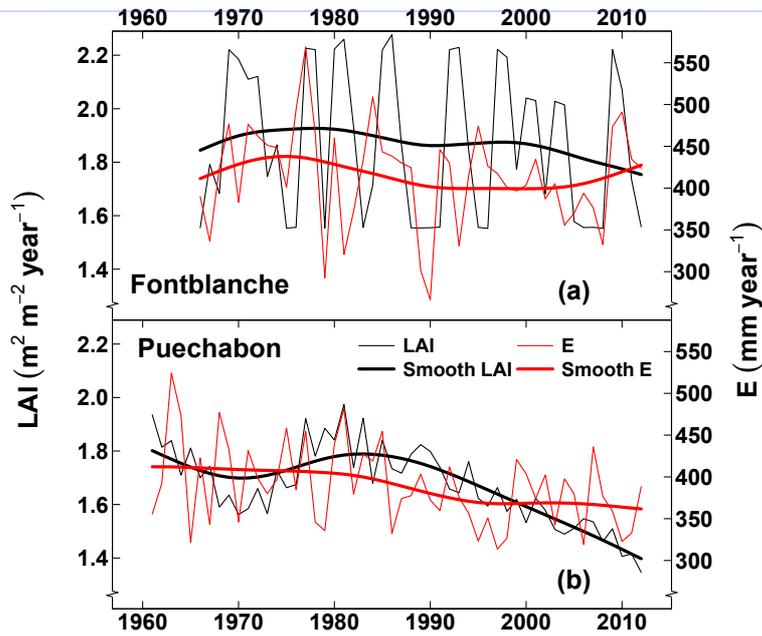
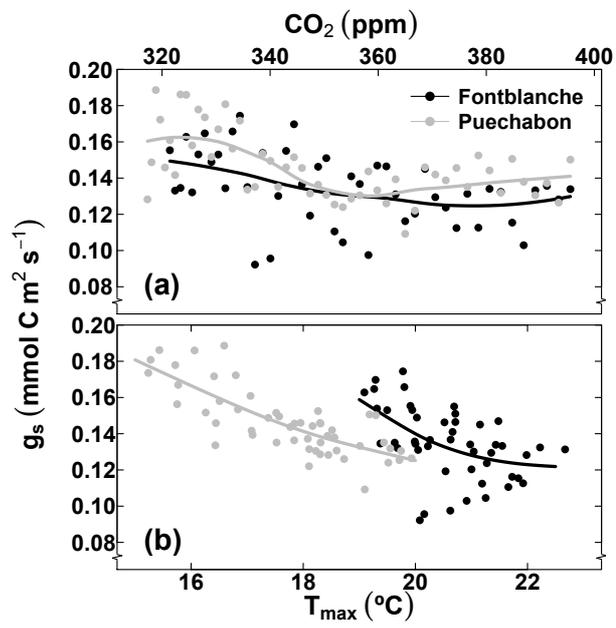


Figure A3. Simulated maximum annual leaf area index LAI ( $\text{m}^2 \cdot \text{m}^{-2}$ ) and total annual stand transpiration E (mm/year) in Fontblanche (a) and Puechabon (b).

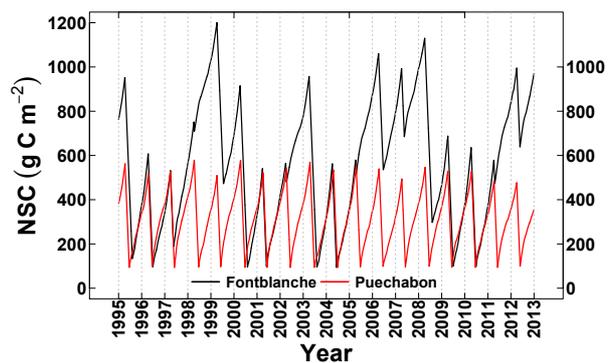


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**Figure A4.** Simulated mean annual stomatal conductance ( $g_s$ ) as a function of mean [CO<sub>2</sub>] (a) and mean maximum temperature (b).



**Figure A5.** Simulated non-structural carbohydrate content (NSC) in the storage pool at both sites. The period 1995-2012 is shown to highlight within year variability.



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