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

Dear editor, please see below a detailed response to reviewers’ comments. We have focused to better explain the methods and the analysis as requested by the reviewers. The detailed responses are in bold between lines. When we refer to the “revised version” we mean the version with track changes that we will submit together with the response.

We would like to thank you and the reviewers for your suggestions.
Yours sincerely.

Guillermo Gea-Izquierdo & coauthors

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

Since E is so much smaller than precip (~50% in Fontblanche), one could think that the site is not water limited. What’s the potential ET? Where does the difference between P-ET go? (I presume that’s a flat site, no run-off)

Yes it is a flat site, but both sites are on a calcareous substrate, which means much water will be percolated into the soil and not available for plants. Additionally in the studied site precipitation generally happens on stormy episodes. We set maximum water holding capacity to field measurements carried out within the studied sites (see references within the ms). E values shown in the ms are of similar magnitude to those in Gaucherel et al. 2008 for a similar ecosystem.

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


We have a few models that link assimilation with growth. Why another one? What’s the justification for deriving such a new model? How does it compare with other models? Could the results obtained from this model not have been obtained by using the existing ones?

The model we used is not new. It was based on an existing one (MAIDEN; Misson 2004) in which we have made a number of developments in order to improve model performance in the light of the data used and hypotheses assessed. We have cited other models in the discussion to show how they perform in terms of goodness-of-fit (lines 570-574). To check how they perform more in detail compared to our results they should need to be analysed on “ad-hoc” modeling comparison. Likely, our results of GPP should be similar to those process-based forest models based on similar photosynthesis equations, but differ in the allocation pattern particularly with those models considering allocation constant.

I find Fig. 5 quite puzzling as it seems to indicate that an extreme drought is the most favorable environment for growth (at least, for allocation to growth), yet water scarcity is likely to limit growth under those conditions. I presume AN under those conditions will be close to zero anyway because of respiration, but what’s the theoretical basis for assuming that growth (driven by turgor) is less sensitive than allocation to the hot and dry?

Please, note that in Fig 5 we show the opposite, namely that more humid conditions lead to more carbon allocated to stem growth and less to storage. Therefore, we agree with your comment.

A minor comment: I found the nomenclature a bit confusing. For instance, the authors refer to allocation to stem and allocation to storage as different things, yet a large part of storage happens in the stem. I presume the authors mean allocation to stem growth?

Yes, this is true. We modify this now for the sake of clarity, please, see e.g. new lines 23, 89, 329

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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 is difficult to have a record of annual growth of the overall parts of the tree (branches, secondary shoots, roots, etc...). However, it’s difficult to discard this important annual sink of carbon if a realistic model has to be elaborated.

We change now “limit carbon allocation” to “change patterns in carbon allocation”, e.g. see line 44.
Primary growth is included either in what we called “allocation to the canopy” or in “allocation to roots”. See e.g. line 313. We agree this is a critical point that merits further development when there is availability of such data.

Specific comments: Line 13 of abstract what kind of environmental changes are being considered by authors? Temperature increase in future? Concentration of CO2 in atmosphere? Drought? Evaporative demand? Recurrence of dry periods? All together? Authors must be more explicit.

We now state “to enhancement in water stress”, which is driven by higher temperatures and also lower precipitation at one site (Puechabon). See new line 29.
Line 15 Details of how ecosystem WUE was estimated should be pointed out. Please, see lines 418-419 (the last in the M-M) where we specify how we calculate WUE and iWUE following Beer et al. (2009)

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

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

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

Minor comment authors change abbreviator from An to Ac without a clear rationale. In addition, I do not see necessary to include the sub-index (i) in the formulations. It’s clear most parameters are variables which value depend of some constants or other functional variables. It can be inferred from lines 196-199 that An=Ac-Rd, and that Rd=f(Ac). We 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 Cc instead of Ci in the model of Farquhar in order to take into account effect of some functional parameters as mesophyll conductance to CO2. This seems not to be relevant for authors, though a comment is included
in passing when coupling stomatal conductance with photosynthesis from a modified version of Leuning (1995) equation (line 4 page 2754). At least a brief comment on the matter should be included to justify the use of Ci instead of Cc in the Farquhar model.

Yes, this is also true. Please, see new lines 208-213 and 245-248 where we further explain how this is address in the model and acknowledge the effect of possible simplifications applied.

It’s unclear how authors split total LAI in sun and shade components. If a co-efficient of extinction is used to model in continuous LAI though the crown by following the Beer–Lambert law, how it’s established the threshold to consider leaves of sun or shade type.

Total LAI is divided on sunny and shaded leaves. The amount of sunny leaves follows the expression in line 253 and then shaded leaves are just the total LAI minus LAIsunny (line 254, it was not properly expressed before). Photosynthesis is calculated for both leaves (sunny, shaded) and then integrated to the amount (i.e. proportion of LAI) of sunny and shaded leaves considered. There is no threshold, just LAI is divided in sunny and shaded components and integrated to get canopy values.

The model considers different allocation of carbon canopy, stem, roots or storage of non-structural carbohydrates (NSC), but losses as respiration are consider at the overall tree without any consideration of the specific respiratory patterns of the different carbon sinks (equation 7 in page 2754).

Yes, this is 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 not seems to be the case. How authors explain this mismatch between the two proxies of water use efficiency.

We have rewritten this point because it was not clear: there is a close match in the high-frequency annual response in both sites but there is a long-term 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 gs, E+soil evaporation (=ET) and GPP determine this relationship, and just the last three are influenced by changes in LAI simulated.

Discussion In line 20 page 2761 What are authors meaning when they refer to leaf activity? Photosynthetic activity? Respiration? Phenological phase? Please make a more precise use of physiological concepts. Stomatal conductance is coupled to other diffusional and biochemical processes that affect carbon uptake.

We add “photosynthetic capacity” to be more precise (please, see line 488)

In line 21 page 2761, the model does not simulate carbohydrate storage. At the most, it simulates carbon allocation.

Yes, the model calculates carbon allocated to storage dynamically as a function of environmental variability and in relation to carbon allocation to other plant components.

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

**We now consider this point on lines 508-509**

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

**Yes, we agree this is an interesting point to address in models**

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

**We add now a statement on this subject, lines 627-630**

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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.

Photons is indeed downscaling 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 downscaling 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, 19: 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, 17: [CO2] should be defined properly the first time it is used, presumably as atmospheric CO2 mixing ratio.

Done, line 61
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

"CO2" is often written with referring as to whether a flux or a mixing ratio is being considered. Presumably in this instance you mean flux, but this should be explicit every time you use it.

Added, see line 87

What is "at a greater scale" referring to? Spatial? Temporal? How big?

Spatial, at the regional scale (line 105)

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

Please give value of Kb used. C917

Line 254

Yes, that was a mistake that now has been corrected along the manuscript

We delete now “well-coupled” for clarity

The model analyses carbon allocation at the stand level together for both species (lines 389-392) at Fontblanche
I don’t think it is possible using Fig. A4 to separate a pure CO2 effect on gs, from the effect of [CO2] on temperature? But it would be easy to make such a separation using factorial experiments (e.g. fixed [CO2] or fixed climate).

Yes, we agree, that is what we state in that sentence “that they apply simultaneously”, line 592

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

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

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

There is a scattering of grammatical errors throughout, but I do not believe these sufficient to require copy-editing, instead I list them below.

pg. 2747, l15: "translated into a parallel increase"
Done

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

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

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

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

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

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

pg. 2752, l15: "compensation point"
Corrected

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

pg. 2753, l9: Presumably this means "reduced lower leaf replacement rates in response to long-term water stress"?
Yes, “leave” should be “leaf” instead
pg. 2754, l21: "...phenological phases during the year..."
Modified

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

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

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

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

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

pg. 2765, l6: Bouchard et al. (2014) is not in the reference list.
That should be “Boucher”, now corrected
Modelling the climatic drivers determining photosynthesis and carbon allocation in evergreen Mediterranean forests using multiproxy long time series

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Abstract

Climatic drivers limit several important physiological processes involved in ecosystem carbon dynamics including gross primary productivity (GPP) and carbon allocation in vegetation. Climatic variability limits these two processes differently. We developed an existing mechanistic model to analyse photosynthesis and variability in carbon allocation in two evergreen species at two Mediterranean forests. The model was calibrated using a combination of eddy covariance CO2 flux data, dendrochronological time series of secondary growth and forest inventory data. The model was modified to be climate explicit in the key processes addressing acclimation of photosynthesis and the pattern of C allocation, particularly to water stress. It succeeded to fit both the high- and the low-frequency response of stand GPP and carbon allocation to stem growth. This would support its capability to address both C-source and C-sink limitations. Simulations suggest a decrease in mean stomatal conductance in response to recent environmental changes.
enhancement in water stress and an increase in mean annual intrinsic water use efficiency (iWUE) in both species during the last 50 years. However, this was not translated into a parallel increase in ecosystem water use efficiency (WUE). Interannual variability of WUE followed closely that of iWUE at both sites. Nevertheless, long-term decadal variability of WUE followed the long-term decrease in annual GPP matching the local trend in annual precipitation observed since the 1970s at one site. In contrast, at the site where long-term precipitation remained stable, GPP and WUE did not show a negative trend and the trees buffered the climatic variability. In our simulations these temporal changes would be related to acclimation processes to climate at the canopy level including modifications in LAI and stomatal conductance, but also partly related to increasing [CO₂] because the model includes biochemical equations where photosynthesis is directly linked to [CO₂]. Long-term trends in GPP did not match those in growth, in agreement with the C-sink hypothesis. There is a great potential to use the model with abundant dendrochronological data and analyse forest performance under climate change. This would help to understand how different interfering environmental factors produce instability in the pattern of carbon allocation, hence the climatic signal expressed in tree-rings.

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

Global change challenges forest performance because it can enhance forest vulnerability (IPCC 2013). Trees modify multiple mechanisms at different scales to tackle with environmental stress, including changes in photosynthesis and carbon allocation within plants (Breda et al. 2006; Niinemets 2007; Chen et al. 2013). Many factors affect the different physiological processes driving forest performance. Among them, the net effect of rising $\text{CO}_2$ mixing ratio ($[\text{CO}_2]$) and climate change is meaningful to determine the forests’ capacity of acclimation to enhanced xericity (Peñuelas et al. 2011; Keenan et al. 2011; Fatichi et al. 2014). Forest process-based models have been developed to mimic these mechanisms. They can include different levels of complexity but generally implement calculations of leaf photosynthesis upscaled to the canopy and carbon allocated to different plant compartments (Le Roux et al. 2001; Schaefer et al. 2012; De Kauwe et al. 2013). Although there is evidence that the tree performance depends to some extent on stored carbohydrates (Breda et al. 2006; McDowell et al. 2013; Dickman et al. 2014), these models have received some criticism when used to understand plant performance in response to climate change. This is in part because they are C-source oriented, therefore can exhibit certain limitations to represent the C-sink hypothesis (i.e., that growth rates are limited by environmental factors such as water stress, minimum temperature or nutrient availability rather than by carbohydrate availability) and address dysfunctions related to the tree hydraulics (Millard et al. 2007; Breshears et al. 2009; Sala et al 2012; Körner et al. 2013; McDowell et al. 2013; Fatichi et al. 2014).

Complex process-based models profit from multiproxy calibration, particularly when such data are applied at different spatio-temporal scales (Peng et al. 2011). The temporal scale can be approached using time growth series of dendrochronological data.
However the analysis of the past always adds uncertainties related to the influence of unknown stand conditions to properly scale productivity. Flux data including stand productivity can be estimated using the eddy covariance technique (Baldocchi 2003). These data overcome many of the limitations of dendroecological data (e.g. intra-annual resolution, control of stand conditions and scaling of net productivity) but they lack their spatial and temporal coverage. Thus, CO₂ flux data can be used to implement unbiased models of canopy photosynthesis, and then combined with dendroecological data to study how carbon is allocated to stem growth as a function of environmental forcing (Friedlingstein et al. 1999; Chen et al. 2013, McMurtrie & Dewar 2013).

Mechanistic models can be also used to analyse the environmental factors determining instability in the climate-growth response (D’Arrigo et al. 2008). Different process-based models have been applied with dendroecological data used either in forward or inverse mode (see Guiot et al. 2014 for a review). Among these models, the process-based model MAIDEN (Misson 2004) was originally developed using dendroecological data. The model explicitly includes [CO₂] to calculate photosynthesis (hence its influence on carbon allocation) and includes a carbohydrate storage reservoir. The latter being one of its strengths compared to other models (Vaganov et al. 2006; Sala et al. 2012; Guiot et al. 2014). It has been previously employed to analyse growth variability in one temperate and two Mediterranean species (Misson et al. 2004; Gaucherel et al. 2008) and recently on inverse mode (also including C and O stable isotopes) to reconstruct past climate (Boucher et al. 2014). However, it requires further development to ensure that it provides unbiased estimates of forest productivity and assesses uncertainties in the response of trees to climatic variability at a greater spatial scale at the regional level. Particularly, its parameterization would need improvement if...
the model is applied to assess how climate modulates forest performance and the pattern of C allocation within plants (Niinemets & Valladares 2004; Fatichi et al. 2014).

In this study we use multiproxy data to develop a process-based model and investigate how evergreen Mediterranean forests have modified stand photosynthesis and carbon allocation in response to interacting climatic factors and enhanced [CO₂] in the recent past. The first objective was to develop a process-based model based on MAIDEN (Misson 2004). Within the new version of the model, photosynthesis, carbon allocation, canopy turnover and phenology are now calculated using climate explicit functions with a mechanistic basis. The model is adapted to give unbiased estimates of canopy photosynthesis and stem growth using instrumental data. Specifically, within the new model formulation: (1) photosynthesis is penalized by prolonged water stress conditions through reductions in leaf area index (LAI) and maximum photosynthetic capacity; (2) the pattern of carbon allocation is directly determined by soil water content (i.e. water stress) and temperature through nonlinear relationships; (3) these relationships can be contrasting for different phenophases and affect independently photosynthesis and the pattern of C allocation. Once the model was developed, a second objective was to analyse how [CO₂] and climatic variability affect the temporal instability in annual forest productivity, water use efficiency and carbon allocation. We hypothesise that they will exhibit differences in their long-term variability in relation to recent climate change driven by different functional acclimation processes within trees.

Material and methods

Study sites and climatic data

The study sites were two evergreen Mediterranean monitored forests in Southern France where CO₂, water vapour and energy fluxes are measured using the Eddy
covariance technique (Baldocchi 2003). Both sites are included in FLUXNET (http://fluxnet.ornl.gov/). The first site Fontblanche (43.2° N, 5.7° E, 420 m) is a mixed stand where *Pinus halepensis* Mill. dominates the open top canopy layer reaching about 12 m. *Quercus ilex* L. forms a lower canopy layer reaching about 6 m and there is a sparse shrub understory including *Quercus coccifera* L. (Simioni et al. 2013). The second site, Puechabon (43.4°N, 3.4° E, 270 m), is a dense coppice in which overstory is dominated by *Q. ilex* with density around 6,000 stems/ha (Rambal et al. 2004; Limousin et al. 2012). Both forests grow on rocky and shallow soils with low retention capacity and of Jurassic limestone origin. The climate is Mediterranean, with a water stress period in summer, cold or mild winters and most precipitation occurring between September and May. Meteorological data were obtained from the neighbouring stations of St. Martin de Londres (for Puechabon) and Aubagne (for Fontblanche). According to those data Puechabon is colder and receives more precipitation than Fontblanche (Table 1). Meteorological data showed a decrease in total rainfall since the 1960s in Puechabon but no trend in Fontblanche. Both sites exhibit a positive trend in temperatures more evident for the maximum values (Figure A1).

We assumed that GPP is driven by the top pine and/or oak layers and that the percentage of LAI related to the understory shrub layer will behave like that of the oak species (evergreen, shrubby). For Fontblanche we considered a maximum leaf area index (*LAI*_max) of 2.2 m²·m⁻² (3 m²·m⁻² plant area index, PAI), composed by a 70% of pine and 30% of oak (Simioni et al. 2013). For Puechabon we considered a *LAI*_max of 2.0 m²·m⁻² (2.8 m²·m⁻² PAI) monospecific of *Q. ilex* (Baldocchi et al. 2010; Limousin et al. 2012). Specific leaf area (*SLA*) considered was 0.0045 m²·g⁻¹ for *Q. ilex* and 0.0037 m²·g⁻¹ for *P. halepensis*, respectively (Hoff & Rambal 2003; Maseyk et al. 2008).
The model

We used MAIDEN (Misson 2004), a stand productivity mechanistic model driven by a number of functions and parameters representing different processes. The model inputs are precipitation, maximum and minimum temperature and CO₂ with a daily time step. This model has been previously implemented for monospecific forests including two oaks and one pine species using dendroecological chronologies of growth and, when available, stand transpiration estimates from sap-flow sensors (Misson et al. 2004; Gaucherel et al. 2008). However, the model has never been compared to actual CO₂ data to ensure that it provides unbiased estimates of forest productivity. In this study, the model was further developed to match ground-based observations and generalize model use by modifying the photosynthesis and allocation modules (including the different phenophases) in relation to climatic drivers. To properly scale model outputs and get unbiased estimates of stand productivity we used CO₂ eddy covariance fluxes (Baldocchi 2003). Different parameters were calibrated to different data sources, including some species-dependent and some site-dependent parameters, as follows. The transpiration rate (E) of day j is calculated using a conductance approach as:

\[ E(j) = g_s(j) \cdot VPD(j) / P_{atm}(j) \]

where \( P_{atm} \) is atmospheric pressure and \( g_s \) and \( VPD \) are stomatal conductance and vapour pressure deficit, respectively, as described below (Misson 2004). Those other equations used to calculate micrometeorological covariates, soil humidity and photosynthetic active radiation, as well as those functions describing the water cycle (including soil evaporation and plant transpiration) are explained in the original model formulation from Misson (2004). Therefore they won’t be described here. The rest of the model was modified as follows.

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

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

$$W_j(i) = \frac{J_{max}(i) \cdot (C_i(i) - \Gamma(i))}{4C_i(i) + B\Gamma(i)} \tag{E2};$$

where $C_i$ is the CO$_2$ intercellular concentration, $\Gamma$ is the [CO$_2$] compensation point for photosynthesis in the absence of dark respiration, and $K_c$ and $K_o$ are the kinetic Michaelis-Menten constants for carboxylation and oxygenation, respectively. $V_{cmax}$ and $J_{max}$ are temperature dependent parameters as follows. Photosynthesis is known to respond to the carbon concentration within chloroplasts $C_i$ rather than to $C_i$. We keep through the paper the notation presented here in [E1] and [E2] but discuss below how mesophyll conductance is taken into account empirically in relation to water stress when calculating $g_s$ and acknowledge the possible limitations of our approach (Reichstein et al. 2002; Grassi & Magnani 2005; Flexas et al. 2006; Sun et al. 2014).

Climate influences leaf photosynthesis calculations through the temperature dependence of different parameters (Bernacchi et al. 2001; Nobel 2009). $\Gamma$, $K_c$ and $K_o$ were modelled using Arrhenius functions of daily mean temperature ($T_{day}$, in °C) with parameters as in De Pury & Farquhar (1997). We modelled $J_{max}$ as a fixed rate of $V_{cmax}$ ($J_{max}(i) = J_{conf} \cdot V_{cmax}(i)$) after comparing with different temperature dependent
formulations (De Pury & Farquhar 1997; Maseyk et al. 2008). The model behaviour was better when the temperature dependence of $V_{\text{max}}$ was modelled using a logistic function (Gea-Izquierdo et al. 2010) rather than an exponential function as in Misson (2004):

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

$V_{\text{max}}$, $V_b$ and $V_{ip}$ are parameters to be estimated, with $V_{\text{max}}$ being the asymptote and $V_{ip}$ the inflection point. $\theta_p$ is a soil water stress function dependent on soil moisture conditions of the previous year. It takes into account down-regulation of photosynthesis in response to protracted drought through its impact on the photosynthetic capacity of active LAI in evergreen species caused by constraints in $V_{\text{max}}$ produced by irreversible photoinhibition, modifications in leaf stoichiometry and/or aging of standing foliage through lower leaf replacement rates in response to long-term water stress (Sala & Tenhunen 1996; Niinemets & Valladares 2004; Niinemets 2007; Vaz et al. 2010).

$\theta_p = 1 - \exp(p_{str} \cdot SWC_{180}) \quad [E4]$, where $p_{str}$ is a parameter to be estimated and $SWC_{180}$ is the mean soil water content (mm) from July to December of the previous year.

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

$$g_s(i) = \frac{g_1 \cdot A_n(i)}{(C_s(i) - \Gamma(i)) \cdot (1 + \text{VPD}(i)/\text{VPD}_0)} \cdot \theta_\theta(i) \quad [E5],$$

$g_1$ and VPD$_0$ are parameters, VPD($i$) is daily vapour pressure deficit, $C_s$ is the leaf surface [CO$_2$]; $\theta_\theta$ is a non-linear soil water stress function as:

$$\theta_\theta(i) = \frac{1}{1 + \exp(soll_\theta \cdot (\text{SWC}(i) - solli_\theta))} \quad [E6].$$
soil\(_b\) and soil\(_p\) are parameters and SWC\((i)\) is daily soil water content (mm). \(\theta_p\) accounts for variability in gas exchange under drought conditions which cannot be taken into account only through stomatal control, e.g. related to mesophyll conductance or stomatal patchiness. Therefore, with this empirical expression we partly represent the effect of CO\(_2\) fractionation during mesophyll conductance under water stress, acknowledging that this will be likely more complex under environmental stress (Reichstein et al. 2002; Grassi & Magnani 2005; Flexas et al. 2006; Sun et al. 2014). The coupled photosynthesis-stomatal conductance system of equations was estimated separately for sun and shade leaves. Canopy photosynthesis was integrated using LAI divided into its sunlit and shaded fractions (De Pury & Farquhar 1997). Transmission and absorption of irradiance was calculated following the Beer-Lambert law as a function of LAI, with LAI\(_{sun}=\text{(1-exp(-LAI))}\cdot K_b\) (\(K_b\) is the beam light extinction coefficient, which was set to 0.8) and LAI\(_{shade}=\text{LAI}_\text{total}-\text{LAI}_\text{sun}\) (Misson 2004). In the mixed stand (Fontblanche), photosynthesis was calculated separately for Q. ilex and P. halepensis, and then integrated to get stand estimates of forest productivity.

Modelling the effect of climatic forcing on carbon allocation

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

\[
R_a(i)=\max\{0.3, f(i)\}, \text{ with } f(i) = 0.47 \cdot A_n(i) \cdot (1 - \exp(p_{prepl} \cdot T_{max}(i)) \text{ [E7]};
\]
where $p_{respi}$ is a parameter. Net photosynthesis is calculated for day $i$ as $A_N(i) = A_n(i) - R_d(i)$. The model simulates several phenological phases during the year (see Figure 1):

[P1] winter period where all photosynthates assimilated daily $A_N(i)$ are allocated to the storage reservoir (NSCs) but there is no accumulation of growing degree days (GDD).

[P2] winter period where all $A_N(i)$ are allocated to storage (i.e. the same as in [P1]) but in opposition to [P1] there is active accumulation of GDD which define the threshold $GDD_1$ to trigger the next phenophase [P3] (budburst, leaf-flush).

[P3] budburst, where carbon available $C_T(i) = A_N(i) + C_{bud}$ (C$_{bud}$ is daily C storage utilized from buds, a parameter) is either allocated to the canopy, to roots or to the stem.

[P4] once the canopy has been completed in [P3], the next phenophase [P4] starts; in this period daily photosynthates $A_N(i)$ are allocated either to the stem or to storage;

[P5] the last phenophase [P5] starts when the photoperiod (parameter) crosses a minimum threshold in fall. In this phase root mortality occurs. Otherwise [P5] is similar to [P1] and [P2], in the sense that all $A_N(i)$ is used for storage until next year [P3] starts.

Allocation of carbon to different plant compartments is complex because it can be decoupled from photosynthetic production depending on different factors, some of them climatic, acting at different temporal scales (Friedlingstein et al. 1999; Sala et al. 2012; Chen et al. 2013; McMurtrie & Dewar 2013). In this new version of the model we set the different allocation relationships as nonlinear functions of temperature and soil water content, $h(i) = f_1(T_{max}) f_2(SWC)$, in [P3] and [P4]. Following the functional relationships described in Gea-Izquierdo et al. (2013), this means that now we take into account homeostatic acclimation processes at the canopy level related to LAI dependence on water availability (Hoff & Rambal 1993; Sala & Tenhunen 1996; Reichstein et al. 2003). LAI is negatively related to long-term drought because litterfall is negatively linked to water stress (Limousin et al. 2009; Misson et al. 2011) and bud
size depends on climate influencing the period of bud formation (Montserrat-Martí et al. 2009). Therefore the actual carbon that can be allocated to the canopy in [P3] of year j (Allo\(_{\text{canopy}}(j)\)) was set as a function of previous year moisture conditions (\(\theta_{\text{LAI}}(j)\)), and maximum carbon that can be allocated to the canopy (Max\(_{\text{canopy}}\)). Max\(_{\text{canopy}}\) is calculated from LAI\(_{\text{max}}\) and SLA, and Allo\(_{\text{canopy}}(j)=\theta_{\text{LAI}}(j)\cdot\text{Max}_{\text{canopy}}\), where:

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

\(p_{\text{LAI}}\) is a parameter to be calibrated representing the threshold over which \(\theta_{\text{LAI}}(j) = 1\), and \(\text{SWC}_{250}\) is mean soil water content for May-December of previous year.

Leaf turnover is variable within years and partly related to water availability (Limousin et al. 2009, 2012). We considered a mean leaf turnover rate of 3 years for pines and 2 for oaks. To model within year variability in leaf phenology (i.e. leaf growth and litterfall) we followed Maseyk et al. (2008) and Limousin et al. (2009) (Figure 1). Allocation to the canopy (i.e. including primary growth) in [P3] is calculated as:

\[
C_{\text{canopy}}(i) = C_{\text{r}}(i) \cdot (1-0.2 \cdot h_{1,i}(i)) \cdot \text{Ratio}_{\text{root/leaf}}; \quad \text{Ratio}_{\text{root/leaf}} \text{ was fixed to 1.5 for both species (Misson et al. 2004; Oursivcual, unpublished data).}
\]

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

\(p_{\text{moist}}, p_{\text{temp}}\) and \(p_{\text{std}}\) are parameters representing the scale of the SWC and the optimum and dispersion of the \(T_{\text{max}}\) functions respectively. The carbon allocated to the stem (C\(_{\text{stem}}\)) in [P3] is C\(_{\text{stem}}(i) = C_{\text{r}}(i) \cdot 0.2 \cdot h_{1,i}(i) \cdot h_{2,i}(i)\), where:

\[
h_{2,i}(i) = (1 - \exp(st_{\text{moist}} \cdot \text{SWC}(i)) \cdot \left(\exp\left(-0.5 \cdot \frac{T_{\text{max}}(i) - st_{\text{temp}}}{st_{\text{std}}\text{temp}}\right)^2\right)) \quad [E10];
\]

with \(h_{2,i}(i)\) as in [E9]; \(st_{\text{moist}}, st_{\text{temp}}\) and \(st_{\text{std}}\) are parameters as in \(h_{1,i}(i)\). The carbon allocated to roots in [P3] is set complementary to that of the other compartments to close the carbon budget within the tree, i.e.: C\(_{\text{root}}(i) = C_{\text{r}}(i) - C_{\text{stem}}(i) - C_{\text{canopy}}(i)\).
Finally, in [P4] carbon assimilated daily $A_N(i)$ is allocated either to stem growth or to storage until changing to [P5]. There since in [P1] and [P2] again all $A_N(i)$ is only allocated to storage until [P3] next year (Misson 2004). In [P4], the amount of carbon to be allocated to stem growth is now also set as a function of climatic forcing:

$$C_{stem}(i) = A_N(i) \cdot (1 - h_4(i))$$

$$C_{stor}(i) = A_N(i) \cdot h_4(i)$$

with:

$$h_4(i) = \left(1 - \exp \left(st_{4temp} \cdot T_{max}(i)\right) \cdot \left(\exp \left(-0.5 \cdot \frac{SWC(i)}{st_{4sid.mois}}\right)\right)^2\right)$$

$st_{4temp}$ and $st_{4sid.temp}$ are parameters as from [E10].

Eddy covariance CO$_2$ flux and dendrochronological data

The process-based model was calibrated using daily gross primary productivity (GPP), dendrochronological data and inventory data. To develop the model, in a first step those functions used to model daily stand photosynthesis (i.e. [E1] to [E9]) were calibrated against GPP values. GPP estimates were obtained from half-hourly net CO$_2$ flux measurements (NEP). GPP was obtained as the difference between measured net ecosystem productivity and calculated ecosystem respiration (Reichstein et al. 2005). Negative GPP values were corrected following Schaefer et al. (2012). Half-hourly GPP data were integrated to obtain daily estimates for the period 2001-2013 (Puechabon, methods detailed in Allard et al. (2008)) and 2008-2012 (Fontblanche) (Table 1).

In a second step, those functions used to model how carbon assimilated and/or storage is allocated to growth of the tree stem (i.e. [E10] and [E11]) were developed using calculated annual stem biomass increment time series. Stem biomass increment chronologies were built combining dendroecological data and forest inventory data collected at each site. We built one chronology for Q. ilex in Puechabon, a second for Q. ilex in Fontblanche and a third one for P. halepensis at Fontblanche (Figure 2). For pines, two perpendicular cores were extracted using an increment borer from 25 trees in
fall 2013 whereas for oaks we used crosssections. In Fontblanche, 15 oak stems were
felled and basal sections collected in spring 2014. A total of 17 oak stems from
Puechabon were logged in 2005 and 2008. The age and diameter distributions of the
studied forests are depicted in Figure A2.

All samples were processed using standard dendrochronological methods (Fritts
1976). Annual growth (RW) was measured using a stereomicroscope and a moving
table switched to a computer. RW crossdating was visually and statistically verified.
RW estimates were transformed to basal area increments (BAI, cm²·year⁻¹). Mean BAI
chronologies were obtained by averaging individual tree BAI time series. In
Fontblanche BAI during the period 1987-1995 was standardized relative to the mean
calculated after excluding that period (Figure 2). BAI data were standardized because
we did not find a climatic explanation for the abrupt growth peak observed in
Fontblanche during that period (Figure 2). Therefore we assumed that it had been
caused by a release event (i.e. reduction in competition) produced by the death of
neighbours as a consequence of winter frost during 1985 and 1987 (Vennetier, pers.
comm., 2014). These two frosts were reflected by the presence of characteristic frost
rings in most individuals from Fontblanche.

To scale BAI chronologies to the same units as annual stem biomass (which is an
output of the model) we used plot inventory data collected around the flux towers at the
two sites. Inventory data included stem diameter for all trees and tree height collected
for a subsample every two years during 2007-2011 in Fontblanche, and annual diameter
estimates for the period 1986-2011 for Puechabon. Individual annual biomass
increments were estimated by subtracting stem biomass at consecutive years and then
stand stem biomass increment (SBI, g C m⁻²·year⁻¹) built integrating plot data. Stem
biomass was calculated using allometric functions. For pines, we calculated stem
biomass using diameter and estimated stem height assuming that the tree bole follows a paraboloid shape (Li et al. 2014). For oaks, stem biomass was calculated following Rambal et al. (2004). Once SBI had been estimated for the years when we had available inventory data, BAI chronologies were correlatively scaled to SBI units (g C m$^{-2}$·year$^{-1}$). We built two mean stand SBI chronologies, one for each site, meaning that we analysed carbon allocation within stands, not differentiating between species in Fontblanche. These two SBI chronologies were used to calibrate sitewise [E10] and [E11].

Model development and analyses

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

To compare model output with stem biomass chronologies as estimated from dendroecological data we used only the period where we had available daily meteorological data (1960-2013), which was also a period that did not include juvenile years with increasing BAI (BAIs reached an asymptote after increasing the first 15-20
juvenile years, Figure 2). The model does not take into account how size differences in allometry or ontogeny affect carbon allocation (Chen et al. 2013). We tried to keep the model as simple as possible also because we had no such data to calibrate ontogenic effects. Hence the model is designed for non-juvenile stands with canopies that reached a steady state with asymptotic LAI\textsubscript{max}. For the same reasons it does not take into account how changes in management affect carbon allocation. The model was analysed in terms of goodness of fit. Additionally, for the period where we had available daily meteorological data we simulated time series of GPP, ecosystem water use efficiency \((WUE = GPP/ET\text{, with ET=actual evapotranspiration})\) and intrinsic water use efficiency of sun leaves \((iWUE = A_n/g_s)\) calculated following Beer et al. (2009).

Results

The studied evergreen forests exhibit a bimodal pattern in GPP with maxima in spring and autumn (Figure 3) as often observed in Mediterranean ecosystems (e.g. Baldocchi et al. 2010). GPP was above zero almost every day of the year, including winter, particularly in the milder site, Fontblanche (Table 1). This means that there is active photosynthesis all year round in these evergreen forests, including both periods of climatic stress with low temperature and short photoperiod in winter, and with low moisture availability in summer (Figure 3). Mean annual GPP was 1431.4±305.4 g C m\textsuperscript{-2} year\textsuperscript{-1} and precipitation 642.7±169.7 mm in Fontblanche; whereas it was 1207.3±206.7 g C m\textsuperscript{-2} year\textsuperscript{-1} and 1002.6±328.2 mm in Puechabon (see Table 1 for more details). Mean GPP was higher at Fontblanche because carbon assimilation was greater in the low temperature winter period but similar the rest of the year (Figure 3). Stem growth did not show any long-term (decadal) growth trend for any of the species studied (Figure 2).
The model accurately represented the low frequency response of GPP: both the seasonal variability in GPP within years and variability in GPP among years (Figure 4). The model explained over 50% of the annual biomass growth variance, and 46% and 59% of daily GPP in Fontblanche and Puechabon, respectively (Figure 4). This means that we were able to mimic the daily, seasonal and long-term trends in stand productivity with unbiased estimates but also to model how carbon is allocated to stem growth along the year at the different phenophases described. The model assumed species-specific carbon allocation responses set to the different plant compartments as nonlinear functions of temperature and soil moisture. These relationships were biologically meaningful in the sense that photosynthesis and carbon allocation could be decoupled to some extent as a function of climatic variability. Once the canopy has been formed in spring, the model allocated more carbon to the stem and less to storage when less severe stress occurs, i.e. with decreasing temperatures and more humid conditions (Figure 5).

Both sites exhibited an increase in temperature particularly evident in the maximum values but only Puechabon suffered a decrease in annual precipitation between 1960 and 2012 (Figure A1). In the model, the studied forests acclimated to changing climatic conditions in the last decades coupling different physiological traits and simulated annual GPP greatly followed the overall trends in precipitation observed. In Fontblanche, which is milder and receives less precipitation, GPP remained stable since the 1960s and presented no apparent long-term trend (Figure 6). In contrast, in the coldest and rainiest site (Puechabon) the model simulated a decrease in GPP (Figure 6), which was driven by the prevailing decrease in precipitation observed since the 1960s (Figure A1). This reduction of GPP was partly a consequence of decreased LAI in response to enhanced long-term water stress (Figure A3; Limousin et al. 2009; Misson...
Simulated long-term decadal trends in mean annual stomatal conductance were similar and decreasing at the two sites with greater water stress as a consequence of enhanced temperatures (Figure 6). The two species studied showed a long-term increase in simulated iWUE (Figure 7) following the decrease in simulated gs (Figure 6). The interannual variability of WUE and iWUE were highly and positively correlated (Figure 7). However, in the long-term they followed a different pattern particularly in Puechabon where there was a recent decline in WUE (not observed in iWUE) forced by trends in ET and GPP (Figure 7). This means that the recent reduction in simulated GPP was proportionally greater than that of simulated ET (Figure 6; Figure A3).

Discussion

Linking photosynthetic production to carbon allocation as a function of climate

The model calculates stand productivity and carbon allocation to stem growth in response to climate and [CO₂] with realism. It is particularly well suited to mimic the effect of water stress in plant performance by the explicit assessment of different acclimation processes at the canopy level including changes in stomatal conductance and photosynthetic capacity (Sala & Tenhunen 1996; Reichstein et al. 2003; Limousin et al. 2010; Misson et al. 2011). Additionally, the model simulates carbohydrate storage dynamically as a function of environmental variability. Climate can affect differently the carbon dynamics and pattern of C-allocation to different tree compartments at different phenophases. In the model the storage reservoir is an active sink for assimilated carbon during some periods of the year and a source in spring to be used in primary and secondary growth (Figure A5). Additionally stem growth is limited by climatic constraints (in [P3] and [P4]) rather than just by the amount of available carbohydrates (Millard et al. 2007). This means that water stress and optimum
temperature directly affect the modelled processes assuming that cell-wall expansion in the xylem can relate to climatic variability differently than photosynthetic production (Sala et al. 2012). The model showed C-limitation (for primary growth) the years when $LAI_{max}$ was not achieved (i.e., a limitation in LAI is driven by limitations in the C supply in spring), e.g., all years in Puechabon for the period shown in Figure A5 (1995–2012) but only those years in Fontblanche when the minimum value considered as a threshold was reached. Therefore both C-source (photosynthesis) and C-sink (just related to growth, other sinks such as volatile organic compounds or root exudates are not explicitly included in the model) limitations can be assessed at different years within one site and even at different periods within the same year (Millard et al. 2007; Sala et al. 2012; Chen et al. 2013; Fatichi et al. 2014). This hypothesis seems plausible as drought stress affects both C-source (e.g., through reduced stomatal conductance) and C-sink limitations (e.g., cell water turgor, hydraulic performance) (McDowell et al. 2013). Whether the pattern of C-storage simulated is realistic is something that needs to be validated against actual data. However, the flexible way in which stored C is modelled has much potentiality to improve ecosystem models that only view a carbon-source limitation (Sala et al. 2012; Friend et al. 2014).

Water stress is generally considered the greatest limitation for Mediterranean ecosystems, driving an intimate relation between precipitation and both growth and photosynthesis (Breda et al. 2006; Pereira et al. 2007; Baldocchi et al. 2010; Gea-Izquierdo & Cañellas 2014). Our results show that a long-term decrease in precipitation triggered a decrease in simulated GPP at the more rainy and continental site. However, this decline was not expressed in the growth-trends. This means that long-term productivity and allocation of C to secondary growth were decoupled and did not match (Sala et al. 2012; Chen et al. 2013; Fatichi et al. 2014). The existence of trade-offs
between carbon assimilation and allocation in relation to environmental variability
dynamics (e.g. Piovesan et al. 2008; Peñuelas et al. 2008; Gea-Izquierdo & Cañellas
2014). GPP was greater in the site receiving less precipitation, which could be related to
differences in soil retention capacity. However both soils are calcareous, shallow and
stony and differences in GPP were greatly explained by less limitation for carbon
assimilation of low winter temperatures at the warmest site (Fontblanche). They can
also be a result of different species composition (oak vs. pine-oak). LAI is greater at the
site yielding higher annual GPP. Nonetheless, had this factor been responsible for the
observed differences in winter photosynthesis, there would have also been differences
in spring photosynthesis, which was not the case (Figure 3).

A better understanding of the underlying processes determining carbon allocation
will benefice process-based models (Sala et al. 2012; Fatichi et al. 2014). Model
parameters were within the range found in the literature, bearing in mind that using a
daily time step to study differential processes or not distinguishing between leaf ages
will affect the scaling of parameters such as $J_{\text{max}}/V_{\text{cmax}}$ or $R_d$ (De Pury & Farquhar 1997;
Grassi & Magnani 2005; Masseyk et al. 2008; Vaz et al. 2010). Daily climatic data are
readily available at a greater spatial scale than data with a higher temporal resolution,
which increases applicability of daily models. Model performance could be improved
by addressing respiration changes related to ontogeny and allometry, nutrient limitations
(e.g. N/P) on photosynthesis, or including more complex up-scaling of leaf-level
photosynthesis (Niinemets et al. 1999; Niinemets 2007; Chen et al. 2013; McMurtrie &
Dewar 2013). However, it is difficult to find suitable data to calibrate such processes.
Similarly, it would be challenging to include allocation to reproductive effort in the
carbon budget. This is because, even if it is influenced by water stress in the studied
forests (Pérez-Ramos et al. 2010), there is still great uncertainty in the causal factors driving multi-annual variability in fruit production (Koenig and Knops 2000). Addressing stand dynamics would also help to generalize model applicability. Stand disturbances modifying stand competition can leave an imprint in growth for more than a decade whereas they do not seem to affect stand GPP over more than one or two years if the disturbance is moderate (Misson et al. 2005; Granier et al. 2008). In response to changes in competition the trees modify carbon allocation or keep the root:shoot ratio constant to enhance productivity on a per-tree basis but up to an asymptotic stand GPP.

Still, the model behaviour was good compared with other studies that addressed ontogenetic changes in the carbon-allocation response to photosynthesis (Li et al. 2014) and similar or better than that of other mechanistic approaches calibrated to standardized dendroecological data (Misson et al. 2004; Evans et al. 2006; Gaucherel et al. 2008; Tolwinski-Ward et al. 2011; Touchan et al. 2012).

Forest performance in response to recent climate change and [CO2] enhancement

Few studies under natural conditions observed a net increase of growth rates in response to enhanced CO2 levels since the late 1800s, meaning that other factors such as water stress and/or N/P were more limiting for photosynthesis and/or allocation to growth than [CO2] (Niinemets et al. 1999; Peñuelas et al. 2011; McMurtrie & Dewar 2013; Lévesque et al. 2014). Yet the forests have increased their iWUE. This can be partly a passive consequence of enhanced [CO2] but higher iWUE observed in more water stressed sites suggests that climate is co-responsible for an active acclimation of physiological plant processes (Keenan et al. 2013; Leonardi et al. 2013; Saurer et al. 2014). These processes would include a higher stomatal control like in our results where in turn we did not observe any increase in long-term carbon assimilation. The mean
annual stomatal conductance simulated was driven by climate but also decreased simultaneously in time with increasing [CO₂] (Appendix A4). Furthermore, there is
debate on whether there has been an increase in ecosystem WUE in response to recent changes in [CO₂] under a warming climate (Beer et al. 2009; Reichstein et al. 2002; Keenan et al. 2013). In our results the high-frequency of WUE followed that of iWUE, but there was some mismatch between the two traits in the low-frequency. We observed an increase in simulated annual WUE for the period 1980-2000 at the site where precipitation remained stable, whereas there was a decrease in WUE following that in GPP particularly evident in the site experiencing a drier climate in recent years. This trend was not observed in iWUE, which means that reductions in GPP and gs were proportionally greater than those in ET (Figure 6, Figure 7, Appendix A3).

Higher CO₂ concentrations enhance photosynthesis with the equations used to calculate leaf photosynthesis in biochemical models (e.g. Gaucherel et al. 2008; Keenan et al. 2011; Leonardi et al. 2013; Boucher et al. 2014). Thus, the absence of a long-term increase in GPP and growth would not mean that enhanced [CO₂] was not beneficial for model outputs (particularly in the case of C-source limitation) but that the net control exerted by other factors such as climatically driven stress was more limiting than that of [CO₂] availability; growth and photosynthesis would have been lower had we used constant [CO₂] with the same model parameters. The absence of any modification in the growth trends, even if there is changes in WUE, would express sink limitation mostly related to hydraulic constraints (Peñuelas et al. 2011; Sala et al. 2012; Keenan et al. 2013). Often, the trees express a growth decline at those sites where there is an enhancement in long-term water stress that dominates species performance (e.g. Bigler et al. 2006; Piovesan et al. 2008; Gea-Izquierdo et al. 2014). In contrast, it has been observed under certain conditions that trees have increased growth with warming since
the 1850s (Salzer et al. 2009; Gea-Izquierdo & Cañellas 2014). These studies suggest the existence of a positive effect of warming rather than that of [CO₂] fertilization upon growth in forests where water stress is not the most limiting factor. Our study sites are located within the Northern limit of the Mediterranean Region, meaning that the two species studied occupy drier and warmer areas more to the South. The two species have different functional characteristics, e.g., oaks are anisohydric whereas pines tend to be isohydric. This confers them different capacities of adaptation to climate change, which means that they should play different roles in future stand dynamics. Our results express the existence of trade-offs in response to climate at different phenological periods. This is important since synergistic environmental stresses acting at different periods can trigger tree mortality (McDowell et al. 2013; Voltas et al. 2013). Model sensitivity analysis could be performed to discuss the influence of specific factors such as climate or [CO₂] causing instability in the climate-growth response (D’Arrigo et al. 2008; Boucher et al. 2014). However, [CO₂] enhancement and climate warming are mixed in analysis performed using data from field studies, which can make the isolation of their effect problematic. The model can be applied using abundant dendrochronological data used to determine the site-dependent parameters. This would give much flexibility to investigate growth trends and forest performance in response to global change at a larger scale.

Conclusions

By developing an original process-based model with carbon allocation relationships explicitly expressed as functions of climate, we accurately simulated gross primary productivity and allocation of carbon to secondary growth in evergreen Mediterranean forests. Different processes were modelled as functions of environmental variability,
The studied forests expressed trade-offs in carbon allocation to different plant compartments in response to stress in different seasons, namely with low temperatures and a short photoperiod in winter, and with moisture shortage in summer. We modelled a decreasing time trend in stomatal conductance, which would suggest a partly active increase of iWUE in the forests studied. Interannual variability in WUE followed closely that of iWUE. However, WUE exhibited a decreasing trend at the site where we simulated a decrease in LAI and GPP in response to a decrease in annual precipitation since the 1980s. Long-term GPP remained at similar levels in the last 50 years just in one stand whereas it declined in the forest suffering a reduction in precipitation. This suggests different acclimation processes at the canopy level and in the pattern of allocation in response to enhanced xericity and increasing CO₂ levels, which could not counterbalance the negative effect of warming just in one site. Tree growth was partly decoupled from stand productivity, highlighting that it can be risky to accept growth as a direct proxy to GPP. The model is flexible enough to assess both C-source and C-sink limitations and includes a dynamic estimation of stored C. These features would improve ecosystem models with a fixed C-source formulation. By calibrating a limited number of parameters related to carbon allocation the model has great potential to be used with abundant dendroecological data to characterise past instability in the growth response in relation to environmental variability and simulate future forest response under different climatic scenarios.

Acknowledgements

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ECCOREV, the labex IRDHEI and OHM-BMP also supported the study. We are grateful to Roland Huc for sharing data from Fontblanche.

References


Modeling acclimation of photosynthesis to temperature in evergreen conifer forests.


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

<table>
<thead>
<tr>
<th></th>
<th>Fontblanche</th>
<th>Puechabon</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Flux Data</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Period</td>
<td>2008-2012</td>
<td>2001-2013</td>
</tr>
<tr>
<td>GPP annual (g C m(^{-2}) year(^{-1}))</td>
<td>1431.4 (305.4)</td>
<td>1207.3 (206.7)</td>
</tr>
<tr>
<td><strong>Climate</strong></td>
<td></td>
<td></td>
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<td>Period</td>
<td>1964-2012</td>
<td>1954-2013</td>
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<tr>
<td>Precipitation (mm)</td>
<td>642.7 (169.7)</td>
<td>1002.6 (328.2)</td>
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<tr>
<td>Tmax (ºC)</td>
<td>20.6 (0.9)</td>
<td>17.8 (1.26)</td>
</tr>
<tr>
<td>Tmin (ºC)</td>
<td>8.8 (0.5)</td>
<td>8.1 (0.8)</td>
</tr>
<tr>
<td><strong>Growth Data</strong></td>
<td></td>
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<td>Species</td>
<td><em>P. halepensis</em></td>
<td><em>Q. ilex</em></td>
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<td>15/30</td>
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<tr>
<td>Length</td>
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<tr>
<td>RW (mm)</td>
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<td><em>Q. ilex</em></td>
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</tr>
<tr>
<td></td>
<td>1941-2005</td>
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Table 2. Model parameters. Those parameter differing between sites were optimized either with GPP data (photosynthesis and allocation module) or with growth-based biomass increment chronologies (allocation module). The rest were common parameters for both sites and selected while developing the model in the first step for Fontblanche using GPP data (represented in ‘Cal’ with a ‘-‘). Meaning of parameters, equation number (E#) and phenophase [P#] are as in the text in Material and Methods.

Fontb=Fontblanche; Puech=Puechabon; Cal=local parameters to be calibrated with GPP or stem biomass increment data (SBI).

<table>
<thead>
<tr>
<th>Process</th>
<th>Process/Equation #</th>
<th>Parameter</th>
<th>Fontb</th>
<th>Puech</th>
<th>Units</th>
<th>Cal</th>
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<td>Photosynthesis</td>
<td>Leaf photosynthesis [E2]</td>
<td>$J_{\text{lef}}$</td>
<td>QUIL</td>
<td>1.59</td>
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<tr>
<td></td>
<td></td>
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<td>PIHA</td>
<td>1.44</td>
<td>-</td>
<td>-</td>
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<td></td>
<td>Leaf photosynthesis [E3]</td>
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<td>QUIL</td>
<td>32.3</td>
<td>µmol C m$^{-2}$ s$^{-1}$</td>
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<td></td>
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<td>QUIL</td>
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<td>°C$^{-1}$</td>
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<td>$V_p$</td>
<td>QUIL</td>
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<td></td>
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<td>PIHA</td>
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<td>-0.05</td>
<td>mm$^{-1}$</td>
<td>-</td>
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<td>Stomatal conductance [E5]</td>
<td>$g_s$</td>
<td>QUIL</td>
<td>7.5</td>
<td>-</td>
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<td>Water stress [E6]</td>
<td>Soil$\text{H}$</td>
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<td>Respiration [E7]</td>
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<td>-</td>
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<td>Stress LAI [E8]</td>
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<td>[P2]</td>
<td>$GDD_{\text{t}}$</td>
<td>203.3</td>
<td>°C</td>
<td>-</td>
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<td>Stored carbon buds [P3]</td>
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<td>7</td>
<td>g C day$^{-1}$</td>
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<td></td>
<td>Photoperiod</td>
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<td>9.5</td>
<td>hours</td>
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<td>Allocation canopy [P3], [E9]</td>
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<td>75</td>
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<td>GPP</td>
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<td></td>
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<td>6.3</td>
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<td>SBI</td>
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<tr>
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<td>Allocation stor/stem [P4], [E11]</td>
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<td></td>
<td>$s_{\text{IP}}$</td>
<td>0.060</td>
<td>-0.097</td>
<td>°C$^{-1}$</td>
<td>SBI</td>
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</table>
**Figure 1.** Outline of the different phenological phases (P1 to P5) and carbon allocation in the model within a given year. $A_n$ = net daily carbon assimilation; NSC = storage (non-structural carbohydrates); GDD = growing degree days; $GDD_l$ = parameter determining shift from P2 to P3 (see text); $C = $ carbon allocated either to the stem, canopy or roots; $d = $ day of year. Solid arrows correspond to allocation within the plant whereas dashed arrows correspond to litterfall (canopy or roots). $f_3$ and $f_4$ are nonlinear functions of soil water content and temperature determining carbon allocation to different compartments (see text for more details).
Figure 2. Growth (basal area increment, BAI, cm²·year⁻¹) and biomass allocated to the tree stem (g·cm⁻²·year⁻¹) of *Q. ilex* and *P. halepensis* at Fontblanche (growth shown in (a), biomass in (b)) and *Q. ilex* at Puechabon (growth and stem biomass shown in (c)). A vertical dashed line marks the release event in Fontblanche produced by the enhanced winter mortality in 1985 in (a). Dark lines for BAI correspond to yearly means while grey polygons show confidence intervals (at 95%) on the standard errors of the mean.
**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.
**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, \( \rho_{\text{low 15}} \)=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-h4(i) (i.e. h4(i) is the portion of allocated carbon to storage) from Cstem(i) = Ad(i)·[(1-h4(i))] as from [E11]. The modifier [0,1] is a function of soil water content (SWC) and maximum temperature (Tmax) 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.
Figure A1. Mean climatic time series in the last 50 years. (a) annual precipitation; (b) and (c) annual maximum (Tmax) and minimum (Tmin) 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.
**Figure A3.** Simulated maximum annual leaf area index LAI (m²·m⁻²) and total annual stand transpiration E (mm/year) in Fontblanche (a) and Puechabon (b).
Figure A4. Simulated mean annual stomatal conductance ($g_s$) as a function of mean [CO$_2$] (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.