© 2019 This manuscript version is made available under the CC-BY-NC-ND 4.0 license
http://creativecommons.org/licenses/by-nc-nd/4.0

Post-print of the paper published in:

Ecological Modelling 407, 108737.

https://doi.org/10.1016/

j.ecolmodel.2019.108737

CO_2 fertilization plays a minor role in long-term carbon accumulation patterns in temperate pine forests in the southwestern Pyrenees

Yueh-Hsin Lo[1], Juan A. Blanco[1], Ester González de Andrés[1], J. Bosco Imbert[1], Federico J. Castillo[1]

[1]Institute for Multidisciplinary Research in Applied biology, Universidad Pública de Navarra, Campus de Arrosadía, Pamplona, Navarra, 31006, Spain

Contact author:

Dr. Juan A. Blanco

Dep. Ciencias, Universidad Pública de Navarra

Campus de Arrosadía, Pamplona, Navarra, 31006, Spain

E-mail: juan.blanco@unavarra.es

Tel: +34 948 16 98 59

Fax: +34 948 16 89 30

Keywords:
ecosystem-level model, FORECAST Climate, ecosystem carbon, CO_2 fertilization effect, climate change.

Abstract

Isolating the long-term fertilization effect of CO_2 from other climate- and site-related effects on tree growth has been proven a challenging task. To isolate long-term effects of [CO_2] on water use efficiency at ecosystem level, we used the FORECAST Climate forest model, calibrated for Scots pine (*Pinus sylvestris* L.) forests in the southwestern Pyrenees, growing at a Mediterranean montane site and at a continental subalpine site. Future climate scenarios (RCP 4.5 and RCP 8.5) were generated using a battery of six climate models to estimate daily values of temperature and precipitation in a 90-year series. A factorial experiment was designed to disentangle the importance on C pools of three growing limiting factors (nitrogen limitation, climate (temperature + precipitation) limitation and atmospheric CO_2 concentration). The relative importance of each factor was quantified by comparing the scenario with the limitation of each individual factor turned on with the non-limitation scenario. Positive CO_2 fertilization due to improvement in water use efficiency was detected by the model, but its quantitative impact improving tree growth was minimum: its average increase in ecosystem C pools ranged from 0.3 to 0.9%. At the site with cooler climate conditions (continental), the main limitation for tree growth was climate. Such limitation will be reduced under climate change and the ecosystem will store more carbon. At the site with milder climate conditions (Mediterranean), N availability was the main limiting factor albeit modulated by water availability. Such limitation could be reduced under climate change as N cycling could accelerate (higher litterfall production and decomposition rates) but also increase if droughts become more frequent and severe. In addition, the magnitude of the uncertainty related to climate model selection was much more important than CO_2 fertilization, indicating that atmospheric processes are more important than tree physiological processes when defining how much carbon could be gained (or lost) in forests under climate change. In conclusion, due to the small changes in forest C pools caused by variation of atmospheric CO_2 concentrations compared to changes caused by other growth limiting factors (nutrients, climate), reducing uncertainty related to climate projections seems a more efficient way to reduce uncertainty in tree growth projections than increasing forest model complexity.

1. Introduction

Under global climate change, European forestry is facing new challenges related to environmental, climatic, and socio-economic changes. Assessing climate-management–growth relationships is of high importance in order to understand how European forests might respond to these changes. Since the beginning of the 19th century, CO_2 concentration in the atmosphere has increased dramatically (IPCC, 2013). In addition, industrial activities have also changed other atmospheric components, such as nitrogen oxides, sulphur, ozone and other trace elements. Such changes have already altered European trees growth rates (Pretzsch et al., 2014).

Despite the general concerns on how potential future temperature and precipitation changes may affect forest ecosystems, one major debate is how elevated CO_2 could affect forest productivity and global carbon cycles (Gedalof and Berg, 2010; Marshall and Linder, 2013). The general belief is that increasing atmospheric CO_2 concentrations will increase tree growth by making photosynthesis more efficient and reducing the time that stomata have to stay open, therefore reducing water losses by transpiration (Katul et al., 2010). Several effects of increasing atmospheric CO_2 concentrations have been documented, such as direct leaf biochemical effects, soil moisture savings due to stomatal closure and changes in leaf area index (Fatichi et al., 2016). Direct leaf biochemical effects have been researched in depth, but indirect effects are hard to isolate (Ainsworth and Long, 2004; Norby and Zak, 2011). The combined direct and indirect effects have been labelled as CO_2 fertilization (Holden et al., 2013), a definition that we used for the rest of this paper. Such fertilization effect could increase forests´ role as carbon sinks in the global carbon budget (Gedalof and Berg, 2010; McMahon et al., 2010). However, inconsistent results have been reported on the size or even the existence of such effect, depending on which scale (i.e. global, continental, landscape, ecosystem, or stand), tools or objects (e.g. model, remote sensing, forest inventory, tree rings) were used for detecting the CO_2 fertilization effect. So far, none of them has reached a consistent conclusion (Baig et al., 2015).

At the small scale, field experiments have shown that CO_2 fertilization increases plant growth in some ecosystems (Cole et al., 2010), but the effect may be modulated by nutrient limitation (Fleischmann et al., 2010; Jonard et al., 2015; Norby et al., 2010). At larger scales, model simulations have also showed the potential for higher CO_2 concentration to increase forest productivity (Bugmann and Bigler, 2011; Piao et al., 2009). However, other evidence has indicated that tree growth increases by climate change are not related to CO_2 fertilization, but to temperature increase, stronger drought resistance, or nutrient fertilization (Bertini et al., 2011; Ise and Moorcroft, 2010; Magalhães et al., 2014; Poulter et al., 2013; Salzer et al., 2009). Moreover, some experiments on growth under elevated CO_2 concentration have shown no effect (Bader et al., 2013; Booth, 2013), or even growth decrease (Esmail and Oelbermann, 2011). In fact, it has been argued that the generalized belief on CO_2 fertilization effects could even be due to sampling bias (Brienen et al., 2012).

Given the lack of long-term field studies in southwestern European forests and the uncertainty in changing climatic conditions, forest growth models provide one of the best available methods to examine long-term patterns of forest growth and development, and their potential behavior under alternative climate change scenarios. Hybrid models combining ecological processes and empirical data can be effective tools for projecting development under untested growing conditions, novel silvicultural regimes, and alternative species combinations and proportions (Blanco et al., 2015). However, large uncertainties still exist in the projected climate change when downscaled for different regions. Therefore, to estimate such uncertainty when modelling long-term growth patterns in forest ecosystems, ensembles of climate change predictions have recently been used successfully (AlRahahleh et al., 2018; González de Andrés et al., 2017). These studies have shown how the uncertainty related to climate model selection can account up to a 25% of variability in tree growth estimation in 100-year-long projections.

All things considered, the intensity of effects related to CO_2 fertilization would be affected by site and stand conditions, and would be accumulative over time as trees grow. These features point out to the need for research tools able to identify the relative importance of different limiting factors

on tree growth but also to take into account their interactions, and how they are affected by new climate conditions. Such tools are ecosystem-level forest models that have a good representation of the most important ecological processes (Bravo-Oviedo et al., 2011; Pretzsch, 2009). Predicting changes in soil nutrients, moisture, carbon cycles, trees and vegetation from other vegetation strata at scales meaningful for forest management involves greater complexity than is included in most operational stand-level empirical models (Kimmins et al., 2008; Lo et al., 2010), the ones usually used by the forestry industry and administrations. As a consequence, current forest planning tools generally fail to account for direct and indirect consequences of climate change (Medlyn et al., 2011), yet these could have very significant effects on tree species distributions, productivity and forest structure in southwestern Europe, as well as worldwide (Lindner et al., 2010; Reyer et al., 2010).

Based on current literature, we hypothesize that current seemingly conflicting evidence of the effect of rising CO_2 concentration can be harmonized when the CO_2 fertilization effect is isolated, its interactions with other plant growth limiting factors (nutrients, temperature, light, moisture) are accounted for, and its influence on the C pools at ecosystem level (vegetation + soil) are taken into account (i.e. adequate model complexity, Kimmins et al., 2008). However, we also hypothesize that uncertainty related to climate model selection may be of the same magnitude than the uncertainty related to model complexity. To test these hypotheses, our research has the following specific objectives: (a) isolating the potential effect of increasing CO_2 levels on tree growth in Scots pine stands in the Pyrenean region; (b) testing how nutrient and water availability may modulate such potential CO_2 fertilization effect; (c) estimating the uncertainty in C sequestered in different ecosystem pools due to climate model selection.

To reach these objectives, we used an ecosystem-level model as a virtual lab to separate the effects of nutrient, water, temperature and CO_2 limitation by simulating different scenarios with each limiting factor sequentially switched off, to rank their importance on ecosystem processes, with a focus on tree growth. To do so, we have employed the process-based, ecosystem-level model FORECAST Climate (Seely et al., 2015) to simulate the development of forest ecosystems under a

reference climate and different climate change scenarios derived from six global circulation models (GCMs) and two representative concentration pathways (RCPs). The model simulates CO_2 fertilization through its effects on water use efficiency, as this effect is well established whereas other direct and indirect effects are still being debated (Seely et al. 2015, and explanation below). FORECAST Climate is able to simulate the flow of water and energy through various forest layers including explicit representations of the balance between inputs from precipitation and seepage, and outputs by canopy interception, evapotranspiration, plant uptake, percolation and runoff. The model has been successfully tested and applied for a wide variety of forest ecosystems (Blanco et al., 2015; Dordel et al., 2011; Lo et al., 2015; Seely et al., 2015, Kang et al. 2017 and references therein).

2. Materials and Methods

2.1 The FORECAST Climate Model

FORECAST Climate (Seely et al., 2015) is an ecological model that simulates forests at stand level. FORECAST Climate builds up from its model antecessor FORECAST (Kimmins et al., 1999) by including a water-energy module (formerly the stand-alone model ForWaDy, Seely et al., 1997). FORECAST Climate is a management-oriented, forest growth and ecosystem dynamics simulator that operates at stand level and annual time steps. It keeps track of nutrient and water cycles in the forests, taking into account how light availability affects matter circulation. The model simulates forest growth using a hybrid approach, as it merges the use of empirical data (i.e. growth and yield tables and field data) modified by the simulation of the most important ecological processes (Mäkelä et al., 2000). A detailed discussion of this approach and the full model have been described before (Kimmins et al., 1999, 2010) and a summary is available in the Supplementary Information.

In FORECAST Climate, tree growth is limited by available light and nutrients (Figure S1 in the Supplementary Information) and the model uses a mass balance approach to simulate nutrient cycling. Rates of key ecosystem processes are calculated at an annual time step from a combination

of historical bioassay data (biomass accumulation in component pools, stand density, etc.) and measures of certain ecosystem variables (e.g., decomposition rates, photosynthetic saturation curves) by relating ‘‘biologically active’’ biomass components (foliage and small roots) with calculations of nutrient uptake, the capture of light energy, and net primary production. In this way the model generates a set of growth properties for each tree and plant species which includes, among others, 1) photosynthetic efficiency per unit of foliage biomass based on relationships between foliage biomass, simulated self-shading, and net primary productivity after accounting for litterfall and mortality, 2) nutrient uptake requirements based on rates of biomass accumulation and nutrient concentrations in different biomass components on different site qualities, and 3) light-related measures of tree and branch mortality derived from stand density input data in combination with simulated canopy light profiles.

As a non-spatial model, FORECAST Climate simulates plant biomass as homogeneously distributed in the stand, piled in different canopy layers determined by top and bottom height of each plant species present. Light availability is estimated for each biomass layer (each of them with 25 cm height) as solar radiation is absorbed by plant biomass. Light-induced mortality occurs in those canopy layers for which input radiation is lower that required to maintain photosynthesis (a user-defined parameter; Kimmins, 1993).

Annual vegetation growth is estimated by comparing nutrient demands (as defined by potential growth based on previous-year biomass) and light availability (calculated by radiation diffusion through the canopy structure) with actual nutrient availability (nutrients present in the soil every time step). Nutrient limitation appears when nutrient demands are higher than nutrient availability. Then, available nutrients are divided among the different plant species depending on their demand and root occupancy (Kimmins et al., 1999). Actual biomass growth is then calculated, and carbon allocation for next year is distributed depending on site quality. The model simulates the dynamics of all major forest carbon stocks (aboveground biomass, belowground biomass, litter, dead wood and soil organic carbon). It complies with the carbon estimation methods outlined by the IPCC (Penman et al., 2003). See Kimmins et al. (1999) for further details.

In addition to light limitation and nutrient cycling, the FORECAST Climate model also contains a two-dimensional forest hydrology sub-model that simulates forest hydrology main dynamics on a daily time step under a given set of climatic and vegetation conditions. It takes into account species-specific estimates of leaf area index, canopy radiation interception, and soil occupation by fine root biomass to calculate water and energy transfers along the canopy and soil profiles. The model also provides information regarding the formation of soil organic matter and its distribution within specific soil layers.

FORECAST Climate calculates potential evapotranspiration (PET) using an empirically-based energy budget approach, estimating net shortwave solar radiation interception based on leaf area index and weather variables (see Table S2 for a full list of variables). PET is estimated separately for the canopy, understory, and forest floor. To simulate hydrological dynamics in the forest floor and rooting zone, the soil is simulated as composed by different layers (Figure S2 in Supporting Information). Each layer´s physical properties (infiltration rate, moisture content, moisture holding capacity, permanent wilting point) define water storage and vertical movement through soil. For each day and each plant species, water stress is calculated as the relative difference between potential energy-limited transpiration demand and actual transpiration. Daily indices for water availability and competition for water resources are computed and then converted into annual estimations to modify annual vegetation and organic matter decomposition rates (Seely et al., 2015, Supporting Information).

Simulation of CO_2 fertilization is restricted to improvements on water use efficiency. As higher atmospheric CO_2 concentrations are associated with lower stomatal water vapour conductance, and greater water use efficiency, such processes are represented in FORECAST Climate using a function that modifies canopy resistance in each plant species in relation to atmospheric CO_2. The reason for this approach is that, although increases in photosynthetic efficiency due to increased CO_2 have been reported and are expected as carboxylation in C3 plants is not saturated, respiration rates increase with raising temperatures (concomitant to increased CO_2) at higher rates than carboxylation (Collalti et al., 2018). In fact, photosynthetic rates can also be reduced by higher

temperatures (Way and Oren, 2010). Respiration also increases with tree age as standing tissue increases, and as a consequence leaf biomass is more important for NPP than C assimilation (Dong et al., 2019). In addition, acclimation to higher CO_2 concentrations in plants has been reported (Ainsworth and Long, 2004), causing that increased photosynthetic rates last for only a few years, particularly in N-limited plants. On the other hand, similar responses to increased CO_2 concentration in C3 and C4 plants (which are almost carbon-saturated at present-day CO_2 concentrations) indicate that increased productivity is mostly caused via increased water use efficiency (Degener, 2015). Therefore, increased photosynthetic rates do not necessarily translate into increased biomass (Korner, 2003; Fatichi et al., 2016). Negligible effects of CO_2 fertilization in water-limited ecosystems have also been reported (Dong et al., 2019). Finally, recent research has pointed that increased productivity by higher photosynthetic rates can translate into faster tree growth but also shorter tree longevity, causing a neutral or even negative overall effect on forest stand biomass at the long term (Bugmann and Bigler, 2011; Chaste et al., 2019). All these facts indicate that CO_2 fertilization at stand level and long time scales is likely a water more than a carbon issue (Holtum and Winter, 2010), supporting our simulation approach.

FORECAST Climate has a modular architecture, allowing switching on or off the two modules simulating nutrient limitation and water/energy limitation, whereas the light limitation is the engine of the model and therefore must always be turned on. A detailed description of all physiological processes and the approaches followed to simulated them can be found in Kimmins (1993), Seely et al. (1997), Kimmins et al. (1999) and Seely et al. (2015). The original FORECAST model has been extensively used in different forest types around the world (see Kimmins et al., 2010). The water-energy module has been validated against field-measured soil moisture data (Dordel et al., 2011; Seely et al., 2015; Titus et al., 2006). Particularly, the model has been evaluated for Scots pine (*Pinus sylvestris* L.) forests in the southwestern Pyrenees, providing acceptable performance for a battery of ecological variables (Blanco et al., 2006, 2017; Candel-Perez et al., 2017; Gárate and Blanco, 2013; González de Andrés et al., 2017; Lo et al., 2015a)

2.2 Model calibration and study sites.

Most of the values used to calibrate the FORECAST Climate model for Scot pine forests came from long-term research plots monitored since 1999 by the Ecology and Environment Group of the Public University of Navarra (Pamplona, Spain). Research plots are located in the higher Ebro Basin, in northern Spain, in the southwestern Pyrenees. Eighteen research plots are placed at two different sites with distinct geo-climatic features, providing data to calibrate the model for two distinct sites, typical of the southwestern Pyrenees. The first site (near the village of Aspurz) has cool Mediterranean climate (Papadakis 1970), 680 m altitude, 10% average slope, average annual temperature (Tm) of 12.0 ºC and annual precipitation (Pa) of 900 mm. The second site (near the village of Garde) has a cool continental climate (Papadakis 1970) at 1380 m altitude, 45% slope, Tm 8.2ºC and Pa 1300 mm (Figure 1). At both sites Scots pine is the dominant species, with a presence of beech trees in the lower canopy and understory layers. A detailed description of the research sites can be found in the Supporting Information (Table S1). From these long-term research sites, calibration data to parameterize the FORECAST Climate model were obtained through different field research, with bibliographical sources used to calibrate parameters not measured directly. A detailed list of the calibration sources can be found in the Supporting Information (Tables S2, S3 and S4).

2.3. Disentangling CO_2 effects on C pools with scenario simulation

A battery of simulations was designed to isolate the individual influence of three limiting factors on tree growth: nutrient availability (for simplicity represented by N available in soil, see Lo et al., [2015a], and section 4.3 for reasons supporting this assumption and its consequences), climate (water availability and temperature) and carbon (atmospheric CO_2 concentration). The simulations were designed to switch off alternatively each of the limiting factors, and then running the simulations with all of them on or off simultaneously. When the nutrient and climate model were switched off, FORECAST Climate worked as a light-only model. To isolate the influence of CO_2, two different types of climate scenarios were created: one with the projected increasing atmospheric

CO_2, and another one with the same precipitation, radiation and temperature values but with CO_2 set constant at 400 ppm. This approach allowed isolating and ranking the influence of each limiting factor. To account for climate influence, the simulations were repeated for no change (baseline), moderate (RCP 4.5) and severe (RCP 8.5) climate change. Climate simulations accounted for variations in precipitation and temperature, but not in other weather variables such as relative humidity, solar radiation or wind as there are not predictions available for the region. To account for site influence, simulations were repeated for both Mediterranean and continental research forests. Baseline climate data were obtained from nearby weather stations for the period 1975-2004 (Figure 1). Climate change scenarios were generated for the period 2015-2104 by downscaling future regional predictions that modified historical records. To account for uncertainty in climate predictions related to climate model selection, the simulations were repeated using climate estimates from six different major climate models (Table S5). The procedure is detailed in the Supporting Information.

Target variables used to compare the importance of each growth-limiting factor were: 1) total ecosystem carbon (defined as the sum of total carbon in trees, understory vegetation, litter, humus and coarse woody debris [CWD]); 2) aboveground carbon (carbon contained in aboveground parts of trees and understory vegetation); 3) litter + CWD carbon (defined as carbon in snags, logs and decomposing organic matter); and 4) belowground carbon (defined as the sum of carbon in humus plus vegetation roots). The light-only scenario was used as the baseline for carbon accumulation. Average reductions in carbon pools due to each growth-limiting factor for the whole simulated period were calculated as weighted averages, calculating first differences between simulations for each year and then calculating the weighted average of those annual differences using the value of each C pool of the light-only scenario for each year as weight.

3. Results

3.1. Estimated importance of different growth limiting factors on accumulated ecosystem C

At the Mediterranean site, when only nutrient limitation was added, accumulated C decreased in the whole ecosystem, litter + CWD, and aboveground pools, but increased in the belowground pool (Figure 2). Nutrient limitation was still the most influencing factor on reducing accumulated C in all the pools (Figure 2). The more extreme the climate scenario, the more important the individual effects of climate and CO_2 became, but N still was the most influencing factor in all situations (a reduction between 12 to 17% in C pools compared to the light-only scenario), except for belowground C, for which climate was the most limiting factor. When the three limiting factors were simulated together, ecosystem C and litter + CWD C pools showed the highest C reduction for both climate scenarios, and belowground C under RCP 8.5. However, aboveground C for both climate scenarios and belowground C for RCP 4.5 showed reductions of C pools smaller when simulating the three limiting factors than when simulating individual factors, indicating the capacity among factors to counteract some negative effects (Table 1).

However, at the continental site, nitrogen was less limiting than at the Mediterranean site for ecosystem, litter + CWD, and aboveground pools. However, nitrogen was more limiting than at the Mediterranean site for belowground C (Figure 3). For all the C pools considered, climate was the most limiting factor. In spite of it, for the belowground C pool, N limitation under climate change was reduced and caused an increase of the pool size. CO_2 had some positive effect on increasing accumulated C, but the effect was very small. However, unlike at the Mediterranean site, climate limitation had similar importance irrespective of which climate scenario was simulated.

Table 1 presents differences in size effects (as percentages) among different limiting factors, summarized for the whole simulated period. At the ecosystem level, under mild climate change at the Mediterranean and continental sites, ecosystem C was reduced 14.8% and 10.7% respectively, when the model was running at maximum complexity (i.e. N limitation, climatic limitation due to precipitation and temperature, and CO_2 fertilization simulated together). For the moderate climate scenario (RCP 4.5), at Mediterranean site nutrient limitation was the most important factor and it

accounted for 12.2% reduction, climate limitation accounted for 8.2% reduction and CO_2 fertilization accounted for a mere 0.7% increase in ecosystem C. On the other hand, at the continental site, climate limitation was the most important factor, reducing ecosystem C by 14.5%, whereas N limitation reduced ecosystem C by 2.2% and CO_2 fertilization increased it by 0.3%.

We subsequently ran the model with a more extreme climate change scenario (RCP 8.5), and the results showed less ecosystem C reduction (12.3% and 7.4% for Mediterranean and continental sites, respectively), indicating a counterbalancing effect among factors. At the Mediterranean site, nutrient limitation still accounted for the largest ecosystem C loss (12.7%) while climate limitation account for less ecosystem C loss (8.0%) and CO_2 fertilization increased ecosystem C by 1.2%. At the continental site, climate limitation was still the most important factor, but the effect was reduced to 12.1% loss. Nutrient limitation reduced ecosystem C about the same (2.3%) and CO_2 fertilization increased ecosystem C by 0.6%.

Looking deeper at different carbon pools at the Mediterranean site (i.e. litter and CWD, aboveground and belowground), no matter which climate scenario was used, litter and CWD lost the most C (20.0% and 19.7% for RCP 4.5 and RCP 8.5 scenarios, respectively). At the continental site, with a mild climate change scenario, the aboveground pool lost the most carbon (13.3%) while under a more extreme climate scenario it was the belowground pool the one losing the most carbon (10.5%). Looking at each limiting factor separately, at the Mediterranean site, N limitation played a role stronger than the other factors (climate and CO_2) for the litter + CWD, and aboveground C pools, while for the belowground C pool, climate played the most important role. In all the cases, CO_2 fertilization played a minor role in increasing accumulated C. At the continental site, climate played the most important role in all carbon pools and CO_2 still played a minor role in increasing C pools.

An important point to highlight is the differential importance of model complexity (number of limiting factors simulated simultaneously) depending on site conditions. At the Mediterranean site, adding extra factors always resulted in larger divergence from the light-only limitation, and more so under the severe climate change scenario (Figure 2). However, at the continental site, the use of the

whole model (light, nutrients, and climate including CO_2) estimated that trees would grow more than with light-only limitation in the severe climate change scenario, but not in the RCP 4.5 scenario (Figure 3).

3.2. Effects of uncertainty related to climate model selection

Uncertainties in predicting C pools patterns due to climate model selection are shown in Figures 4 and 5, which depict the upper and lower limits of the 95% confidence intervals of the average predictions (showed in Figure 2 and 3) for the complexity scenarios that included climate as a factor. For all C pools, the selection of climate models caused a variability in model predictions larger at the Mediterranean that at the continental site. At the Mediterranean site, belowground C had the smallest variation, whereas C in litter and CWD showed the largest uncertainty. At the continental site, the largest uncertainty was found for the aboveground C, whereas the smallest was estimated for litter and CWD carbon. Comparing different climate change scenarios, the variability caused by climate model selection was larger when simulating the RCP 8.5 than the RCP 4.5 at both forest types. In addition, forest model complexity interacted with uncertainty related to climate model selection, which was reduced when the full forest model (light, N, and climate with CO_2) was applied.

4. Discussion

4.1. Effects of different growth limiting factors on C pools

We quantitatively estimated the possible importance of different growth limiting factors on accumulated C in different pools in two contrasting SW European Scots pine forests. Trees growing at the Mediterranean site mainly suffer from N competition, while at the continental site the most growth-limiting factor is climate. Although such results may seem counterintuitive at first sight, in fact, they point out to each local Scots pine population having adjusted their maximum potential growth (the light-only scenario) to the most important growth conditioning factor (drought at the Mediterranean site, N at the continental site, Blanco, 2004; Blanco et al., 2011; Cardil et al., 2018;

Primicia et al., 2013). This fact indicates that trees have adapted and acclimated to unfavorable growing condition (Camarero et al., 2015; Moreno et al., 2018). Therefore, additional limitation in those factors is not as impacting on actual growth as shortages in other environmental factors. From our simulations, it can be seen that when only N limitation is added into the model, the ecosystem C pool is reduced (particularly at the Mediterranean site) as the forest has not enough N to support all its potential growth. This result agrees with the progressive N limitation hypothesis proposed by Luo et al. (2004) and also with Liebig´s law of minimum. However, N limitation is likely causing the underground root system to explore more soil, therefore, increasing belowground C. At the continental site, where trees already have slower growth rates, the additional loss of potential accumulated C not achieved by N limitation is not as important as at the Mediterranean site, except for the belowground C pool. This is likely caused by a more intense nutrient limitation as the soil at this site is poorer in N (Table S1; Blanco et al., 2015, 2011). In addition, at this site N limitation causes an increase in litter and CWD carbon, caused by increased mortality due to competition for N in the less fertile soil.

After adding climate limitation (simulated as temperature and water controls on tree growth and litter decomposition, Seely et al., 2015), and simulating different climate change scenarios (which will cause climate to become warmer and drier at these two sites) we estimated that the effects of different limiting factors affected both ecosystems in different ways. At the Mediterranean site, adding climate and nutrient limitation together caused bigger differences between the realized accumulated C and the potential accumulated C than those estimated by the light-only limitation simulation. A point to keep in mind is that N competition could be linked to water scarcity during part of the growing season. A feature that defines many temperate forests, and particularly those in the Mediterranean climate, is the existence of seasonal droughts (Perry et al., 2008). From our research at the experimental sites, we know that at the Mediterranean site the rate of nutrient cycling is limited by low temperatures early in the growing season, when there is abundant water, but becomes limited by low water later in the growing season (Blanco et al., 2011; Primicia et al., 2013).

Therefore, even though there is some evidence that CO_2 enrichment can cause growth increase (see references and results above), it appears that such increase would be irrelevant compared to the extra losses due to more frequent and severe drought events (Lim et al., 2015; Thornton et al., 2007). However, although we could expect that RCP 8.5 will reduce even more total accumulated C than RCP 4.5, our results indicate the opposite. Such counter-intuitive result could arise because trees do not respond to environmental change in a linear relationship, as competition modulates their responses (Fernández-de-Uña et al., 2015). Hence, it is important to distinguish the differential effects of climate change on aboveground C (mostly in trees) and on dead organic matter C (litter + CWD). Increased mortality due to drought would likely reduce standing C reserves, but on the other hand, it will increase litter and woody debris fall. As these materials (particularly CWD) have relatively low decomposition rates and climate change could reduce them even more by decreasing soil moisture (Almagro et al., 2015; Blanco et al., 2011; Saura-Mas et al., 2012), at an ecosystem scale C reserves could even increase, by transferring a portion from standing to fallen C material (Suzuki et al., 2019). Nonetheless, if longer time scales are simulated, it is likely that the C transferred from the canopy to the soil will also be lost over time. However, uncertainty related to climate predictions would also increase if longer time scales are used.

As Scots pine is the most widely distributed pine species globally, our results can have implications for other regions as well. Although Scots pine is tolerant to poor soils, frost and drought, it could also take advantage of improved growth conditions in future climates, particularly in northern sites were temperature could rise, accelerating nutrient cycling, but without an important increase in drought stress (Matala et al. 2005, 2006). However, in Central and Mediterranean Europe, our results agree with previous modelling exercises showing drought as important limiting factor in nutrient-poor low-elevation sites (Wellpot et al., 2005; Ameztegui et al. 2017). At these drought-prone sites, CO_2 would play a minor role by producing a slight alleviation of water stress (Gärdenäs and Jansson, 1995). All these modelling results combined support Körner´s (2003) position that environmental conditions restraining tissue formation are the actual limitation for tree growth, whereas C assimilation is close to saturated in most forests around the world, except likely

xeric forests during dry seasons.

4.2 Is there a relevant CO_2 fertilization effect?

The CO_2 fertilization effect can be separated into a direct effect by increasing the speed of photosynthesis rate (Norby et al., 1999) and an indirect effect on stomata conductance and then affecting water use efficiency (Farquhar et al., 1989). Several experiments had shown that CO_2 fertilization increased the photosynthesis rate but later on, such rate either stabilized or decreased due to shortages of other growth factors (e.g. nutrient or moisture) (Norby et al., 2010; Peñuelas et al., 2011; Sun et al., 2018). Other field experiment have also shown that CO_2 fertilization changed water use efficiency and therefore increased (under moderate water stress) or decreased (under severe water stress) tree growth performances (Drake et al., 2017; Rezaie et al., 2018; Silva et al., 2010). In addition, observed increases in plant biomass under elevated CO_2 concentrations have shown that such increases are mostly due to reduced water limitation (Degener, 2015; Holtum and Winter, 2010) or could translate into shorter tree life spans, and therefore cancelling out fertilization effects at stand level (Bugmann and Bigler, 2011; Chaste et al. ,2019). In our model, we did not simulate the change of photosynthesis rate but rather the change of water use efficiency, but we still found a net CO_2 fertilization influence, benefiting both Mediterranean and continental ecosystems. However, such influence was small (0.7% average increase in ecosystem C). Such increase was easily overridden by other limiting factors causing reductions of accumulated C. Similar findings have been published worldwide (Brito et al., 2016; Dong et al., 2019; Exbrayat et al., 2018; Peñuelas et al., 2017). Therefore, when talking about the CO_2 fertilization effect, its importance depends on the spatial and temporal scale, and it also depends on the age and physiological character of the species and the site conditions (Yang et al., 2016; Zhu et al., 2016). In any case, the real question is to which point such physiological effect actually has the potential to modify ecosystem C pools in a relevant way. According to our results, in southwestern European conifer forests such potential is quite small.

Classical reviews on the potential yield increase in crops have indicated that production could

increase up to 32% due to CO_2 fertilization (Degener, 2015; Hartwell Allen et al., 1996). However, such impressive growth increase in agricultural crops is achieved under intensive fertilization and irrigation regimes. Net increase in tree growth due to CO_2 fertilization will be unlikely, as the main growth limiting factor in a warmer world would be water availability, and specifically in the Mediterranean area, where droughts are increasingly more frequent and severe. In addition, the continued N deposition levels, at least in European (Pretzsch et al., 2018) and Asian (Wei et al., 2012) forests, will even exacerbate the limiting nature of water (Dziedek et al., 2016; Huang et al., 2016). Such increased but unbalanced growth will have direct translation into reduced tree longevity (Bugmann and Bigler, 2011) and increased tree mortality (Allen et al., 2010; Klein and Hartmann, 2018; Pretzsch et al., 2014b).

The most noticeable relative change in C stocks at the Mediterranean forests would be the increase of C stored in litter and CWD. Such increase is directly related to increased mortality and litterfall rates caused by droughts. Our estimations of increased mortality agree with other modelling exercises for Mediterranean conifers (Davi and Cailleret, 2017). Indeed, such effect has already been detected at the experimental sites (Blanco et al., 2011; Primicia et al., 2016). Changes in other ecosystem C pools were small, in particular for underground C, agreeing with previous reports from empirical studies (Agathokleous et al., 2016; Lotfiomran et al., 2016), which did not detect significant increase in root biomass in trees under enriched CO_2 atmosphere. For understory, C pools (data not shown, but are included in the aboveground and belowground pool), we did not find significant changes, agreeing with empirical data from free-air-CO_2-enrichment (FACE) experiments (Kim et al., 2016).

If effective mitigation plans to increase atmospheric CO_2 fixation need to be set in the near future to reduce climate change effects, it is important to know how different growth limiting factors affect growth performance and more specifically, C fixation. The complex interaction between CO_2, climate change, and C pools indicates the need to focus not only on trees, but also specially on deadwood and soils as the main reservoir to store C in forests (Blanco, 2018; Virto and Blanco, 2018). Even though our quantitative estimation should be taken with caution, we can

conclude that under the current climate change rate, the ecosystem C gained from CO_2 fertilization or warmer temperatures (longer growing season) do not override C losses due to drought stress or insufficient nutrient supply. This statement agrees with previous results from FACE experiments (Holtum and Winter, 2010). However, small CO_2 effects that may not be relevant for tree productivity at local scale could still be significant at regional scales by making current sites still suitable for tree species under climate change (Keenan et al., 2011).

In any case, future forest management could take advantage of CO_2 fertilization if the other two most important limiting factors (nutrient limitation and water limitation) are somehow alleviated. As due to economy neither irrigation nor fertilization are practical in most European forests, and particularly in mountainous areas, alternative practices could be mixing pines with other species, such as European beech (*Fagus sylvatica* L.) to accelerate N cycling as broadleaves have higher leave contents and faster decomposition rates. Such nutrient accelerating effect in mixed forests has already been reported at these same sites (González de Andrés et al., 2019). Similarly, mixing pine with beech could also reduce water stress in pine by reducing intra-specific competition for water (González de Andrés et al., 2017, 2018). Another alternative could be thinning pines to increase water availability (Ameztegui et al., 2017), although thinning effects are complex and not intuitive in mixedwoods as water interception and nutrient flows are also modified (Cardil et al., 2018).

4.3 Uncertainty and modelling limitations

There are two main uncertainty sources in the simulations presented here: 1) forest model complexity (the different limiting factors simulated simultaneously), 2) climate model selection, used to estimate future climate variables. As our results show, forest model complexity has an important influence on estimated C pools. Although *a priori* it seems that the more complex the model is, the more realistic its simulations would be, it is worth noticing that increasing model complexity also increases uncertainty derived from calibrating more parameters and also the uncertainty related to model structure (Saltelli et al., 2007). Therefore, a model should be as

complex as necessary to answer the question posed by the model user, but not more complex (Kimmins et al., 2008). In our case, turning on the modules that allowed the simulation of climate and nutrients was the only way to explore the consequences of the interactions among those factors on C pools.

On the other hand, the uncertainty related to climate model selection is in fact external to the exercise of modelling tree growth, as FORECAST Climate uses the outputs from the climate models as inputs to estimate water and energy flows. In that sense, giving the important uncertainty detected in our simulations for some variables, the choice of climate model seems more important than the inclusion of the CO_2 fertilization effect. In addition to uncertainty in climate model selection (Prudhomme and Davies, 2009), there is also uncertainty in the method used to downscale climate projections to local landscape scale (Etemadi et al., 2014), the one meaningful for stand-level forest models. In fact, Prudhomme and Davies (2009) suggested ignoring sources of uncertainty that are of smaller scale than uncertainty due to climate model selection, and pointed out the need for climate modelling uncertainty should be accounted to provide sound, scientifically based advice for decision makers. A recommended way to incorporate uncertainty due to model selection is the use of model ensembles (Suzuki-Parker et al., 2018; Wang et al., 2014), and as the case presented here. On the other hand, a more general implication of our results is that the most efficient way to improve predictions of forests C pool patterns is by reducing uncertainty in climate models (Teng et al., 2012), rather than by expanding complexity in forest models. However, it is also worth pointing out that global simulation uncertainty was also reduced when using the full forest model (including simultaneously light, nutrients, climate with CO_2), which indicates FORECAST Climate´s capacity to counterbalance uncertainty related to climate to some extent by simulating more accurately the relationships between climate and the rest of growth-related variables, as has also been reported before for previous model versions (Blanco et al., 2007).

As in all modelling exercises, there were some limitations when using the FORECAST Climate model. For example, the representation of underground mycorrhizal system or the simulation of hydraulic redistribution among soil layers is not included in the model. Both of these

could be important factors regulating ecosystem function in some forest ecosystems (Neumann and Cardon, 2012; Simard et al., 2012). Indeed, mycorrhizal hyphae can have surface area that is at least comparable than leaf area (Perry et al., 2008), and therefore C pools. These facts imply that changes in belowground C pools (particularly roots) would affect changes in mycorrhizae and *vice versa*. In addition, drought-related mortality is empirically estimated, which combined with the lack of spatial representation of trees may cause that the model could not represent adequately neighboring effects important in Iberian forests (González de Andrés et al., 2018; Ruiz-Benito et al., 2013) and therefore changes in deadwood C pools.

Finally, our objective was to create a ranking of importance among the three most important tree growth-limiting factors, but in natural forests, such factors cannot be separated. Undeniably, water and nutrient flows are linked through the root absorption rates and soil solution (Gessler et al., 2017). Moreover, in our studies, we have limited simulating nutrient limitation to the effect of N. This was based on previous empirical studies at these two sites indicating that N is a limiting nutrient here (Blanco et al., 2009; Primicia et al., 2014), but also P, with a relatively more important role in the Mediterranean site. In fact, our most recent research is indicating that phosphorous could also be limiting (González de Andrés et al., 2019), supporting previous estimations that these forest may be reaching a N-saturated status (Blanco et al., 2017), a phenomenon seen in many other European forests (Sardans et al., 2016).

5. Conclusion:

The complex interactions among climate (precipitation, temperature, atmospheric CO_2) and nutrients had not been studied in an integrative way at ecosystem-level before. Our most important advancement beyond the state of the art is the ranking and quantification of the CO_2 fertilization effect compared with other growth limiting factors. Almost all the literature generated for Scots pine forests in SW Europe is focused on empirical-only, inventory-related measures, which do not provide ecophysiological explanations or estimation of future changes in efficiency of using different growth resources (nutrients, water, temperature, carbon).

Our results indicated that the CO_2 fertilization effect, while positively affecting ecosystem C accumulation, could counteract only a minor part of the growth limitation imposed by N and climate. In addition, the ranking in importance of N and climate is directly inverse to the present importance of such limitation. In other words, in forests which are poor in N but precipitation is not a limiting factor, soil moisture could account for the biggest portion of growth limitation under climate change condition. Similarly, in forests where enough N is available but soil moisture is low, trees have acclimated to water limitation and therefore apparently they are less ready to deal with N limitation. In conclusion, trees focus their efforts on overcoming the current limiting factors, but that strategy leaves them unadapted to other events that would made factors usually non-limiting to become scarce. Such situation is expected owing to the process of global change generated by anthropic activities.

Finally, our results also point that if accurate estimations of future C pools in forests are needed, the most effective way is to reduce the uncertainty related to climate model selection, namely, to reduce the disagreement between different climate model estimations. Such way seems much more efficient to reduce uncertainty when estimating forest C pools that the addition of detailed ecophysiological processes in process-based forest models (such as CO_2 fertilization), which imply big efforts in modelling development and calibration but do not noticeably change predicted temporal trajectories of forest C pools.

Acknowledgments

The authors wish to thank all the previous graduate and undergraduate students working at UPNA' s Ecology and Environment Group who had made possible to gather the 19-year long databases used for model calibration. Funding for this research has been provided by the Spanish Ministry of Economy and Competitiveness (projects AGL2012-33465, AGL2016-76463-P), a Ramón y Cajal contract (ref. RYC-2011-08082) and Marie Curie Actions (ref CIG-2012-326718-ECOPYREN3, H2020-MSCA-IF-2014-DENDRONUTRIENT).

References:

Agathokleous, E., Watanabe, M., Nakaji, T., Wang, X., Satoh, F., Koike, T., 2016. Impact of elevated CO_2 on root traits of a sapling community of three birches and an oak: a free-air-CO_2 enrichment (FACE) in northern Japan. Trees 30, 353–362. https://doi.org/10.1007/s00468-015-1272-6

Ainsworth, E.A., Long, S.P., 2004. What have we learned from 15 years of free-air CO_2 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO_2. New Phytol. 165, 351–372. https://doi.org/10.1111/j.1469-8137.2004.01224.x

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., Mcdowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, T., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S.W., Semerci, A., Cobb, N., Allen, C.D., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For. Ecol. Manage. 259, 660–684. https://doi.org/10.1016/j.foreco.2009.09.001

Almagro, M., Maestre, F.T., Martínez-López, J., Valencia, E., Rey, A., 2015. Climate change may reduce litter decomposition while enhancing the contribution of photodegradation in dry perennial Mediterranean grasslands. Soil Biol. Biochem. 90, 214–223. https://doi.org/10.1016/j.soilbio.2015.08.006

ALRahahleh, L., Kilpeläinen, A., Ikonen, V.-P., Strandman, H., Venäläinen, A., Peltola, H., 2018. Effects of CMIP5 Projections on Volume Growth, Carbon Stock and Timber Yield in Managed Scots Pine, Norway Spruce and Silver Birch Stands under Southern and Northern Boreal Conditions. Forests 9, 208. https://doi.org/10.3390/f9040208

Ameztegui, A., Cabon, A., De Cáceres, M., Coll, L. 2017. Managing stand density to enhance the adaptability of Scots pine stands to climate change: A modelling approach. Ecol. Model. 356, 141-150. http://dx.doi.org/10.1016/j.ecolmodel.2017.04.006

Bader, M.K.F., Leuzinger, S., Keel, S.G., Siegwolf, R.T.W., Hagedorn, F., Schleppi, P., Koerner,

C., 2013. Central European hardwood trees in a high-CO_2 future: synthesis of an 8-year forest canopy CO_2 enrichment project. J. Ecol. 101, 1509–1519. https://doi.org/10.1111/1365-2745.12149

Baig, S., Medlyn, B.E., Mercado, L.M., Zaehle, S., 2015. Does the growth response of woody plants to elevated CO_2 increase with temperature? A model-oriented meta-analysis. Glob. Chang. Biol. 21, 4303–4319. https://doi.org/10.1111/gcb.12962

Bertini, G., Amoriello, T., Fabbio, G., Piovosi, M., 2011. Forest growth and climate change: evidences from the ICP-Forests intensive monitoring in Italy. iForest 4, 262–267. https://doi.org/10.3832/IFOR0596-004

Blanco, J.A., 2018. Managing Forest Soils for Carbon Sequestration: Insights From Modeling Forests Around the Globe, in: Muñoz, M.Á., Zornoza, R. (Eds.), Soil Management and Climate Change. Elsevier Inc, pp. 237–252. https://doi.org/10.1016/B978-0-12-812128-3.00016-1

Blanco, J.A., 2004. The Practice of Forest Thinning and Its Influence on Nutrient Cycling in Two Scots Pine Stands in the Pyrenees of Navarre. Public University of Navarra.

Blanco, J.A., Emeterio, L.S., González de Andrés, E., Imbert, J.B., Larraínzar, E., Peralta, J., Lo, Y.-H., Castillo, F.J., 2017. Are Pyrenean mixed Scots pine / European beech forests in the path to being N-saturated? Rev. Ecosistemas 26, 66–78. https://doi.org/10.7818/RE.2014.26-1.00

Blanco, J.A., González de Andrés, E., San Emeterio, L., Lo, Y.-H., 2015. Modelling mixed forest stands: Methodological challenges and approaches. Dev. Environ. Model. 27, 189–215. https://doi.org/10.1016/B978-0-444-63536-5.00009-0

Blanco, J.A., Imbert, J.B., Castillo, F.J., 2011. Thinning affects *Pinus sylvestris* needle decomposition rates and chemistry differently depending on site conditions. Biogeochemistry 106, 397–414. https://doi.org/10.1007/s10533-010-9518-2

Blanco, J.A., Imbert, J.B., Castillo, F.J., 2009. Thinning affects nutrient resorption and nutrient-use efficiency in two *Pinus sylvestris* stands in the Pyrenees. Ecol. Appl. 19, 682–698. https://doi.org/10.1890/1051-0761-19.3.682

Blanco, J.A., Olarieta, J.R., Kimmins, J.P.H., 2006. Assessment of Long-Term Sustainability of Forest Management in Scots Pine Forests in the Pyrenees : an Ecosystem-Level Simulation Approach, in: Carrera, E., deFelipe, J.., Sureda, B., Tollin, N. (Eds.), International Conference on Sustainibility Measurement and Modelling ICSMM 06. Barcelona.

Blanco, J.A., Seely, B., Welham, C., Kimmins, J.P.H., Seebacher, T.M., 2007. Testing the performance of a forest ecosystem model (FORECAST) against 29 years of field data in a Pseudotsuga menziesii plantation. Can. J. For. Res. 37, 1808–1820. https://doi.org/10.1139/X07-041

Booth, T.H., 2013. Eucalypt plantations and climate change. For. Ecol. Manage. 301, 28–34. https://doi.org/10.1016/J.FORECO.2012.04.004

Bravo-Oviedo, A., Roig, S., Bravo, F., Montero, G., Del-Río, M., 2011. Environmental variability and its relationship to site index in Mediterranean maritime pine. For. Syst. 20, 50. https://doi.org/10.5424/fs/2011201-9106

Brienen, R.J.W., Gloor, E., Zuidema, P.A., 2012. Detecting evidence for CO_2 fertilization from tree ring studies: The potential role of sampling biases. Global Biogeochem. Cycles 26, GB1025. https://doi.org/10.1029/2011GB004143

Brito, P., Grams, T.E.E., Matysssek, R., Jimenez, M.S., Gonzalez-Rodriguez, A.M., Oberhuber, W., Wieser, G., 2016. Increased water use efficiency does not prevent growth decline of *Pinus canariensis* in a semi-arid treeline ecotone in Tenerife, Canary Islands (Spain). Ann. For. Sci. 73, 741–749. https://doi.org/10.1007/s13595-016-0562-5

Bugmann, H., Bigler, C., 2011. Will the CO_2 fertilization effect in forests be offset by reduced tree longevity? Oecologia 165, 533–544. https://doi.org/10.1007/s00442-010-1837-4

Camarero, J.J., Gazol, A., Galván, J.D., Sangüesa-Barreda, G., Gutiérrez, E., 2015. Disparate effects of global-change drivers on mountain conifer forests: warming-induced growth enhancement in young trees vs. CO_2 fertilization in old trees from wet sites. Glob. Chang. Biol. 21, 738–749. https://doi.org/10.1111/gcb.12787

Candel-Perez, D., Blanco, J.A., Gonzalez De Andres, E., Lo, Y.-H., Imbert, J.B., Castillo, F.J.,

2017. Simulating the interaction among initial stand density and water and nutrient flows to understand the development of *Pinus sylvestris* and *Fagus sylvatica* mixedwoods under climate change. Ecosistemas 26. https://doi.org/10.7818/ECOS.2017.26-2.05

Cardil, A., Imbert, J.B., Camarero, J.J., Primicia, I., Castillo, F., 2018. Temporal interactions among throughfall, type of canopy and thinning drive radial growth in an Iberian mixed pine-beech forest. Agric. For. Meteorol. 252, 62–74. https://doi.org/10.1016/J.AGRFORMET.2018.01.004

Chaste, E., Girardin, M.P., Kaplan, J.O., Bergeron, Y., Hély, C. 2019. Increases in heat-induced tree mortality could drive reductions of biomass resources in Canada´s managed boreal forest. Landscape Ecol. 34. 403-426. https://doi.org/10.1007/S10980-019-00780-4

Cole, C.T., Anderson, J.E., Lindroth, R.L., Waller, D.M., 2010. Rising concentrations of atmospheric CO_2 have increased growth in natural stands of quaking aspen (*Populus tremuloides*). Glob. Chang. Biol. 16, 2186–2197. https://doi.org/10.1111/j.1365-2486.2009.02103.x

Collalti, A., Trotta, C., Keenan, T.C., Ibrom, A., Bond-Lamberty, B., Grote, R., Vicca, S., Reyer, C.P.O., Migliavacca, M., Veroustraete, F., Anav, Al., Campioli, M., Scoccimarro, E., Sigut, L., Grieco, E., Cescatti, A., Matteucci, G. 2018 Thinning can reduce losses in carbon use efficiency and carbon stocks in managed forests under warmer climate. J. Adv. Model. Earth Sys. 10, 2427-2452. https://doi.org/10.1002/2018MS001275

Davi, H., Cailleret, M., 2017. Assessing drought-driven mortality trees with physiological process-based models. Agric. For. Meteorol. 232, 279–290. https://doi.org/10.1016/j.agrformet.2016.08.019

Degener, J.F., 2015. Atmospheric CO_2 fertilization effects on biomass yields of 10 crops in northern Germany. Front. Environ. Sci. 3, 48. https://doi.org/10.3389/fenvs.2015.00048

Dordel, J., Seely, B., Simard, S.W., 2011. Relationships between simulated water stress and mortality and growth rates in underplanted Toona ciliata Roem. in subtropical Argentinean plantations. Ecol. Modell. 222, 3226–3235. https://doi.org/10.1016/J.ECOLMODEL.2011.05.027

Drake, B.L., Hanson, D.T., Lowrey, T.K., Sharp, Z.D., 2017. The carbon fertilization effect over a century of anthropogenic CO_2 emissions: higher intracellular CO_2 and more drought resistance among invasive and native grass species contrasts with increased water use efficiency for woody plants in the US Southwest. Glob. Chang. Biol. 23, 782–792. https://doi.org/10.1111/gcb.13449

Dong, Z., Driscoll, C.T., Johnson, S.L., Campbell, J.L., Pourmokhtarian, A., Stoner, A.M.K., Hayhoe, K. 2019 Projections of water, carbon, and nitrogen dynamics under future climate change in an old-growth Douglas-fir forest in the western Cascade Range using a biogeochemical model. Sci. Tot. Environ. 656, 608-624. https://doi.org/10.1016/j.scitotenv.2018.11.377

Dziedek, C., Härdtle, W., Oheimb, G.von, Fichtner, A., 2016. Nitrogen Addition Enhances Drought Sensitivity of Young Deciduous Tree Species. Front. Plant Sci. 7, 1100. https://doi.org/10.3389/FPLS.2016.01100

Esmail, S., Oelbermann, M., 2011. The impact of climate change on the growth of tropical agroforestry tree seedlings. Agrofor. Syst. 83, 235–244. https://doi.org/10.1007/s10457-011-9424-1

Etemadi, H., Samadi, S., Sharifikia, M., 2014. Uncertainty analysis of statistical downscaling models using general circulation model over an international wetland. Clim. Dyn. 42, 2899–2920. https://doi.org/10.1007/s00382-013-1855-0

EUFORGEN, 2009. Distribution map of Scots pine (*Pinus sylvestris*) [WWW Document]. URL http://www.euforgen.org/species/pinus-sylvestris/ (accessed 3.27.19).

Exbrayat, J.-F., Bloom, A.A., Falloon, P., Ito, A., Smallman, T.L., Williams, M., 2018. Reliability ensemble averaging of 21st century projections of terrestrial net primary productivity reduces global and regional uncertainties. Earth Syst. Dyn. 9, 153–165. https://doi.org/10.5194/esd-9-153-2018

Farquhar, G.D., Ehleringer, J.R., Hubick, K.T., 1989. Carbon Isotope Discrimination and Photosynthesis. Annu. Rev. Plant Physiol. Plant Mol. Biol. 40, 503–537.

https://doi.org/10.1146/annurev.pp.40.060189.002443

Fatichi, S., Leuzinger, S., Paschalis, A., Langley, J.A., Donnellan Barraclough, A., Hovenden, M.J., 2016. Partitioning direct and indirect effects reveals the response of water-limited ecosystems to elevated CO_2. Proc. Natl. Acad. Sci. U. S. A. 113, 12757–12762. https://doi.org/10.1073/pnas.1605036113

Fernández-de-Uña, L., Cañellas, I., Gea-Izquierdo, G., 2015. Stand Competition Determines How Different Tree Species Will Cope with a Warming Climate. PLoS One 10, e0122255. https://doi.org/10.1371/journal.pone.0122255

Fleischmann, F., Raidl, S., Oßwald, W.F., 2010. Changes in susceptibility of beech (*Fagus sylvatica*) seedlings towards Phytophthora citricola under the influence of elevated atmospheric CO_2 and nitrogen fertilization. Environ. Pollut. 158, 1051–1060. https://doi.org/10.1016/J.ENVPOL.2009.10.004

Gárate, M., Blanco, J.A., 2013. Importance of root biomass characterization when simulating forest ecosystems. Ecosistemas 22, 66–73. https://doi.org/10.7818/ECOS.2013.22-3.10

Gedalof, Z., Berg, A.A., 2010. Tree ring evidence for limited direct CO_2 fertilization of forests over the 20th century. Global Biogeochem. Cycles 24, GB3027. https://doi.org/10.1029/2009GB003699

Gessler, A., Schaub, M., McDowell, N.G., 2017. The role of nutrients in drought-induced tree mortality and recovery. New Phytol. 214, 513–520. https://doi.org/10.1111/nph.14340

González de Andrés, E., Blanco, J.A., Imbert, J.B., Guan, B.T., Lo, Y.H., Castillo, F.J., 2019. ENSO and NAO affect long-term leaf litter dynamics and stoichiometry of Scots pine and European beech mixedwoods. Glob. Chang. Biol. (In press) https://doi.org/10.1111/gcb.14672.

González de Andrés, E., Camarero, J.J., Blanco, J.A., Imbert, J.B., Lo, Y.-H., Sangüesa-Barreda, G., Castillo, F.J., 2018. Tree-to-tree competition in mixed European beech-Scots pine forests has different impacts on growth and water-use efficiency depending on site conditions. J. Ecol. 106, 59–75. https://doi.org/10.1111/1365-2745.12813

González de Andrés, E., Seely, B., Blanco, J.A., Imbert, J.B., Lo, Y.-H., Castillo, F.J., 2017.

Increased complementarity in water-limited environments in Scots pine and European beech mixtures under climate change. Ecohydrology 10, e1810. https://doi.org/10.1002/eco.1810

Hartwell Allen, L.J., Baker, J.T., Boote, K.J., 1996. The CO_2 fertilization effect: higher carbohydrate production and retention as biomass and seed yield, in: Bazzaz, F., Sombroek, W. (Eds.), Global Climate Change and Agricultural Production. Direct and Indirect Effects of Changing Hydrological, Pedological and Plant Physiological Processes. Food And Agriculture Organization Of The United Nations And John Wiley & Sons, Rome and Chichester.

Holden, P.B., Edwards, N.R., Gerten, D., Schaphoff, S., 2013. A model-based constraint on CO_2 fertilisation. Biogeosciences 10, 339–355. https://doi.org/10.5194/bg-10-339-2013

Holtum, J.A.M., Winter, K., 2010. Elevated [CO_2] and forest vegetation: more a water issue than a carbon issue? Funct. Plant Biol. 37, 694–702. https://doi.org/10.1071/FP10001

Huang, Z., Liu, B., Davis, M., Sardans, J., Peñuelas, J., Billings, S., 2016. Long-term nitrogen deposition linked to reduced water use efficiency in forests with low phosphorus availability. New Phytol. 210, 431–442. https://doi.org/10.1111/nph.13785

Intergovernmental Panel on Climate Change (Ed.), 2013. Climate Change 2013 - The Physical Science Basis. Cambridge University Press, Cambridge. https://doi.org/10.1017/CBO9781107415324

Ise, T., Moorcroft, P.R., 2010. Simulating boreal forest dynamics from perspectives of ecophysiology, resource availability, and climate change. Ecol. Res. 25, 501–511. https://doi.org/https://doi.org/10.1007/s11284-009-0680-8

Jonard, M., Fürst, A., Verstraeten, A., Thimonier, A., Timmermann, V., Potočić, N., Waldner, P., Benham, S., Hansen, K., Merilä, P., Ponette, Q., dela Cruz, A.C., Roskams, P., Nicolas, M., Croisé, L., Ingerslev, M., Matteucci, G., Decinti, B., Bascietto, M., Rautio, P., 2015. Tree mineral nutrition is deteriorating in Europe. Glob. Chang. Biol. 21, 418–430. https://doi.org/10.1111/gcb.12657

Kang, H., Seely, B., Wang, G., Cai, Y., Innes, J., Zheng, D., Chen, P., Wang, T. 2017. Simulating the impact of climate change on the growth of Chinese fir plantations in Fujian province,

China. New Zealand J. For. Sci. 47, 20. https://doi.org/10.1186/s40490-017-0102-6

Katul, G., Manzoni, S., Palmroth, S., Oren, R., 2010. A stomatal optimization theory to describe the effects of atmospheric CO_2 on leaf photosynthesis and transpiration. Ann. Bot. 105, 431–442. https://doi.org/10.1093/aob/mcp292

Keenan, T., Maria Serra, J., Lloret, F., Ninyerola, M., Sabate, S., 2011. Predicting the future of forests in the Mediterranean under climate change, with niche- and process-based models: CO_2 matters! Glob. Chang. Biol. 17, 565–579. https://doi.org/10.1111/j.1365-2486.2010.02254.x

Kim, D., Oren, R., Qian, S.S., 2016. Response to CO_2 enrichment of understory vegetation in the shade of forests. Glob. Chang. Biol. 22, 944–956. https://doi.org/10.1111/gcb.13126

Kimmins, J.P.H., 1993. Scientific foundations for the simulation of ecosystem function and management in FORCYTE-11. Forestry Canada, Northern Forestry Centre.

Kimmins, J.P.H., Blanco, J.A., Seely, B., Welham, C., Scoullar, K., 2008. Complexity in modelling forest ecosystems: How much is enough? For. Ecol. Manage. 256, 1646–1658. https://doi.org/10.1016/J.FORECO.2008.03.011

Kimmins, J.P.H., Mailly, D., Seely, B., 1999. Modelling forest ecosystem net primary production: the hybrid simulation approach used in forecast. Ecol. Modell. 122, 195–224. https://doi.org/10.1016/S0304-3800(99)00138-6

Kimmins, J.P.J., Blanco, J., Seely, B., Welham, C., Scoullar, K., 2010. Forecasting Forest Futures: A Hybrid Modelling Approach to the Assessment of Sustainability of Forest Ecosystems and their Values, 1st ed. Routledge.

Klein, T., Hartmann, H., 2018. Climate change drives tree mortality. Science 362, 758. https://doi.org/10.1126/science.aav6508

Körner, C. 2003. Carbon limitation in trees. J. Ecol. 91, 4-17.

Lim, H., Oren, R., Palmroth, S., Tor-ngern, P., Morling, T., Nasholm, T., Lundmark, T., Helmisaari, H.S., Leppalammi-Kujansuu, J., Linder, S., 2015. Inter-annual variability of precipitation constrains the production response of boreal *Pinus sylvestris* to nitrogen fertilization. For. Ecol. Manage. 348, 31–45. https://doi.org/10.1016/j.foreco.2015.03.029

Lindner, M., Maroschek, M., Netherer, S., Kremer, A., Barbati, A., Garcia-Gonzalo, J., Seidl, R., Delzon, S., Corona, P., Kolström, M., Lexer, M.J., Marchetti, M., 2010. Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. For. Ecol. Manage. 259, 698–709. https://doi.org/10.1016/J.FORECO.2009.09.023

Lo, Y.-H., Blanco, J. a., Canals, R.M., González de Andrés, E., San Emeterio, L., Imbert, J.B., Castillo, F.J., 2015a. Land use change effects on carbon and nitrogen stocks in the Pyrenees during the last 150 years: A modeling approach. Ecol. Modell. 312, 322–334. https://doi.org/10.1016/j.ecolmodel.2015.06.005

Lo, Y.-H., Blanco, J.A., Seely, B., Welham, C., Kimmins, J.P.H., 2010. Relationships between climate and tree radial growth in interior British Columbia, Canada. For. Ecol. Manage. 259, 932–942. https://doi.org/https://doi.org/10.1016/j.foreco.2009.11.033

Lo, Y.-H., Blanco, J.A., Welham, C., Wang, M., 2015b. Maintaining Ecosystem Function by Restoring Forest Biodiversity – Reviewing Decision-Support Tools that link Biology, Hydrology and Geochemistry, in: Blanco, J.A., Lo, Y.-H., Roy, S. (Eds.), Biodiversity in Ecosystems - Linking Structure and Function. InTech. https://doi.org/10.5772/59390

Lotfiomran, N., Kohl, M., Fromm, J., 2016. Interaction effect between elevated CO_2 and fertilization on biomass, gas exchange and C/N ratio of European beech (*Fagus sylvatica* L.). Plants 5, 38. https://doi.org/10.3390/plants5030038

Luo, Y., Su, B., Currie, W.S., Dukes, J.S., Finzi, A., Hartwig, U., Hungate, B., McMurtrie, R.E., Oren, R., Parton, W.J., Pataki, D.E., Shaw, R.M., Zak, D.R., Field, C.B., 2004. Progressive Nitrogen Limitation of Ecosystem Responses to Rising Atmospheric Carbon Dioxide. Bioscience 54, 731–739. https://doi.org/10.1641/0006-3568(2004)054[0731:pnloer]2.0.co;2

Magalhães, N. dos S., Marenco, R.A., Camargo, M.A.B., 2014. Do soil fertilization and forest canopy foliage affect the growth and photosynthesis of Amazonian saplings? Sci. Agric. 71, 58–65. https://doi.org/10.1590/S0103-90162014000100008

Mäkelä, A., Landsberg, J., Ek, A., E. Burk, T., Ter-Mikaelian, M., I. Agren, G., Oliver, C., Puttonen, P., 2000. Process-based models for forest ecosystem management: Current state of

the art and challenges for practical implementation. Tree Physiol. 20, 289–298. https://doi.org/10.1093/treephys/20.5-6.289

Marshall, J.D., Linder, S., 2013. Mineral nutrition and elevated CO_2 interact to modify delta C-13, an index of gas exchange, in Norway spruce. Tree Physiol. 33, 1132–1144. https://doi.org/10.1093/treephys/tpt004

Maltala, J., Ojansuu, R., Peltola, H., Sievänen, R., Kellomäki, S. 2005. Introducing effects of temperature and CO2 elevation on tree growth into a statistical gorwth and yield model. Ecol. Model. 181, 173-190. https://doi.org/10.1016/j.ecolmodel.2004.06.030

Matala, J., Ojansuu, R., Peltola, H., Raitio, H., Kellomäki, S. 2006. Modelling the response of tree growth to temperature and CO_2 elevation as related to the fertility and current temperature sum of a site. Ecol. Model. 199, 39-52. https://doi.org/10.1016/j.ecolmodel.2006.06.009

McMahon, S.M., Parker, G.G., Miller, D.R., 2010. Evidence for a recent increase in forest growth. Proc. Natl. Acad. Sci. U. S. A. 107, 3611–5. https://doi.org/10.1073/pnas.0912376107

Medlyn, B.E., Duursma, R.A., Zeppel, M.J.B., 2011. Forest productivity under climate change: a checklist for evaluating model studies. Wiley Interdiscip. Rev. Clim. Chang. 2, 332–355. https://doi.org/10.1002/wcc.108

Moreno, A., Neumann, M., Hasenauer, H., 2018. Climate limits on European forest structure across space and time. Glob. Planet. Change 169, 168–178. https://doi.org/10.1016/J.GLOPLACHA.2018.07.018

Neumann, R.B., Cardon, Z.G., 2012. The magnitude of hydraulic redistribution by plant roots: a review and synthesis of empirical and modeling studies. New Phytol. 194, 337–352. https://doi.org/10.1111/j.1469-8137.2012.04088.x

Norby, R.J., Warren, J.M., Iversen, C.M., Medlyn, B.E., McMurtrie, R.E., 2010. CO_2 enhancement of forest productivity constrained by limited nitrogen availability. Proc. Natl. Acad. Sci. U. S. A. 107, 19368–73. https://doi.org/10.1073/pnas.1006463107

Norby, R.J., Wullschleger, S.D., Gunderson, C.A., Johnson, D.W., Ceulemans, R., 1999. Tree responses to rising CO_2 in field experiments: implications for the future forest. Plant, Cell

Environ. 22, 683–714. https://doi.org/10.1046/j.1365-3040.1999.00391.x

Norby, R.J., Zak, D.R., 2011. Ecological Lessons from Free-Air CO_2 Enrichment (FACE) Experiments. Annu. Rev. Ecol. Evol. Syst. 42, 181–203. https://doi.org/10.1146/annurev-ecolsys-102209-144647

Papadakis, J. 1970. Climates of the world, their classification, similitudes, differences, and geographic distribution. Self-edited, Buenos Aires, 47 p.

Penman, J., Gytarsky, M., Hiraishi, T., Krug, T., Kruger, D., Pipatti, R., Buendia, L., Miwa, K., Ngara, T., Tanabe, K., Wagner, F., 2003. Good Practice Guidance for Land Use, Land-Use Change and Forestry. Institute for Global Environmental Strategies (IGES), Kanagawa, Japan.

Peñuelas, J., Canadell, J.G., Ogaya, R., 2011. Increased water-use efficiency during the 20th century did not translate into enhanced tree growth. Glob. Ecol. Biogeogr. 20, 597–608. https://doi.org/10.1111/j.1466-8238.2010.00608.x

Peñuelas, J., Ciais, P., Canadell, J.G., Janssens, I.A., Fernández-Martínez, M., Carnicer, J., Obersteiner, M., Piao, S., Vautard, R., Sardans, J., 2017. Shifting from a fertilization-dominated to a warming-dominated period. Nat. Ecol. Evol. 1, 1438–1445. https://doi.org/10.1038/s41559-017-0274-8

Perry, D.A., Oren, R., Hart, S.C., 2008. Forest ecosystems. Johns Hopkins University Press.

Piao, S., Ciais, P., Friedlingstein, P., deNoblet-Ducoudré, N., Cadule, P., Viovy, N., Wang, T., 2009. Spatiotemporal patterns of terrestrial carbon cycle during the 20th century. Global Biogeochem. Cycles 23, GB4026. https://doi.org/10.1029/2008GB003339

Poulter, B., Pederson, N., Liu, H., Zhu, Z., D'Arrigo, R., Ciais, P., Davi, N., Frank, D., Leland, C., Myneni, R., Piao, S., Wang, T., D'Arrigo, R., Ciais, P., Davi, N., Frank, D., Leland, C., Myneni, R., Piao, S., Wang, T., 2013. Recent trends in Inner Asian forest dynamics to temperature and precipitation indicate high sensitivity to climate change. Agric. For. Meteorol. 178, 31–45. https://doi.org/10.1016/j.agrformet.2012.12.006

Pretzsch, H., 2009. Forest Dynamics, Growth, and Yield, in: Forest Dynamics, Growth and Yield. Springer Berlin Heidelberg, Berlin, Heidelberg, pp. 1–39. https://doi.org/10.1007/978-3-540-

88307-4_1

Pretzsch, H., Biber, P., Schütze, G., Kemmerer, J., Uhl, E., 2018. Wood density reduced while wood volume growth accelerated in Central European forests since 1870. For. Ecol. Manage. 429, 589–616. https://doi.org/10.1016/J.FORECO.2018.07.045

Pretzsch, H., Biber, P., Schütze, G., Uhl, E., Rötzer, T., 2014. Forest stand growth dynamics in Central Europe have accelerated since 1870. Nat. Commun. 5, 4967. https://doi.org/10.1038/ncomms5967

Primicia, I., Artázcoz, R., Imbert, J.-B., Puertas, F., Traver, M.-C., Castillo, F.-J., 2016. Influence of thinning intensity and canopy type on Scots pine stand and growth dynamics in a mixed managed forest. For. Syst. 25, e057. https://doi.org/10.5424/fs/2016252-07317

Primicia, I., Camarero, J.J., Imbert, J.B., Castillo, F.J., 2013. Effects of thinning and canopy type on growth dynamics of *Pinus sylvestris*: inter-annual variations and intra-annual interactions with microclimate. Eur. J. For. Res. 132, 121–135. https://doi.org/10.1007/s10342-012-0662-1

Primicia, I., Imbert, J.B., Traver, M.C., Castillo, F.J., 2014. Inter-specific competition and management modify the morphology, nutrient content and resorption in Scots pine needles. Eur. J. For. Res. 133, 141–151. https://doi.org/10.1007/s10342-013-0753-7

Prudhomme, C., Davies, H., 2009. Assessing uncertainties in climate change impact analyses on the river flow regimes in the UK. Part 2: future climate. Clim. Change 93, 197–222. https://doi.org/10.1007/s10584-008-9461-6

Reyer, C., Lasch, P., Mohren, G.M.J., Sterck, F.J., 2010. Inter-specific competition in mixed forests of Douglas-fir (*Pseudotsuga menziesii*) and common beech (*Fagus sylvatica*) under climate change — a model-based analysis. Ann. For. Sci. 67, 805–805. https://doi.org/10.1051/forest/2010041

Rezaie, N., D'Andrea, E., Braeuning, A., Matteucci, G., Bombi, P., Lauteri, M., 2018. Do atmospheric CO_2 concentration increase, climate and forest management affect iWUE of common beech? Evidences from carbon isotope analyses in tree rings. Tree Physiol. 38, 1110–1126. https://doi.org/10.1093/treephys/tpy025

Ruiz-Benito, P., Lines, E.R., Gómez-Aparicio, L., Zavala, M.A., Coomes, D.A., 2013. Patterns and Drivers of Tree Mortality in Iberian Forests: Climatic Effects Are Modified by Competition. PLoS One 8, e56843. https://doi.org/10.1371/journal.pone.0056843

Saltelli, A., Ratto, M., Andres, T., Campolongo, F., Cariboni, J., Gatelli, D., Saisana, M., Tarantola, S., 2007. Global Sensitivity Analysis. The Primer. John Wiley & Sons, Ltd, Chichester, UK. https://doi.org/10.1002/9780470725184

Salzer, M.W., Hughes, M.K., Bunn, A.G., Kipfmueller, K.F., 2009. Recent unprecedented tree-ring growth in bristlecone pine at the highest elevations and possible causes. Proc. Natl. Acad. Sci. U. S. A. 106, 20348–53. https://doi.org/10.1073/pnas.0903029106

Sardans, J., Alonso, R., Janssens, I.A., Carnicer, J., Vereseglou, S., Rillig, M.C., Fernández-Martínez, M., Sanders, T.G.M., Peñuelas, J., 2016. Foliar and soil concentrations and stoichiometry of nitrogen and phosphorous across European *Pinus sylvestris* forests: relationships with climate, N deposition and tree growth. Funct. Ecol. 30, 676–689. https://doi.org/10.1111/1365-2435.12541

Saura-Mas, S., Estiarte, M., Peñuelas, J., Lloret, F., 2012. Effects of climate change on leaf litter decomposition across post-fire plant regenerative groups. Environ. Exp. Bot. 77, 274–282. https://doi.org/10.1016/j.envexpbot.2011.11.014

Seely, B., Arp, P., Kimmins, J., 1997. A forest hydrology submodel for simulating the effect of management and climate change on stand water stress., in: A, A., M, T. (Eds.), Proceedings of Empirical and Process - Based Models for Forest, Tree and Stand Growth Simulation. Edicões Salamandra, Lisboa, Oeiras, Portugal, pp. 463–477.

Seely, B., Welham, C., Scoullar, K., 2015. Application of a Hybrid Forest Growth Model to Evaluate Climate Change Impacts on Productivity, Nutrient Cycling and Mortality in a Montane Forest Ecosystem. PLoS One 10, e0135034. https://doi.org/10.1371/journal.pone.0135034

Silva, L.C.R., Anand, M., Leithead, M.D., 2010. Recent Widespread Tree Growth Decline Despite Increasing Atmospheric CO_2. PLoS One 5, e11543.

https://doi.org/10.1371/journal.pone.0011543

Simard, S.W., Beiler, K.J., Bingham, M.A., Deslippe, J.R., Philip, L.J., Teste, F.P., 2012. Mycorrhizal networks: Mechanisms, ecology and modelling. Fungal Biol. Rev. 26, 39–60. https://doi.org/10.1016/J.FBR.2012.01.001

Sun, J., Dai, W., Peng, B., Liu, J., He, T., Jiang, P., Han, S., Bai, E., 2018. Does the accelerated soil N cycling sustain N demand of *Quercus mongolica* after decade-long elevated CO_2 treatment? Biogeochemistry 139, 197–213. https://doi.org/10.1007/s10533-018-0463-9

Suzuki-Parker, A., Kusaka, H., Takayabu, I., Dairaku, K., Ishizaki, N.N., Ham, S., 2018. Contributions of GCM/RCM Uncertainty in Ensemble Dynamical Downscaling for Precipitation in East Asian Summer Monsoon Season. SOLA 14, 97–104. https://doi.org/10.2151/sola.2018-017

Suzuki, S.N., Tsunoda, T., Nishimura, N., Morimoto, J., Suzuki, J.-I., 2019. Dead wood offsets the reduced live wood carbon stock in forests over 50 years after a stand-replacing wind disturbance. For. Ecol. Manage. 432, 94–101. https://doi.org/10.1016/J.FORECO.2018.08.054

Teng, J., Vaze, J., Chiew, F.H.S., Wang, B., Perraud, J.-M., Teng, J., Vaze, J., Chiew, F.H.S., Wang, B., Perraud, J.-M., 2012. Estimating the Relative Uncertainties Sourced from GCMs and Hydrological Models in Modeling Climate Change Impact on Runoff. J. Hydrometeorol. 13, 122–139. https://doi.org/10.1175/JHM-D-11-058.1

Thornton, P.E., Lamarque, J.-F., Rosenbloom, N.A., Mahowald, N.M., 2007. Influence of carbon-nitrogen cycle coupling on land model response to CO_2 fertilization and climate variability. Global Biogeochem. Cycles 21, GB4018. https://doi.org/10.1029/2006GB002868

Titus, B.D., Prescott, C.E., Maynard, D.G., Mitchell, A.K., Bradley, R.L., Feller, M.C., Beese, W.J., Seely, B., Benton, R.A., Senyk, J.P., Hawkins, B.J., Koppenaal, R.S., 2006. Post-harvest nitrogen cycling in clearcut and alternative silvicultural systems in a montane forest in coastal British Columbia. For. Chron. 62, 844–859.

Virto, I., Blanco, J.A., 2018. Maintaining soil organic matter: concepts and perspectives., in: Daniels, J.A. (Ed.), Advances in Environmental Research. Nova Science, New York, pp. 95–

138.

Wang, F., Mladenoff, D.J., Forrester, J.A., Blanco, J.A., Scheller, R.M., Peckham, S.D., Keough, C., Lucash, M.S., Gower, S.T., 2014. Multimodel simulations of forest harvesting effects on long-term productivity and CN cycling in aspen forests. Ecol. Appl. 24, 1374–1389. https://doi.org/10.1890/12-0888.1

Way, D.A., Oren, R., 2010. Differential responses to changes in growth temperature between trees from different functional groups and biomes: a review and synthesis of data. Tree Physiol. 30, 669–688. https://doi.org/10.1093/treephys/tpq015

Wei, X., Blanco, J.A., Jiang, H., Kimmins, J.P.H., 2012. Effects of nitrogen deposition on carbon sequestration in Chinese fir forest ecosystems. Sci. Total Environ. 416, 351–361. https://doi.org/10.1016/j.scitotenv.2011.11.087

Wellpott, A., Imbery, F., Schindler, D., Mayer, H. 2005. Simulation of drought for a Scots pine forests (*Pinus sylvestris* L.) in the southern upper Rhine plain. Meteorologische Zeitschrift 14, 143-150.

Yang, Y., Donohue, R.J., McVicar, T.R., Roderick, M.L., Beck, H.E., 2016. Long-term CO_2 fertilization increases vegetation productivity and has little effect on hydrological partitioning in tropical rainforests. J. Geophys. Res. 121, 2125–2140. https://doi.org/10.1002/2016jg003475

Zhu, Z., Piao, S., Myneni, R.B., Huang, M., Zeng, Z., Canadell, J.G., Ciais, P., Sitch, S., Friedlingstein, P., Arneth, A., Cao, C., Cheng, L., Kato, E., Koven, C., Li, Y., Lian, X., Liu, Y., Liu, R., Mao, J., Pan, Y., Peng, S., Peñuelas, J., Poulter, B., Pugh, T.A.M., Stocker, B.D., Viovy, N., Wang, X., Wang, Y., Xiao, Z., Yang, H., Zaehle, S., Zeng, N., 2016. Greening of the Earth and its drivers. Nat. Clim. Chang. 6, 791–795. https://doi.org/10.1038/nclimate3004

Table 1. Average effect size caused by each growth-limiting factor and the combination of all of them on different carbon pools, at two sites and under two climate scenarios. Values are percentages of the light-only estimation.

Site	Climate Scenario	C pool	Nitrogen	Climate	CO_2	Combined
Mediterranean	RCP 4.5	Ecosystem C	-12.2	-8.2	0.7	-14.8
		Litter + CWD C	-17.0	-10.3	0.1	-20.0
		Belowground C	1.0	-7.7	0.1	-7.4
		Aboveground C	-13.2	-6.3	1.4	-13.1
	RCP 8.5	Ecosystem C	-12.3	-8.0	1.2	-12.3
		Litter + CWD C	-17.3	-11.7	-0.3	-19.7
		Belowground C	1.2	-8.9	0.1	-8.4
		Aboveground C	-13.0	-4.0	2.8	-7.3
Continental	RCP 4.5	Ecosystem C	-2.2	-14.5	0.3	-10.6
		Litter + CWD C	5.4	-10.2	0.2	4.7
		Belowground C	-4.2	-5.1	0.1	-9,4
		Aboveground C	-2.2	-20.7	0.5	-13.3
	RCP 8.5	Ecosystem C	-2.3	-12.1	0.6	-7.4
		Litter + CWD C	5.4	-11.8	0.4	3.5
		Belowground C	-4.2	-6.2	0.1	-10.5
		Aboveground C	-2.1	-15.8	0.8	-6.9

List of figures

Figure 1. The top panel shows the climatic diagrams for the study sites for the period 1975-2004 for the Mediterranean site and the continental site. Y: number of years considered; T: mean annual temperature (ºC); P: mean annual amount of precipitation (mm). Oblique striped area shows months with an absolute minimum temperature below 0 °C. The bottom left panel shows the location of the experimental plots (circles) used to calibrate the FORECSAT Climate, the weather stations providing historical climate (triangles), and the weather stations averaged for climate change scenarios projection (stars). The bottom right panel shows the location of the area in the Iberian Peninsula with the distribution of Scots pine in the region (EUFORGEN, 2009).

Figure 2. Average projections of C pools for a Mediterranean Scots pine forest in the southwestern Pyrenees when different limiting factors are simulated.

Figure 3. Average projections of C pools for a continental Scots pine forest in the southwestern Pyrenees when different limiting factors are simulated.

Figure 4. Confidence intervals (95%) of the average C pool projection for a Mediterranean Scots pine forests in the southwestern Pyrenees when different limiting factors are simulated. The lines with the same color (black, red or blue), represent the upper and lower limits of each simulation type. Shaded areas represent the uncertainty regions for each type, being the priority for showing colors first grey (full model), then red (light + climate + CO_2) and last blue (light + climate).

Figure 5. Confidence intervals (95%) of the average C pool projection for a Mediterranean Scots pine forests in the southwestern Pyrenees when different limiting factors are simulated. The lines with the same color (black, red or blue), represent the upper and lower limits of each type of simulation. Shaded areas represent the uncertainty regions for each type, being the priority for showing colors first grey (full model), then red (light + climate + CO_2) and last blue (light + climate).

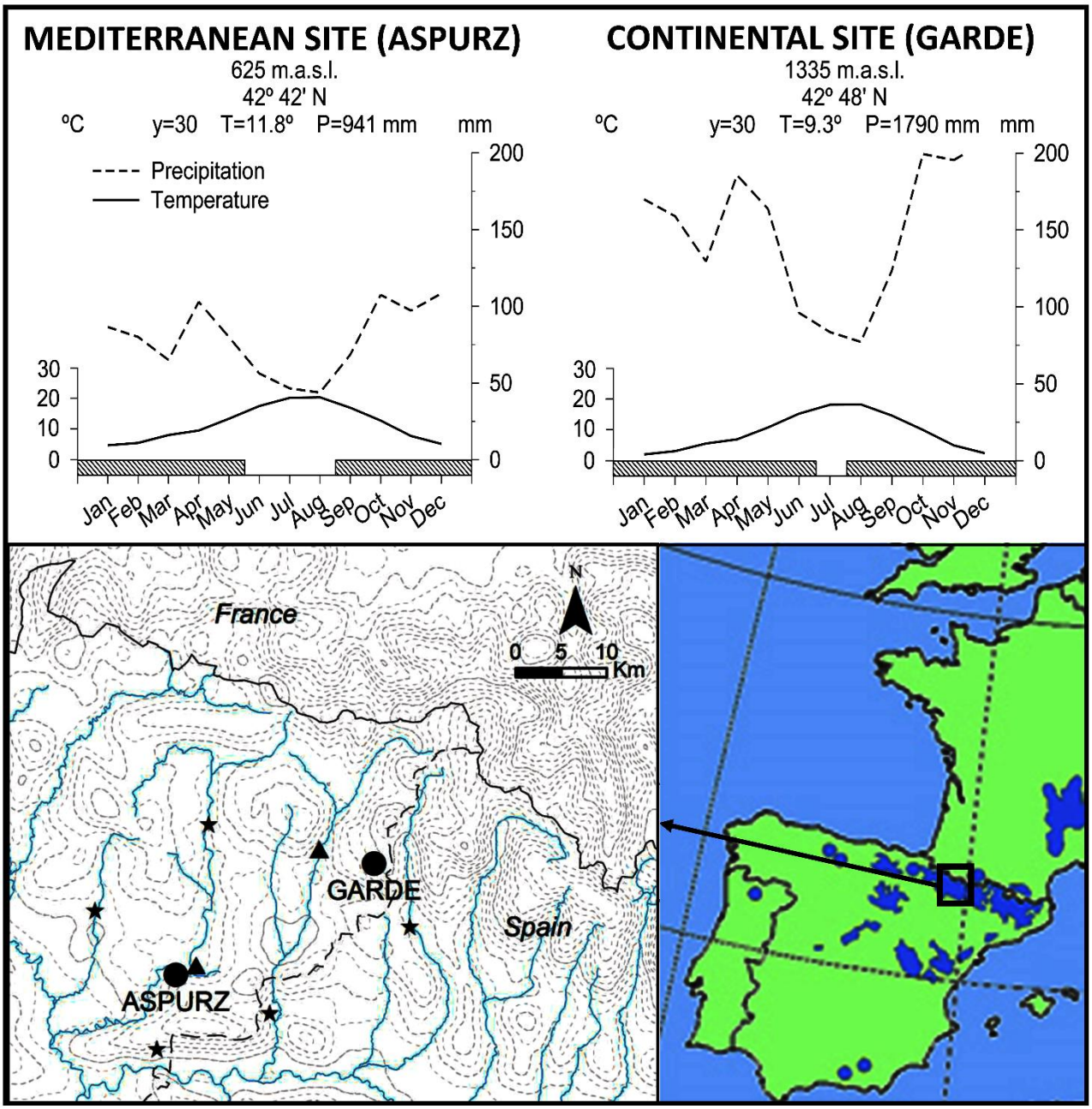
MEDITERRANEAN SITE (ASPURZ)
625 m.a.s.l.
42º 42' N
ºC y=30 T=11.8º P=941 mm mm
Precipitation
Temperature
200
150
100
50
0
30
20
10
0
Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec
CONTINENTAL SITE (GARDE)
1335 m.a.s.l.
42º 48' N
ºC y=30 T=9.3º P=1790 mm mm
France
N
0 5 10
Km
GARDE
Spain
ASPURZ

Figure 1

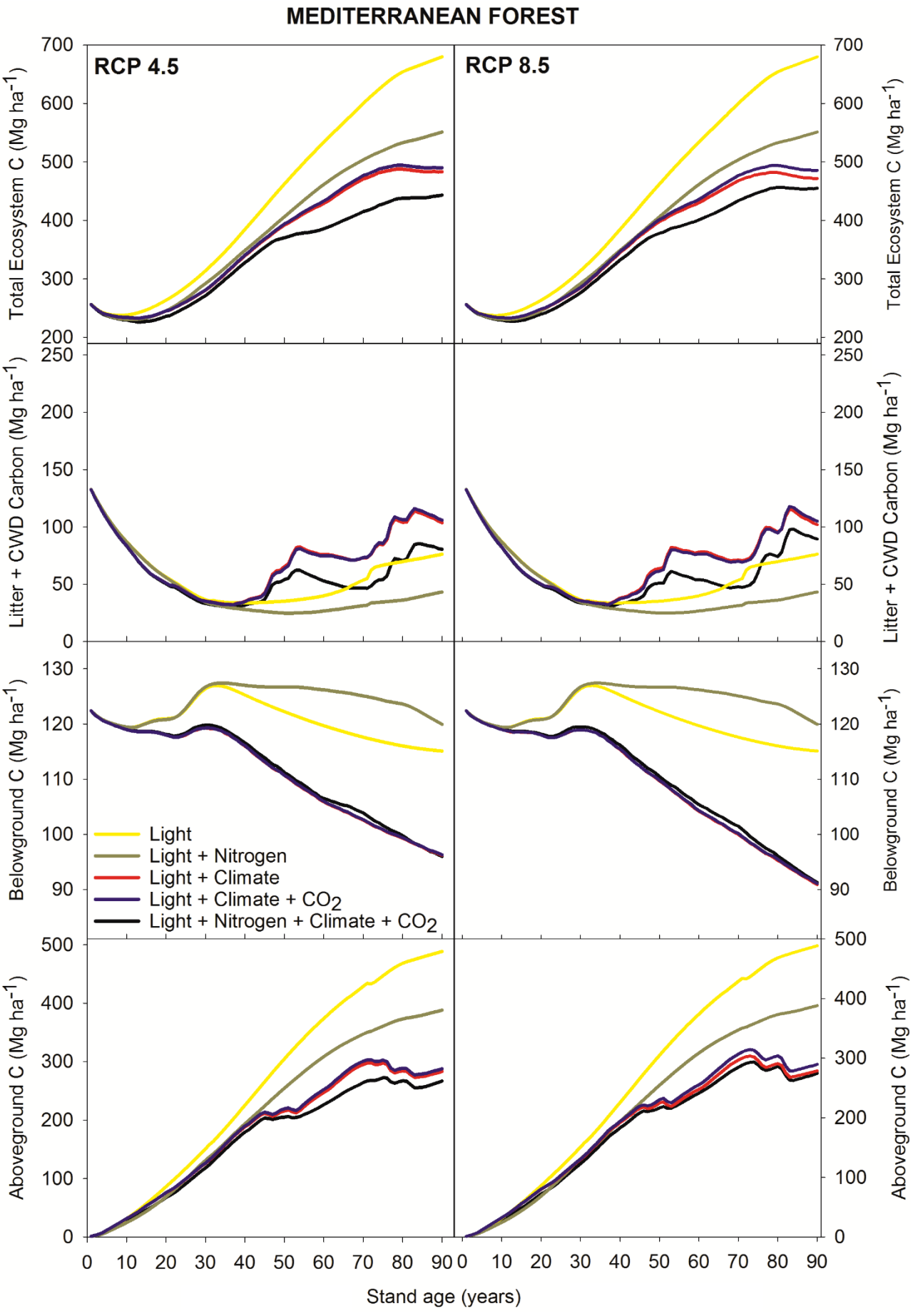
MEDITERRANEAN FOREST
RCP 4.5
RCP 8.5
Total Ecosystem C (Mg ha-1)
Litter + CWD Carbon (Mg ha-1)
Belowground C (Mg ha-1)
Aboveground C (Mg ha-1)
Light
Light + Nitrogen
Light + Climate
Light + Climate + CO2
Light + Nitrogen + Climate + CO2
Stand age (years)

Figure 2.

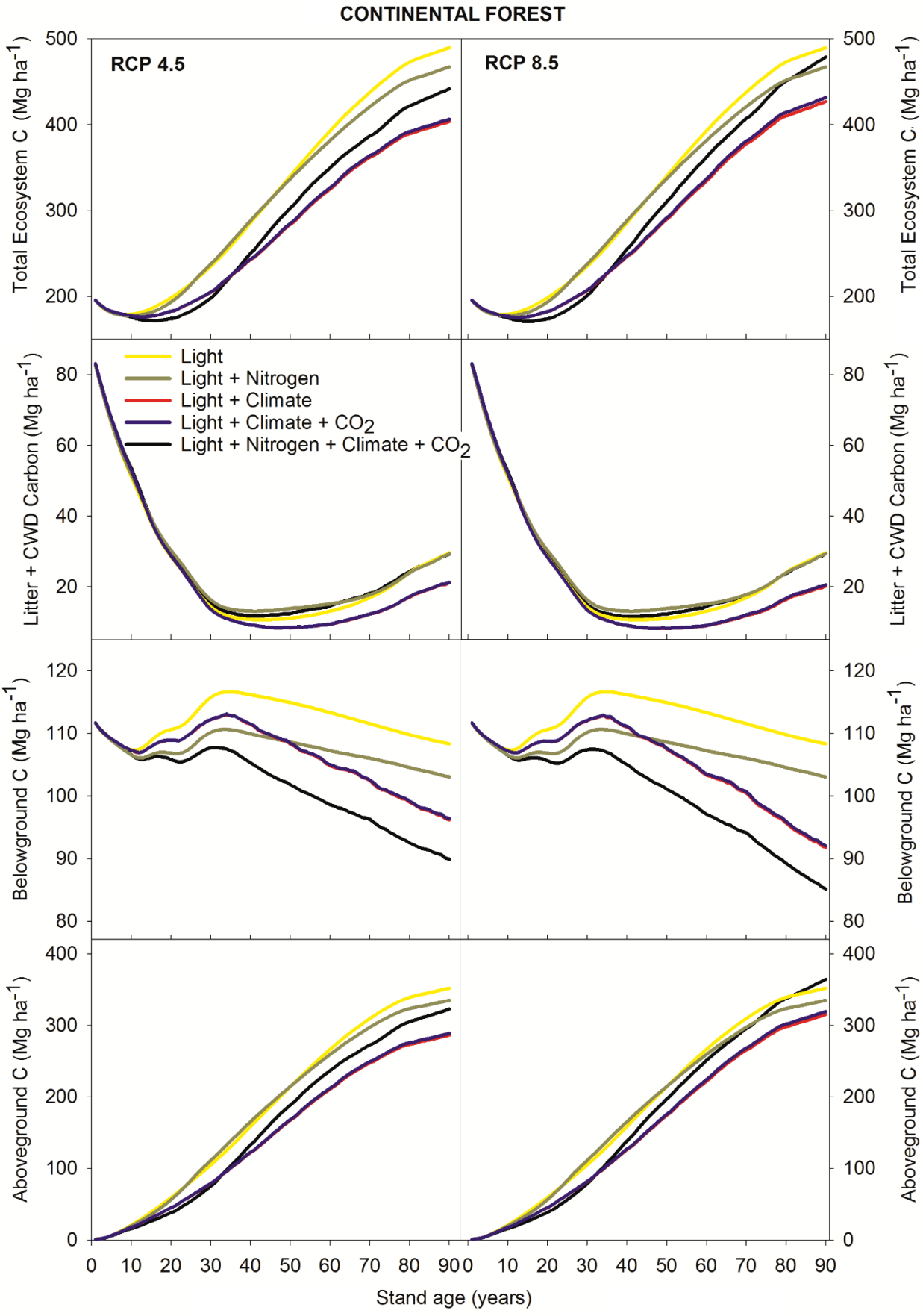
CONTINENTAL FOREST
RCP 4.5
RCP 8.5
Total Ecosystem C (Mg ha-1)
Litter + CWD Carbon (Mg ha-1)
Belowground C (Mg ha-1)
Aboveground C (Mg ha-1)
Light
Light + Nitrogen
Light + Climate
Light + Climate + CO2
Light + Nitrogen + Climate + CO2
Stand age (years)

Figure 3.

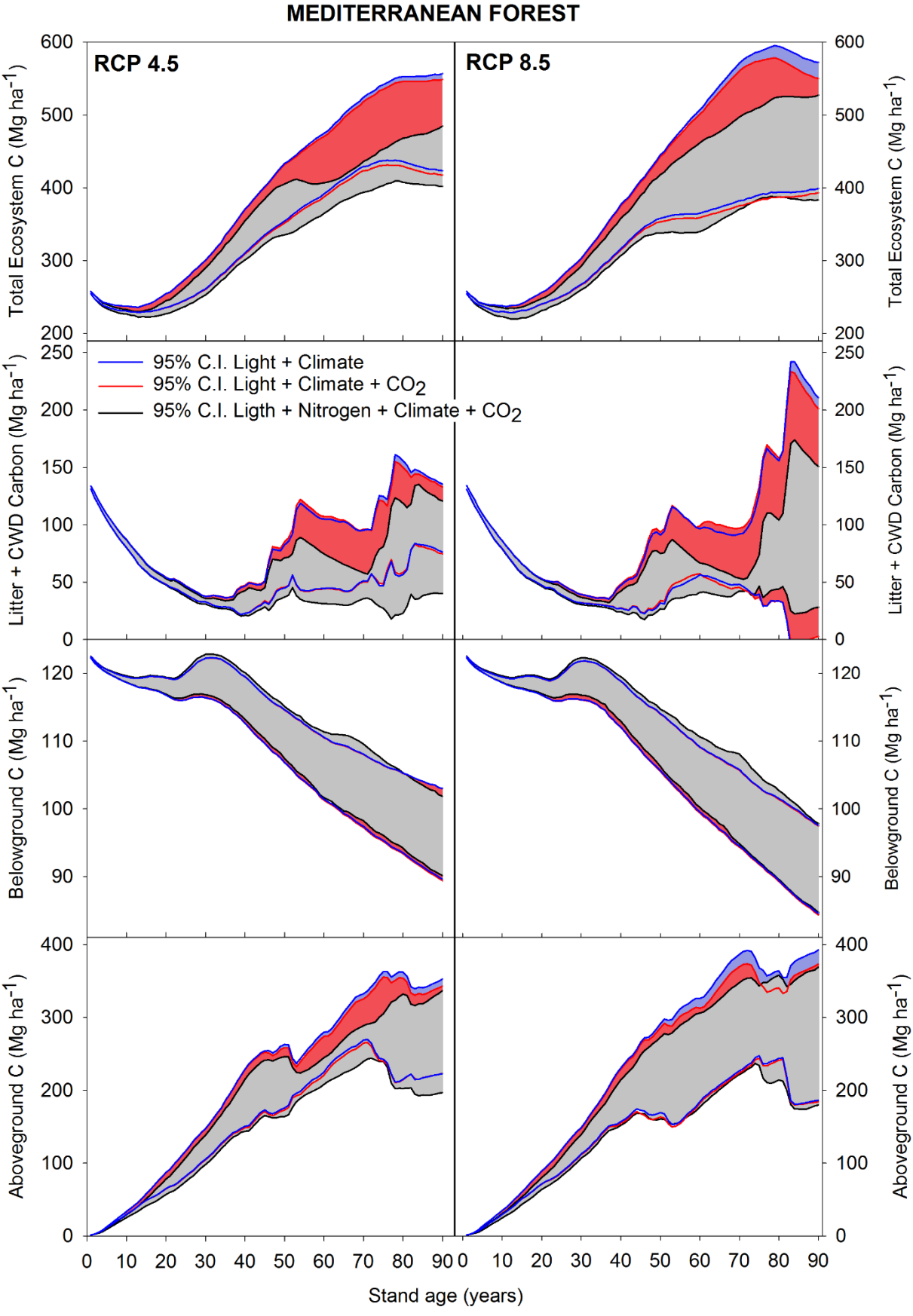
MEDITERRANEAN FOREST
RCP 4.5
RCP 8.5
95% C.I. Light + Climate
95% C.I. Light + Climate + CO2
95% C.I. Ligth + Nitrogen + Climate + CO2
Total Ecosystem C (Mg ha-1)
Litter + CWD Carbon (Mg ha-1)
Belowground C (Mg ha-1)
Aboveground C (Mg ha-1)
Stand age (years)

Figure 4.

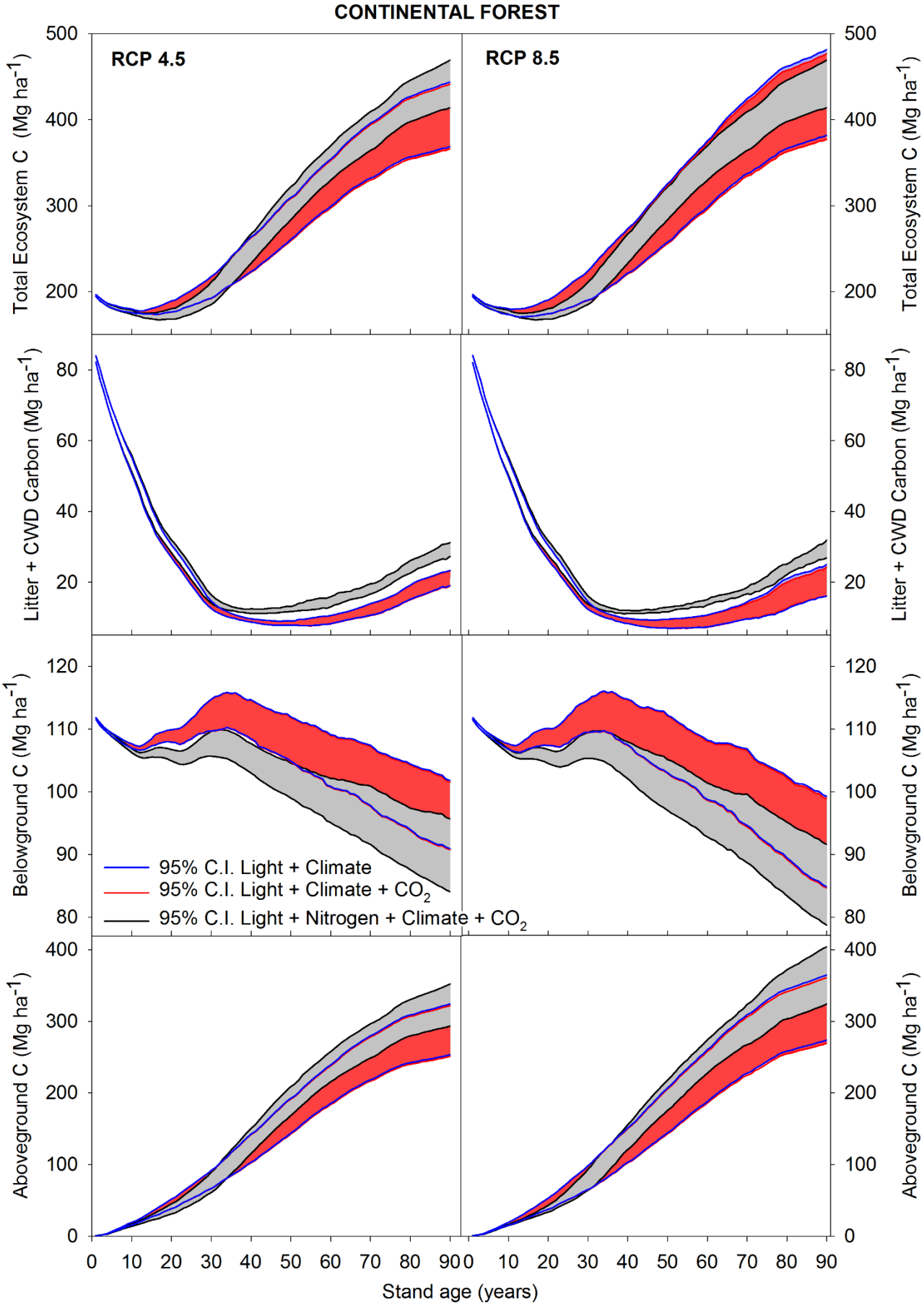
CONTINENTAL FOREST
RCP 4.5
RCP 8.5
Total Ecosystem C (Mg ha-1)
Litter + CWD Carbon (Mg ha-1)
Belowground C (Mg ha-1)
Aboveground C (Mg ha-1)
95% C.I. Light + Climate
95% C.I. Light + Climate + CO2
95% C.I. Light + Nitrogen + Climate + CO2
Stand age (years)

Figure 5.