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Estimation of productivity in pine and oak forests in northern Portugal using Biome-BGC

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Studies about the productivity of forest ecosystems help to quantify sequestered carbon and provide data that are used in forest management. Forests in northern Portugal are an important economic resource, but their productivity in scenarios of future climate change is not yet well understood. The objectives of this study were to evaluate and compare simulated net primary production (NPP) and NPP based on measured data of two tree species located in the Vila Real district forests, pine (*Pinus pinaster* Aiton) and oak (*Quercus pyrenaica* Willd.) and assess their simulated NPP in diverse climate conditions, including future climate scenarios and increasing atmospheric CO_2 concentrations. An ecosystem process model, Biome-BGC, which simulates carbon, nitrogen and water cycles of forest ecosystems close to equilibrium conditions, was used to examine the importance of site and ecophysiological factors on the productivity of these forests. Climate change scenarios and increased CO_2 concentrations were tested to explore potential responses of the studied species. The model provided good estimates of NPP. There was a strong correlation between the simulated and measured NPP values in the pine (15) and oak (15) stands. The NPP of these forests are predicted to increase in the future with a CO_2 increase whereas in a climate with higher temperature and lower soil moisture, the NPP will decrease. These results confirm that precipitation is a very important climate variable to growth and productivity in the Mediterranean forest ecosystems. This study also demonstrated the ability of Biome-BGC to accurately simulate forest ecosystems behaviour and encourages the application of model simulations in Portugal.

Introduction

Forests play an important role in the sequestration of atmospheric carbon dioxide (CO_2) through photosynthesis. The need to monitor and quantify the amount of carbon accumulated within forests has increased, and several studies have been focusing their attention on the effects of forest ecosystems as potential mitigators of environmental change (Melillo *et al.*, 1993; IPCC, 2001; Brown, 2002; Churkina *et al.*, 2003; Ainsworth and Long, 2005; Janssens *et al.*, 2005; Tatarinov and Cienciala, 2006; IPCC, 2007; Chiesi *et al.*, 2010). The effects of climate change on forest ecosystem productivity imply changes in carbon sequestration (Ogaya *et al.*, 2003) and quantifying forest carbon pools, and their variation over time is of fundamental importance in countries subject to Mediterranean climate influence, which is one of the most vulnerable areas to global change (IPCC, 2007).

Climate change studies have predicted increases in atmospheric CO_2 and average annual temperature (Melillo *et al.*, 1993; IPCC WGI, 1996; Santos *et al.*, 2002; Rathgeber *et al.*, 2003). These potential changes are now recognized as one of the most serious problems facing the world and a major challenge for European forestry (Allen *et al.*, 2010; Lindner *et al.*, 2010). Since pre-industrial times the atmospheric CO_2 concentration has increased from 280 to >395 ppmv (parts per million by volume), a 40-per cent change, largely due to carbon emissions from anthropogenic fossil fuel burning and deforestation (IPCC WGI, 1996; Santos *et al.*, 2002; Dlugokencky and Tans, 2014); at the same time, the global average temperature has increased by 0.8°C (Hansen *et al.*, 2006). The current growth of CO_2 is likely to continue in the next decades and may bring CO_2 near to 550 ppm by 2050 and 730–1000 ppm by 2100 (Weigel and Manderscheid, 2012). Stimulation of photosynthesis under the effect of elevated atmospheric CO_2 levels was observed (Weigel and Manderscheid, 2012). This 'CO_2 fertilization effect' could benefit future food production and attenuate potential negative consequences of changes in other climate variables (e.g. temperature increase, more drought events and increase of tropospheric ozone). However, increased photosynthesis may not be sustained over a long-term period under CO_2 enrichment, and a down-regulation often occurs after some time (Calfapietra *et al*., 2005). This is especially true for plants growing under limiting conditions, which do not allow a maintenance of active sinks necessary to accumulate the surplus of carbohydrates produced under elevated CO_2 (Stitt, 1991). Marinari *et al*. (2007) report that the increase of carbon sequestration expected under elevated CO_2 in forests and tree plantation could be limited by nutrient availability, especially of nitrogen. CO_2 enrichment reduced foliar nitrogen and increased the concentration of magnesium, whereas nitrogen fertilization had opposite effects on leaf nitrogen and magnesium concentrations. As Weigel and Manderscheid (2012) stated, attempts to assess the full impact of the various interacting variables of climate change on food production have to understand to what extent crop plants respond to the rapidly changing CO_2 concentration.

To calculate CO_2 sequestered by plants, it is necessary to estimate their net primary production (NPP), an important component in the global carbon cycle. NPP can be measured in terms of biomass or CO_2 exchange. Gas exchange NPP is the rate at which vegetation fixes carbon from the atmosphere (gross primary productivity) minus the rate at which it is returned to the atmosphere by the plants themselves (plant respiration). Biomass NPP is commonly estimated by repeated measurements of biomass accumulations, litter production and herbivory losses in forest stands (Landsberg and Gower, 1997).

Intergovernmental Panel on Climate Change (IPCC) projections through the end of the twenty-first century show that, in the Mediterranean area, the average annual temperature is projected to increase 3–4°C (4–5°C in summer and 2–3°C in winter), and yearly precipitation is expected to drop by up to 20 per cent of the current annual precipitation (up to 50 per cent less in summer whereas winter precipitation is expected to increase) (IPCC, 2001; Christensen *et al*., 2007). Moreover, the frequency, intensity and duration of extreme events are expected to increase, and the region will have more hot days, heat waves, heavy precipitation events and fewer cold days.

General Circulation Models (GCMs) for Portugal, which are used to describe the complex dynamics of mass and energy exchange, momentum and hydrologic cycling within Earth's surface-atmosphere system, predict an upward trend and a significant warming in the twenty-first century, a decrease in precipitation and a change in the annual precipitation cycle (Santos *et al*., 2002). These predicted changes compel us to try to understand the sensitivity of the local forest ecosystems and how the forest species may respond to climate change. The present capacity of the Portuguese forest to store carbon is high under the present climatic conditions, according to Santos *et al*. (2002). Nevertheless, understanding the growth and productivity response to climate change is very important to support forest policies and economic decisions.

Several studies have measured the productivity of Mediterranean forests (Santos *et al*., 2002; Ogaya *et al*., 2003; Chiesi *et al*., 2007; Maselli *et al*., 2009; Chiesi *et al*., 2011a,b; Chiesi *et al*., 2012). Mediterranean forests include both deciduous and evergreen tree species that are characterized by high environmental complexity and an extreme spatio-temporal heterogeneity of their structural and functional features (Chiesi *et al*., 2010). With this high variability in study environments and heterogeneous regions (Bolle *et al*., 2006), their productivity may respond differently to climate change. Experimental climate manipulation studies are one of the approaches to understand the effects of climate change in forests; however, these studies are not only expensive but they are generally developed only on a small scale (<10 km) and the results have to be extrapolated to a bigger, regional scale.

Ecosystem process models, on the other hand, are useful tools to quantify interactions and responses of forests to different climate and edaphic factors and estimate regional and global productivity (Thornton *et al*., 2002; Norby and Luo, 2004; Hasenauer *et al*., 2005; Schmid *et al*., 2006). These models are driven by surface climate variables, employ algorithms to simulate carbon, water and nitrogen cycles and have been, and still are, used to assess forest ecosystem dynamics and how management impacts may affect forest development over time (Peckham *et al*., 2012). Using these models, coupled with site- and species-specific NPP field measurements, it is possible to estimate the impacts of climate change on forest ecosystems productivity (Thornton *et al*., 2002; Bond-Lamberty *et al*., 2005; Bond-Lamberty *et al*., 2007). In this study, we selected the Biome-BGC (Running and Hunt, 1993), among the possible alternatives, due to its specific suitability to simulate water, carbon and nitrogen cycles in different forest ecosystems (White *et al*., 2000; Thornton *et al*., 2002). This model has been widely applied and also used recently to successfully simulate the behaviour of the Mediterranean forest (Chiesi *et al*., 2007; Maselli *et al*., 2009; Chiesi *et al*., 2012).

For various reasons (ecological, economic, etc.), it is necessary to better understand the sensitivity of the different forest regions and forest species to climate change. In Portugal, there is a lack of published studies using forest ecosystem models with future climate projection data to understand the potential effects of climate change on pine (*Pinus pinaster* Aiton) and oak (*Quercus pyrenaica* Willd.) forests and their capacity to store carbon. Pine species are important in Portugal economy. According to the last National Forest Inventory (2005/06), the pine forest area comprises 28 per cent of the total forest area (AFN, 2010). Forests cover 38 per cent of the Vila Real district, and pine is the dominant type (72 per cent). In this district, there are also important mixed oak forests. Oak forests cover 4.7 per cent of the total area in Portugal. *Quercus pyrenaica* occupies ~62 000 ha (Goes, 1991), only 2 per cent of the total area, with the greatest distribution in northern Portugal (Carvalho, 2005). It is well adapted to the climate of Vila Real having 13 per cent of the forest area (the percentage of the Pyrenean oak area also includes some other *Quercus* genera). Oak is also regarded in the region as a valuable timber resource.

The objective of this study was to explore the ability of the ecosystem model Biome-BGC to estimate the annual NPP for pine and oak species in the Vila Real district forests and their dynamics shifts in response to changing climatic conditions. Model NPP estimates were validated against NPP measured by field inventories, and a sensitivity analysis was performed to evaluate which ecophysiological parameters influenced NPP. The model was then used to simulate NPP under climate change scenarios. The results were expected to give a better understanding of these forests' reaction to climate change and Biome-BGC model aptitude to simulate their behaviour.

Material and methods

Study area and field measurements

The study covers an area that represents the environmental variation of the forest type in the Vila Real district, northern Portugal (Figure 1). More information related to each plot is available in Supplementary data, Appendix A.

The study was conducted in stands located on private land, most of them of small size (DGRF, 2006), with no formal management plan, naturally regenerated and with a scattered location in space. They were selected from the National Forest Inventory pool and consist of 15 pine and 15 oak monospecific stands. In 2008, a 500-m^2 plot was established in each stand to collect data for the study. In 2008 and 2009, all the trees, with diameter at breast height (DBH—1.30 m above the ground) $\geq$7.5 cm, were measured with a steel diameter tape and the total height of each tree was also measured with a clinometer. Basal area and density (trees ha^{-1}) were calculated for each plot and averaged for each forest type.

In each plot ($n = 30$), the soil depth was measured in five sampling locations: centre and at 1.0 m from the centre in the four cardinal directions. To analyse the soil texture (sand, silt and clay), soil samples were collected in five plots, randomly selected, for each species.

To determine the relative productivity, the site quality was estimated for pine (height dominant trees at 35 years at breast height) using site index curves from Marques (1991) and for oak (height dominant trees at 30 years at breast height) using site index curves from a study in Galicia (Díaz-Maroto *et al.*, 2010). Galicia is just across the border, in Spain, and has a very similar climate to the study area.

Specific leaf area is an important input parameter in the Biome-BGC model. This parameter is defined as the ratio of fresh foliage surface area to unit dry foliage mass. From a physiological point of view, it is an important parameter in forest canopy architecture because it describes the photosynthetic surface area that can be constructed from unit dry mass of organic matter (Gower *et al.*, 1997; Landsberg and Gower, 1997; Garnier *et al.*, 2001). The specific leaf area was calculated from 10 leaves randomly chosen from the foliage subsample, from all canopy positions in ten trees of each species, randomly chosen in representative plots. The projected leaf areas of the fresh leaf samples were determined using a digital image analyser in the laboratory. These samples were oven-dried at 70°C to a constant dry mass extraction and weight (± 0.01 g). More details about the field measurements are documented (Nunes *et al.*, 2013).

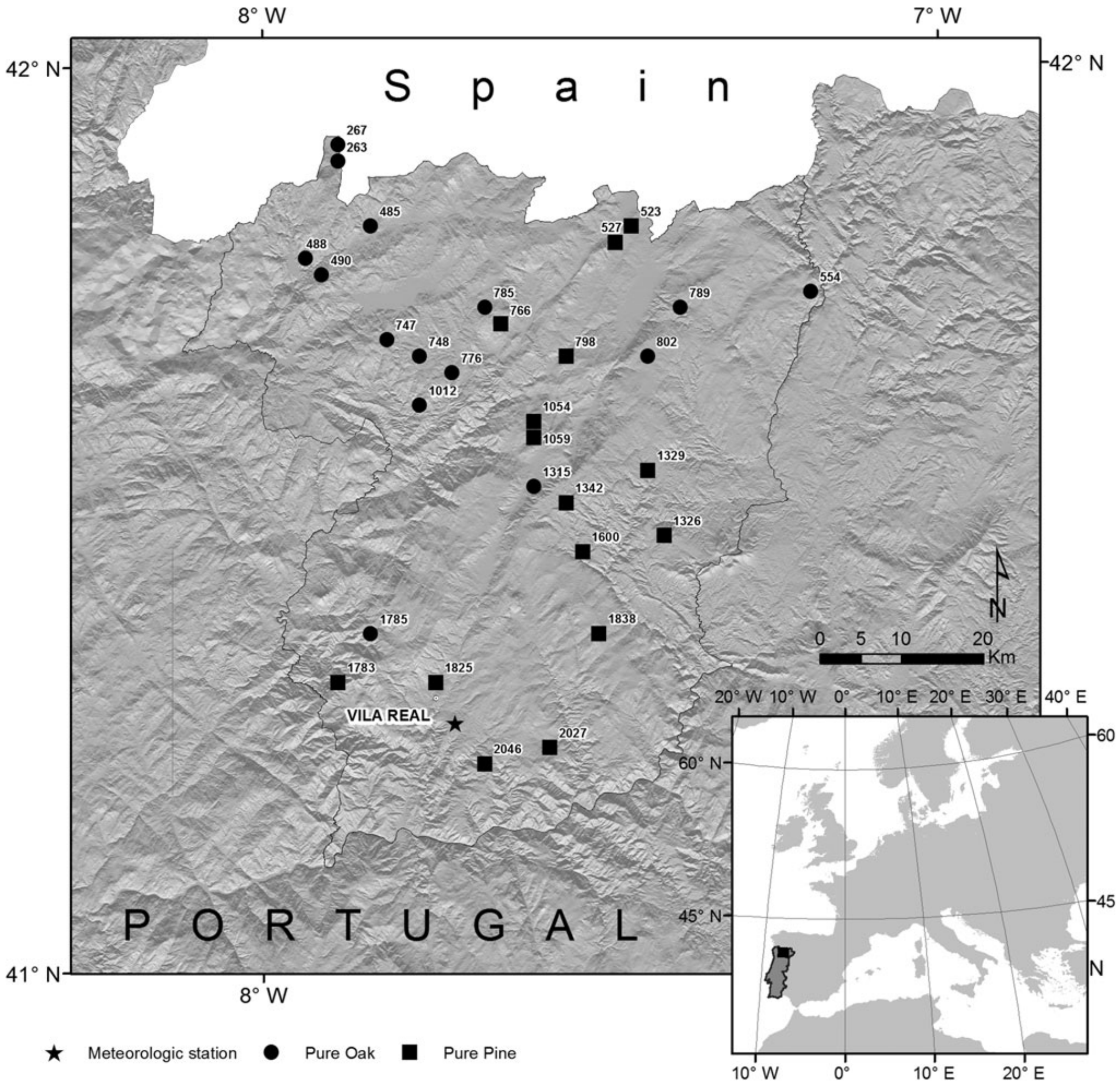

Figure 1 Location of the study stands in the Vila Real district.

Net primary production based on measured data was calculated for all the trees, on the period between 2008 and 2009, as the sum of the average woody biomass increment (ΔB) plus the annual foliage biomass production. In Supplementary data, Appendix B, detailed information is provided.

Meteorological data

The primary driving variables for estimating ecosystem processes with Biome-BGC are the daily meteorological data, including total precipitation (PREC), total incident solar radiation (S_{RAD}), average vapour pressure deficit (VPD), maximum air temperature (T_{max}), minimum air temperature (T_{min}), daytime average air temperature (T_{day}) and daylength (DAYL).

The meteorological data from 1998 to 2012 for the Vila Real meteorological station (41°16′ N, 7°43′W, 560 m a.s.l) were downloaded from the National Climatic Data Center (http://www.ncdc.noaa.gov/), and the daily elements included in the dataset are maximum temperature (T_{max}, °C), minimum temperature (T_{min}, °C), average temperature (T_{day}, °C) and total precipitation (PREC, cm). The mean temperature and total precipitation (± standard error) were calculated for this period to characterize the climate of the study area (Figure 2). The average annual temperature was 13.1°C (± 0.1) and mean annual January and July temperatures averaged 5.9 and 20.5°C, respectively. Total annual precipitation averaged 932.3 mm (± 80.0), but $<$10 per cent occurred between May and September.

Daily meteorological records (maximum temperature, minimum temperature and precipitation) were obtained as previously reported. The daylight average VPD (Pa), daylight average shortwave radiant flux density (S_{RAD}, W m^{-2}) and daylength were not available from the meteorological station. VPD and S_{RAD} were estimated by the methodology described in Supplementary data, Appendix C. Daylength was estimated by using the DAYMET model (www.daymet.ornl.gov) to the same latitude as the Vila Real stations (Thornton and Running, 1999). DAYMET is a model that generates daily gridded surfaces of temperature, precipitation, humidity and radiation over large regions of complex terrain.

The meteorological stations from the Portuguese National Weather Service are sparsely located, and climate information is frequently difficult to retrieve for specific places. So, in order to compile continuous daily climate data for each sampling plot of the study area, a climate simulation model was used. The model mountain microclimate simulator (MTCLIM) was used to extrapolated daily climate data from the Vila Real meteorological station (meteorological base station) to the centre of each study area. More information related to methods of extrapolating climate data is included in Supplementary data, Appendix D.

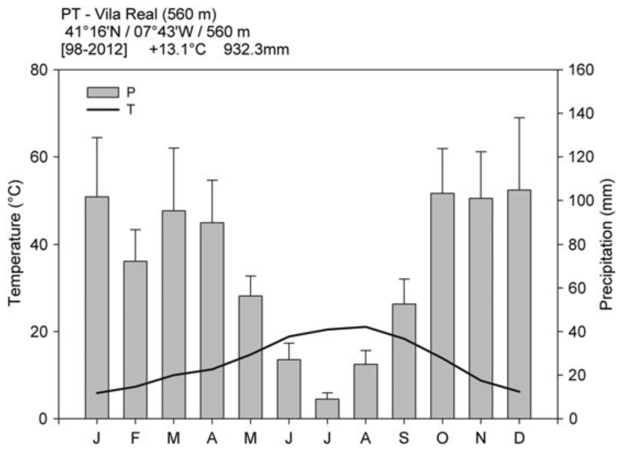

Figure 2 Climate diagram of the Vila Real meteorological station (1998–2012). The bars represent the precipitation (total ± standard error).

Biome-BGC: parameterization and validation

The Biome-BGC (BioGeochemical Cycles) has already been widely used, and good detailed description of the structure and processes of the model have been published in scientific papers (Running and Gower, 1991; White *et al.*, 2000; Thornton *et al.*, 2002).

The Biome-BGC is an ecosystem process-based model (Running and Hunt, 1993) that simulates state and fluxes of water, energy, carbon and nitrogen cycles for vegetation and soil components of terrestrial ecosystems at a daily time step to take advantages of widely available temperature and precipitation data (Running and Gower, 1991; Thornton *et al.*, 2002; Bond-Lamberty *et al.*, 2005). In particular to carbon fluxes, the model produces estimates on carbon allocated in the various ecosystem compartments (stem, leaf, branch, litter, etc.). Eventual climate changes can also be included.

Required input variables for Biome-BGC can be placed in three categories: (1) meteorological inputs, (2) physical site inputs and (3) ecophysiological inputs. The initialization file provides general information about the simulation, including a description of the physical site characteristics and the scenario with the time-frame, ambient CO_2 concentration and nitrogen deposition.

The computation of gross primary production is made using the Farquhar photosynthesis routine (Farquhar *et al.*, 1980), separately for illuminated and shaded foliage, and the NPP is then computed by subtracting the autotrophic respiration. The autotrophic respiration includes the maintenance respiration, calculated as a function of tissue nitrogen concentration (Ryan, 1991), and the growth respiration, which is a function of the amount of carbon allocated to the different plant compartments.

The version of the model currently in use (version 4.2) includes complete parameter settings for the major biomes types (i.e., evergreen needleleaf, evergreen broadleaf, deciduous broadleaf, shrub, C3 and C4 carbon fixation type plants) (White *et al.*, 2000). We parameterized the model to be applicable for pine (*P. pinaster*) and oak (*Q. pyrenaica*) species using site-measured characteristics, such as soil depth, soil texture (sand, slit and clay), geographical position and meteorological data.

Among the Biome-BGC initialization parameters, those related to geographical position, soil depth and meteorological data, extrapolated from the meteorological base station by the MTCLIM model, were modified for each plot, whereas those descriptive of soil features were kept equal to medium conditions due to the lack of information for the entire sampling plots.

Table 1 summarizes the ecophysiological inputs, the third major type of data parameterization, for the studied species. Most of the ecophysiological parameters were referenced by White *et al.* (2000). Due to the absence of species-specific values, most of the values are the genera or default. When well parameterized, Biome-BGC can accurately represent many biome types across the globe but the amount of physiological data required to adequately initialize the model can make it prohibitively difficult to use (White *et al.*, 2000). The canopy average specific leaf area uses specific-species data. We used default values in the following order of preference: *Pinus* spp. or *Quercus* spp. $>$ general *Pinus* or general *Quercus* $>$ coniferous forests (ENF; pine) or temperate broadleaved forests (DBF; oak) $>$ all biome.

All Biome-BGC simulations were performed running the model in a spin-up and run mode, meaning that the first step is to find an internal equilibrium of the model state variables and then make it run (White *et al.*, 2000; Thornton and Rosenbloom, 2005; Pietsch and Hasenauer, 2006). The spin-up simulations were run up to the value of 6000 years in order to minimize the effects of different time to reach steady-state conditions on ecosystem carbon stock pools (White *et al.*, 2000; Tatarinov and Cienciala, 2006). The spin-up run or self-initialization simulation was performed using daily meteorological data between 1998 and 2012 as a reference period, the most recent and complete daily data period for the study area. To define the initial state of the ecosystem, an ecophysiological parameters file, corresponding to the given species and site characteristics, was used. All the estimates provided by the model therefore refer to a forest that

Table 1 Ecophysiological parameter settings used to parameterize Biome-BGC model

Parameter description	Symbol	Units	Pine	Oak
Annual leaf and fine root turnover fraction	LFRT	1 $year^{-1}$	0.26^{δ}	1.0^{δ}
Annual live wood turnover fraction	LWT	1 $year^{-1}$	0.7^{ε}	0.7^{ε}
Annual whole-plant mortality fraction	WPM	1 $year^{-1}$	0.005^{γ}	0.005^{γ}
Annual fire mortality fraction	FM	1 $year^{-1}$	0.005^{δ}	0.0025^{δ}
Allocation requirements				
New fine root C : new leaf C	FRC : LC	Ratio	1.4^{δ}	1.2^{δ}
New stem C : new leaf C	SC : LC	Ratio	2.2^{δ}	2.2^{δ}
New live wood C : new total wood	LWC : TWC	Ratio	0.071^{δ}	0.16^{δ}
New root C : new stem C	CRS : SC	Ratio	0.29^{δ}	0.22^{δ}
Current growth proportion		Prop.	0.5^{δ}	0.5^{δ}
C : N of leaves	$C : N_{leaf}$	kg C kgN^{-1}	42.0^{δ}	27.2^{β}
C : N of leaf litter, after retranslocation	$C : N_{lit}$	Kg C kg N^{-1}	93.0^{δ}	55.0^{δ}
C : N of fine roots	$C : N_{fr}$	kg C kg N^{-1}	58.0^{δ}	63.5^{β}
C : N of live wood	$C : N_{lw}$	kg C kg N^{-1}	50^{δ}	60^{β}
C : N of dead wood	$C : N_{dw}$	kg C kg N^{-1}	730.0^{δ}	451.0^{β}
Leaf litter labile : cellulose : lignin	FR_{lab}: FAR_{cel}: FAR_{lig}	%	$31 : 45 : 24^{\delta}$	$20 : 56 : 24^{\beta}$
Fine root labile : cellulose : lignin	L_{lab}: L_{cel}: L_{lig}	%	$23 : 41 : 36^{\delta}$	$34 : 44 : 22^{\varepsilon}$
Dead wood cellulose : lignin	DW_{cel}: DW_{lig}	%	$71 : 29^{\delta}$	$77 : 23^{\delta}$
Canopy water interception coefficient	W_{int}	1 LAI^{-1} day^{-1}	0.052^{β}	0.045^{ε}
Canopy light extinction coefficient	K	DIM	0.51^{δ}	0.54^{δ}
All-sided: projected leaf area	$LAI_{all: proj}$	DIM	2.6^{δ}	2.0^{δ}
Canopy average SLA (projected area basis)	SLA	m^2 kg C^{-1}	10.5^{s}	34.0^{s}
Ratio of shaded SLA : sunlit SLA	$SLA_{shd: sun}$	DIM	2.0^{ε}	2.0^{ε}
Fraction of leaf N in Rubisco	N_R	%	0.0457^{β}	0.088^{δ}
Maximum stomatal conductance	$g_{s,max}$	m s^{-1}	0.006^{ε}	0.006^{ε}
Cuticular conductance	g_{cut}	m s^{-1}	0.00006^{ε}	0.00006^{ε}
Boundary layer conductance	g_{bl}	m s^{-1}	0.09^{δ}	0.01^{δ}
Leaf water potential: start of conductance reduction	LWP_i	MPa	-0.65^{δ}	-0.34^{δ}
Leaf water potential: complete conductance reduction	LWP_f	MPa	-2.5^{δ}	-2.2^{δ}
VPD: start of conductance reduction	VPD_i	Pa	610^{δ}	1100^{δ}
VPD: complete conductance reduction	VPD_f	Pa	3100^{δ}	3600^{δ}

All values were taken from White *et al.* (2000), unless specified. Superscripts denote values for *Pinus* spp. or *Quercus* spp. (β), evergreen needleleaf or deciduous broadleaf (δ), all forest (γ) and all biome (ε). Superscript (s) denotes specific values measured at study sites.
C, carbon; N, nitrogen; LAI, leaf area index; SLA, specific leaf area; VPD, vapour pressure deficit.

is in ecosystem equilibrium condition. We made the simulation for a 15-year period, the same as the reference period of meteorological data span. A mean out of that period was calculated to obtain the simulated NPP for each plot. Biome-BGC was then validated by comparing simulated NPP to measured NPP (Nunes *et al.*, 2013) in all plots.

Sensitivity test

A model parameter sensitivity analysis for Biome-BGC has already been conducted by White *et al.* (2000). However, it should be stressed that sensitivity analysis for ecophysiological parameters is needed, especially for different environments (Tatarinov and Cienciala, 2006), because many are not measured or are highly uncertain for a given forest type. So, to detect the major effects of ecophysiological parameters on the simulated average annual NPP, a sensitivity analysis was carried out on Biome-BGC. This was made by changing each ecophysiological parameter individually with a 20-per cent variation of each parameter in both directions from its prescribed values (see Table 1). This was made for each species with average site-species data, average soil depth and meteorological data from the Vila Real station (180 simulations: 30 parameters × 3 parameter states (2 directions and 1 reference) × 2 species). The sensitivity of output variables (y) to input parameters (x) (or effects of parameter x on the variable y), $\Delta y/\Delta x$ was calculated as a ratio of output variable change to parameter change (both in per cent). Coefficients of variation for ecophysiological values were also calculated as absolute quantity based on the values selected or calculated from White *et al.* (2000). To understand these sensitivity values, taking into account the absolute quantity ($|\Delta y/\Delta x|$), the parameters were ranked in terms of their effects on the NPP, as parameters with strong effect ($|\Delta y/\Delta x|$ larger than 20 per cent), parameters with medium effect ($|\Delta y/\Delta x|$ between 10 and 20 per cent) and parameters with low effect ($|\Delta y/\Delta x|$ less than 10 per cent) (Tatarinov and Cienciala, 2006).

The effects of temperature and precipitation changes in NPP were also analysed in Biome-BGC taking the average temperature and precipitation as baseline (actual conditions). Precipitation was multiplied by 0.5, 0.75, 1.0 (baseline), 1.5 and 2.0 factors, bringing the total to five levels. In each precipitation level, six temperature steps were used starting with the average temperature as baseline and adding the values of −4.5°C, −3.0°C, −1.5°C, 0°C (baseline), +1.5°C and +3.0°C.

A sensitivity analysis was also used to quantify the effect of soil depth on NPP. Simulations were made for the two species with the soil depth average value and a 20-per cent variation in both directions. The analysis encompassed the actual climate and CO_2 conditions and a scenario of climate change and increased CO_2 concentration (as described in Table 2).

Climate change effects on NPP

To assess the impact of climate change and atmospheric CO_2 concentration increase on the ecosystem processes and which climate variables have more influence on NPP results, seven own scenarios were tested in the model and are identified in Table 2. Climate change scenarios were made taking in account changes in precipitation, temperature and CO_2 concentration. These scenarios were based on the results of the projections from different GCMs with the IPCC scenario IS92a (a scenario that leads to a doubling of the greenhouse gas radiative forcing by the end of the twenty-first century) and regional climate change simulations produced by the HadRM model (regional version of the Hadley Centre climate model for European area), with a horizontal resolution of 50 km (Santos *et al.*, 2002).

The applied change in precipitation was in agreement with the results obtained by the regional model (Santos *et al.*, 2002) that predicted a decrease in annual precipitation in almost the whole of Portugal by up to 15 per cent; therefore, the precipitation considered in the climate change scenario was 0.85 of the actual value. The tested climate change scenario forecasted an increase of 3.0°C in maximum and minimum temperature, consistent with the projections of most GCMs that predict for the Iberian Peninsula an increase between 4 and 7°C by 2100 (Santos *et al.*, 2002) and also consistent with the projections for the Mediterranean zone (where Portugal is included) (Christensen *et al.*, 2007). The $2 \times CO_2$ scenario studied in this work was based on an atmospheric CO_2 of 700 ppmv taking in account the reference value of 365 ppmv (IPCC WGI, 1996; Santos *et al.*, 2002).

In order to identify which climatic variables have more influence on NPP results, climate scenarios were tested, for pine and oak, with different combinations between variables (Table 2), with constant average site-specific conditions, average soil depth and meteorological data from the Vila Real station. Predicted NPP for the species forests were compared with simulation results with reference values of 365 ppmv CO_2 and no changes in temperature and precipitation (under the $C_0T_0P_0$ scenario).

Table 2 Climatic scenarios used in Biome-BGC model

Climatic scenarios[a]	Ambient CO_2 concentration	Temperature	Precipitation
$C_0T_0P_0$	Reference	Reference	Reference
$C_0T_0P_1$	Reference	Reference	−15%
$C_0T_1P_0$	Reference	+3.0°C	Reference
$C_0T_1P_1$	Reference	+3.0°C	−15%
$C_1T_0P_0$	Doubled	Reference	Reference
$C_1T_0P_1$	Doubled	Reference	−15%
$C_1T_1P_0$	Doubled	+3.0°C	Reference
$C_1T_1P_1$	Doubled	+3.0°C	−15%

[a] The first simulation was realized with the current meteorological data from the Vila Real station ($C_0T_0P_0$). The change temperature in +3.0°C was applied in the maximum and minimum temperature.

Results

Stand characteristics

Table 3 summarizes the general stand characteristics in the study area. The analysis showed higher average DBH and total height in pine stands. The basal area and density in oak are lower than those in pine stands. The soil depth in all stands is similar, with an average of 0.8 m. The average site index (height of dominant trees at age 35 for pine and at age 30 for oak) was 15.7 m (±1.0) for pine and 10.6 m (±0.5) for oak. The average age for oak was 55 (±7) years, 17 more years than for pine. Even though oak stands are older than pine stands, they present lower DBH and height values due in part to the slower rate of growth of the oak species. Specific leaf area of current-year foliage for the entire canopy averaged 33 $cm^2\ g^{-1}$ for pine and 179 $cm^2\ g^{-1}$ for oak; the higher value observed for oak was due to the leaves characteristics and shape.

Validation of the measured NPP against model NPP estimates

This study compares the simulated against measured NPP in order to test the reliability of Biome-BGC in the northern Portuguese forests of pine and oak. Observed NPP averaged 397.2 ± 46.3 and 366.3 ± 34.2 $g\ C\ m^{-2}\ year^{-1}$ for pine and oak, respectively. Pine stands averaged higher values than oak stands, but there was no significant difference ($P > 0.05$) between both. Average simulated NPP for pine was 341.6 ± 25.5 $g\ C\ m^{-2}\ year^{-1}$. For oak stands, the model estimated an average NPP of 299.1 ± 25.6 $g\ C\ m^{-2}\ year^{-1}$, which is a reasonable estimate when compared with the observed

Table 3 Summary of structural characteristics of the sampling plots

Forest type	SD (m)	Age	SI	BA ($m^2\ ha^{-1}$)	N	DBH (cm)	Range DBH (cm)		Range H (m)		Soil texture (%)			SLA ($cm^2\ g^{-1}$)
											Sand	Silt	Clay	
Pine														
Mean	0.8	38	15.7	21.0	545	24.2	12.9	38.2	9.5	17.2	78.0	15.6	6.4	32.7
SE	0.1	4	1.0	2.6	122	1.7	1.2	2.5	0.8	1.1				0.86
Oak														
Mean	0.8	55	10.6	10.6	388	22.1	10.3	37.3	6.2	14.1	76.6	18.3	5.1	169.9
SE	0.1	7	0.5	1.5	102	1.9	1.0	3.4	0.5	0.8				8.31

SD, average soil depth; SI, site index according to Marques (1991) for pine and according to Diaz-Maroto *et al.* (2010) for oak; BA, average basal area; N, number of trees per hectare; DBH, average diameter at breast height; H, average tree height; SLA, average specific leaf area.

values. Predicted NPP values were plotted against observed values in Figure 3. The agreement between simulated and observed NPP was strong. For the whole set of analysed plots ($n = 30$ plots), the two species have a $R^2 = 0.88$ and a $S_{yx} = 55.71$ g C m^{-2} year^{-1} ($P < 0.0001$). Analysed by forest type, simulated and measured productivity were positively correlated. Pine had a $R^2 = 0.93$ ($P < 0.0001$), and estimated mean bias was 79.03 g C m^{-2} year^{-1}, or 5.0 per cent of the observed productivity, suggesting that the model slightly underestimated NPP. Oak showed good agreement between simulated and measured NPP: $R^2 = 0.87$ ($P < 0.0001$). Estimated mean bias was 69.71 g C m^{-2} year^{-1}, or 5.3 per cent of the observed productivity, also suggesting that the model slightly underestimated NPP. These data suggest that the model estimates of NPP are reasonable.

Model sensitivity analysis

Our sensitivity analysis shows that the different parameters contributed differently to resulting NPP. The ecophysiological parameters with higher variation on NPP values were the C:N ratio of leaves and fine roots for both species (Table 4). The specific leaf area was also an important ecophysiological parameter for both species, with a NPP variation of 17 and 23 per cent for pine and oak, respectively. The effect of the new fine root carbon to new leaf carbon allocation ratio on NPP was strong in pine species (23 per cent of SA ratio) and small in oak species (7 per cent of SA ratio) but with a high coefficient of variation. A medium effect of canopy light extinction coefficient, new stem carbon to new leaf carbon allocation ratio and C:N ratio of leaf litter was observed on NPP for the oak species only. The effect of nitrogen content in Rubisco on NPP was strong for pine and medium for oak. In pine, a medium effect was also observed on NPP for maximum stomatal conductance. In oak, a medium effect was observed for light extinction coefficient and dead wood cellulose. The effect of other ecophysiological parameters on NPP was small.

The sensitivity analysis showed that, when varying the precipitation and temperature levels for both species, precipitation had a greater influence on NPP (Figure 4). In pine, there was an increase in NPP with an increase in precipitation and productivity was conditioned by the variation in temperature. NPP increase along with precipitation increase is smaller above average temperature than below average temperature. Temperature increases (maximum and minimum) will imply changes leading to a productivity decrease in the ecosystems. Oak had higher NPP with increased precipitation. The highest NPP values were obtained in the oak stands, even with the higher temperatures. The results show that precipitation is an important climate variable in these ecosystems: lower productivity was obtained with lower precipitation.

The NPP response to the soil depth with a 20-per cent variation is presented in Figure 5. This analysis was tested with the actual climate conditions and the combination effects of increased CO_2 and climate changes (corresponding to the $C_1T_1P_1$ scenario). When comparing both species the pine, being a pioneer species, can adapt easier to different edaphic scenarios; oak, on the other hand, being more demanding, is more affected by the soil depth. The response of the two species to the changes in soil depth indicates a positive effect on modelled NPP. Increases in soil depth led to an increase in NPP, particularly for oak. The productivity response to higher soil depth (0.64–0.96 m) was a 25-per cent increase for oak and 16 per cent for pine. The simulations with the climate change scenario show that both species increase productivity when compared with the actual climate conditions. The oak species reached the highest increment with an average of 12-per cent NPP increase over the actual climate conditions for all the tested soil depths.

Simulation under climate change scenarios

The productivity in pine and oak stands shows a similar behaviour in tested climate change scenarios (Figure 6). The effect of temperature alone (under the $C_0T_1P_0$ scenario) decreased the productivity for both species of ~15 per cent for pine and 11 per cent for oak. A decrease in precipitation (under the $C_0T_0P_1$ scenario) leads to a decrease in NPP for both species. The productivity decrease is then roughly 3 per cent. Increase in temperature and decrease in precipitation (under the $C_0T_1P_1$ scenario) decreased NPP by

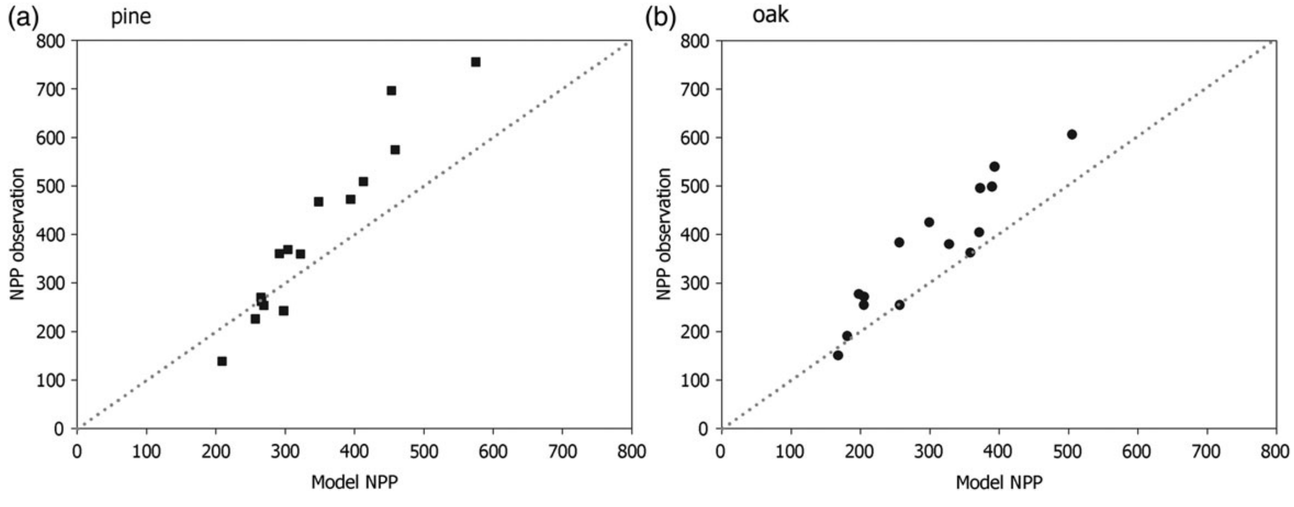

Figure 3 Comparison of modelled NPP (g C m^{-2} year^{-1}) with measured NPP for the analysed plots of pine (a) and oak (b).

Table 4 Sensitivity analysis

Ecophysiological parameter	Pine		Oak	
	SA	CV	SA	CV
Annual leaf turnover fraction	2.34	35.61	0.00	0.00
Annual fine root turnover fraction	2.34	35.61	0.00	0.00
Annual live wood turnover fraction	0.42	0.00	2.85	0.00
Annual whole-plant mortality fraction	0.05	0.00	0.75	0.00
Annual fire mortality fraction	0.60	0.00	0.77	0.00
(ALLOCATION) new fine root C : new leaf C	23.18_1	44.87	6.82	100.00
(ALLOCATION) new stem C : new leaf C	2.62	94.98	12.80_2	42.64
(ALLOCATION) new live wood C : new total wood	0.13	19.72	1.04	52.50
(ALLOCATION) new root C : new stem C	0.54	48.28	1.94	98.36
C : N of leaves	38.84_1	22.36	20.05_1	21.60
C : N of leaf litter, after retranslocation	3.33	25.13	15.72_2	25.28
C : N of fine roots	29.52_1	38.83	23.01_1	31.25
C : N of live wood	0.14	0.00	1.04	0.00
C : N of dead wood	0.35	31.07	4.38	22.00
Leaf litter labile	0.04	38.71	1.74	26.32
Leaf litter cellulose	0.08	10.44	1.09	25.00
Leaf litter lignin	0.12	27.92	2.06	36.67
Fine root labile	0.03	8.24	1.75	8.24
Fine root cellulose	0.10	10.91	3.00	10.91
Fine root lignin	0.06	33.18	3.53	33.18
Dead wood cellulose	1.08	2.68	12.84_2	4.81
Dead wood lignin	0.47	10.69	3.14	21.30
Canopy water interception coefficient	2.37	26.67	0.93	26.67
Canopy light extinction coefficient	0.09	12.09	13.09_2	14.63
All-sided: projected leaf area	2.37	11.28	0.93	0.00
Canopy average SLA (projected area basis)	17.29_2	34.29	22.78_1	34.38
Ratio of shaded SLA : sunlit SLA	0.82	0.00	0.02	0.00
Fraction of leaf N in Rubisco (%)	51.84_1	0.00	19.27_2	0.00
Maximum stomatal conductance	17.30_2	0.00	12.39_2	0.00
Cuticular conductance	0.12	0.00	0.05	0.00
Boundary layer conductance	1.00	0.00	0.05	0.00
Leaf water potential: start of conductance reduction	1.09	46.00	0.44	46.67
Leaf water potential: complete conductance reduction	3.95	71.43	3.55	25.45
VPD: start of conductance reduction	4.46	27.87	4.12	48.18
VPD: complete conductance reduction	1.76	45.16	6.52	22.22

The bottom index indicates the sensitivity ranking.
SA, expressed as ratio % of NPP ± 20%/% of NPP reference, and coefficient of variation (CV, %) results from the selected important ecophysiological parameters affecting the NPP.

17 per cent for pine and 14 per cent for oak. Predicted NPP for both species increased around 26 per cent when atmospheric CO_2 concentration doubled ($C_1T_0P_0$). For both species, the highest NPP values were in the $C_1T_0P_0$ scenario. In $C_1T_1P_0$, pine and oak NPP decreased compared with the scenario $C_1T_0P_0$ although the results were higher compared with $C_0T_0P_0$: 12 per cent for pine and 15 per cent for oak. NPP in the $C_1T_0P_1$ scenario was higher than $C_1T_1P_0$ but lower when compared with $C_1T_0P_0$. NPP results under the scenario $C_1T_1P_1$ were lower for both species compared with $C_1T_0P_0$. According to the results, the values are related to the intensity of their response.

Discussion

Our simulations of forest ecosystem processes showed that the model Biome-BGC is a useful tool to estimate NPP in different forest species (a fast-growing softwood one, the *P. pinaster*; and a slow hardwood one, the *Q. pyrenaica*). Other methodologies for productivity estimation (satellite imagery, field measurements, etc.) require spatially detailed data descriptive of the examined ecosystems, which are often difficult to recover over wide areas and medium/long time periods (Dorigo *et al.*, 2007). Field measurements are also expensive and time-consuming but are critical for

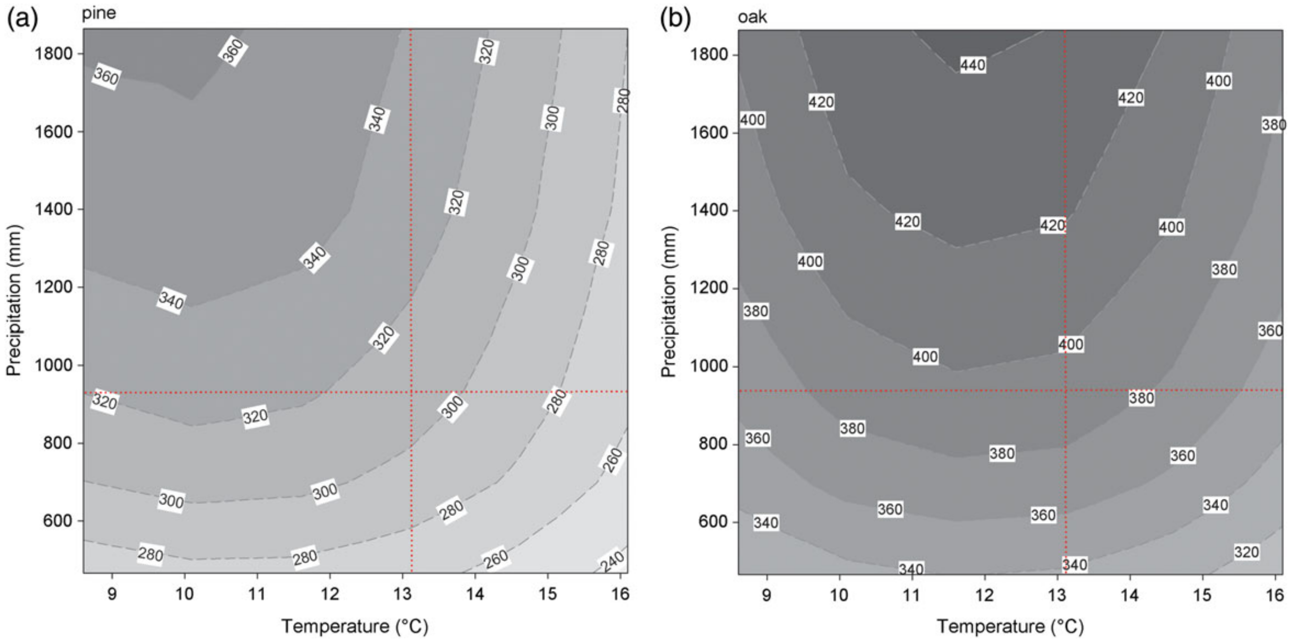

Figure 4 Influence of mean annual temperature and annual precipitation on simulated NPP (g C m^{-2} year^{-1}) for pine (a) and oak (b). The dashed lines indicate the average values of temperature and precipitation. In this figure, the SigmaPlot software was used for a spatial extrapolation of the actual results. Supplementary data, Appendix E presents the actual results.

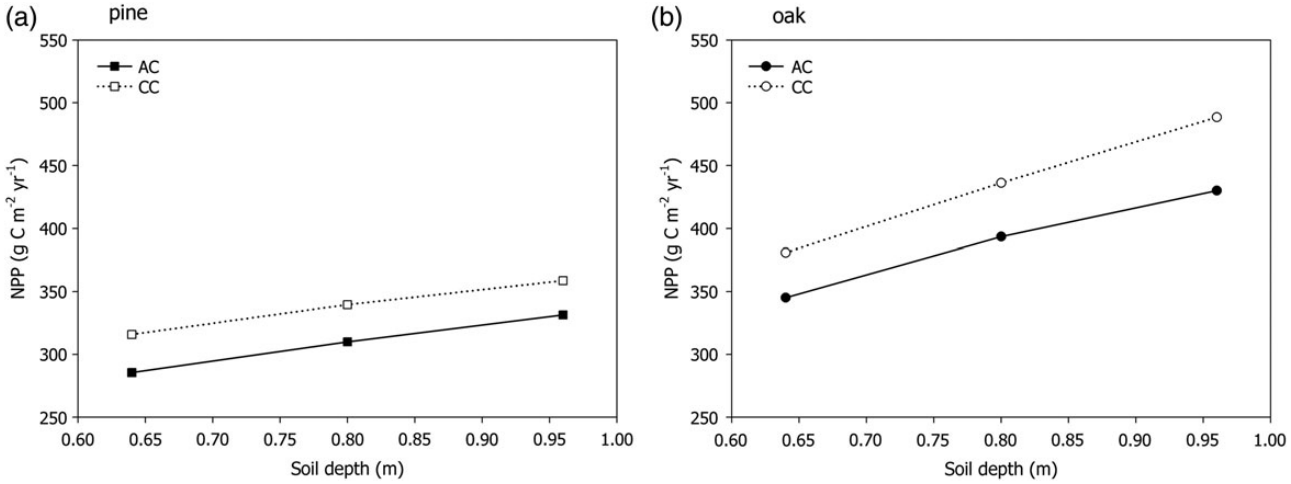

Figure 5 Simulated NPP *vs* soil depth response to climate conditions for pine (a) and oak (b). The AC represents the actual climate conditions ($C_0T_0P_0$), and CC represent the climate change scenario ($C_1T_1P_1$).

model validation. To avoid errors in the measured forest biomass, it is important to adjust allometric equations for component biomass with harvest trees on the study site, because of the potential for intersite variation in tree architecture and wood density (dependent on site conditions and climate variability) (Su *et al.*, 2007).

Accurate simulations by the model require many different parameters (White *et al.*, 2000) and depend on data sources and measured field parameters of the study area (Huiqing *et al.*, 2008). The model identification of equilibrium with local eco-climatic conditions requires the correct setting of soil parameters related to texture and depth (Chiesi *et al.*, 2007), and it is known that forest responses are dependent on site-specific conditions such as climate and soil depth (Churkina *et al.*, 2003; Cienciala and Tatarinov, 2006). Accordingly, in each plot, to have accurate simulations, the soil depth was measured and meteorological data obtained from the MTCLIM model.

Field-based and simulated NPP were positively correlated, and the coefficient of determination of both species was high ($R^2 = 0.93$ for pine and $R^2 = 0.87$ for oak), which means that modelled data are a very good representation of the field data. The

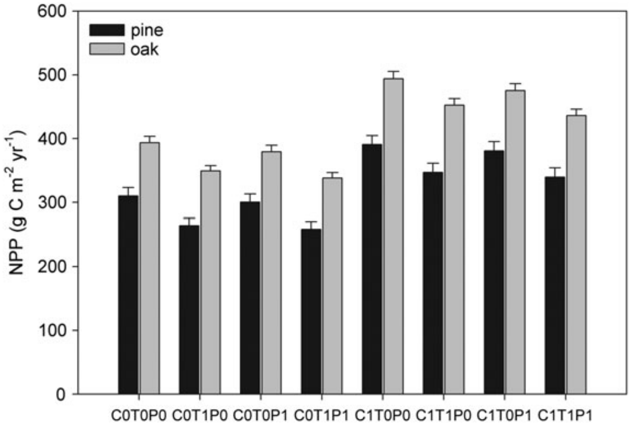

Figure 6 Change in species NPP under the different climate and atmospheric CO_2 changes (see Table 2). The histograms represent the average ± standard error under the scenario $C_xT_xP_x$ simulations.

ability of Biome-BGC to correctly simulate the productivity of the studied forest ecosystems means that it is possible to use this model in a future regional scale analysis of NPP or carbon budgets in Portuguese forests. The accuracy of the model is in agreement with other studies (Thornton *et al.*, 2002; Hanson *et al.*, 2004; Law *et al.*, 2004; Su *et al.*, 2007; Huiqing *et al.*, 2008; Chiesi *et al.*, 2010). The model slightly underestimated the productivity for both species. Cienciala and Tatarinov (2006), however, reported a positive correlation ($R^2 = 0.91$) between modelled and measured aboveground biomass accumulation for 32 plots in managed beech, oak, pine and spruce stands in Europe. We had a similar positive relationship ($R^2 > 0.88$) on 30 plots of oak and pine. Huiqing *et al.* (2008) reported a positive correlation ($R^2 = 0.76$) between modelled and measured NPP of *P. elliotti* forest during 1993–2004. Chiesi *et al.* (2010) also observed a good agreement between measured and estimated forest annual volume increment ($R^2 = 0.81$) for six ecosystem types in Tuscany forests (central Italy). Despite the model tendency to underestimate NPP, we should have in mind that *P. pinaster* is a fast-growing species with a regrowth period of <50 years, whereas *Q. pyrenaica* is a low growing species with a regrowth of >100 years. Additionally, the *P. pinaster* is a pioneer species, which means it allows a wide range of edaphic and climatic conditions to be installed, whereas the *Q. pyrenaica* is much more exigent and requires depth and rich soils.

The sensitivity analysis for the ecophysiological parameters revealed that: specific leaf area, maximum stomatal conductance, C:N ratios of leaves and fine root, and allocation ratios of new fine root carbon to new leaf carbon had the greatest effect on NPP. Tatarinov and Cienciala (2006) reached similar conclusions when studying forest ecosystems of beech, oak, pine and spruce species in Central Europe. White *et al.* (2000) also reported that NPP is sensitive to leaf and fine root C:N, maximum stomatal conductance and specific leaf area. We observed an important effect of leaf N in Rubisco on NPP in both species, similarly to White *et al.* (2000). This effect follows from the fact that the maximum rate of carboxylation in the model is proportional to N content in Rubisco. The effect of the light extinction coefficient was different for both species: it was medium for oak and small for pine. Similar results in evergreen coniferous and deciduous broadleaf forests were found by White *et al.* (2000).

The analysis of the soil depth, within the NPP estimation, indicates a sensitivity effect, which results in higher productivity due to the increase in soil depth. This could be explained by the fact that, in principle, greater soil depth should provide more water availability for the plants and consequently better growth and productivity (Kremer and Running, 1996). In fact, water routeing is straightforward in the Biome-BGC model, excess precipitation is either routed to surface runoff or deep drainage. Shallow soil layer reduces total water-holding capacity and consequently water availability.

The demonstrated capability of the model to simulate the present behaviour of forest ecosystems, as discussed previously, was a necessary prerequisite for the application of this methodology to simulate the effects of different environmental scenarios and to analyse the effects of changing climatic conditions and ambient CO_2 concentrations on ecosystems. Based on this, different environmental scenarios were considered in our simulations: higher temperature, decreased precipitation, increased atmospheric CO_2 concentration and their possible combinations. Several studies analysed the model NPP response to climate change scenarios (Su *et al.*, 2007; Huiqing *et al.*, 2008; Chiesi *et al.*, 2010). According to Melillo *et al.* (1990), climate change is expected to affect the NPP of the world's land ecosystems. Kirschbaum and Fischlin (1996) suggested that forests are highly sensitive to climate change and the first response of ecosystems to climate change and atmospheric CO_2 concentration increase might be an increase in productivity.

Biome-BGC predicted a significant NPP increase (26 per cent) in the scenario of doubled atmospheric CO_2 concentration for both tested species. These results are in agreement with those obtained by: Osborne *et al.* (2000) in a simulation experiment for Mediterranean ecosystems (25-per cent higher NPP when increasing CO_2 from 297 to 360 ppmv); Curtis and Wang (1998), who found a 28.8 ± 2.4-per cent increase, in a meta-analysis on 102 measurements of woody plants total biomass response to elevated CO_2; Ainsworth and Long (2005), who reported a 28-per cent increase in aboveground dry matter production for trees grown under elevated CO_2 concentration, based on the data collected from 120 primary, peer-reviewed articles describing tree physiology and production in 12 large-scale free-air-CO_2-enrichment (FACE) experiments (with simulated CO_2 concentrations from 475 to 600 ppmv); Hättenschwiler and Körner (2003), who observed increased biomass growth in *Prunus laurocerasus*, *Hedera helix* and *Fraxinus excelsior* at two elevated CO_2 concentrations compared with ambient CO_2, in Swiss temperate forests; and Chiesi *et al.* (2010) in a study that simulated effects of increased ambient CO_2 concentration (550 ppmv) on six ecosystems types and indicated an increase in forest production.

For longer periods of time, other simulations have shown that, in increased atmospheric CO_2 concentration scenarios, the increase of NPP is not linear and cannot persist indefinitely at high strength (Cao and Woodward, 1998). The increased CO_2 also leads to water-use efficiency decrease, and the increased heterotrophic respiration leads to a lesser increase in NPP than expected (Cramer *et al.*, 2001). Resources like nitrogen also play an important role in CO_2 increased scenarios. With CO_2 enrichment soil C:N increases and decomposing microorganisms require more nitrogen; this effect can reduce nitrogen mineralization (Hungate *et al.*, 2003) leading to lower growth. Hättenschwiler *et al.* (2002) also expressed doubts over the persistence of the initial growth stimulation forced by the CO_2 enrichment.

When the scenario $C_1T_1P_1$ was tested, the NPP value was higher than that in the reference scenario. Nevertheless, the obtained value was 12 per cent lower than that in the scenario $C_1T_0P_0$. Hence, increases in NPP are mainly due to the effects of elevated CO_2.

When a temperature increase was tested, results showed that NPP decreased around 15 and 11 per cent for pine and oak, respectively. Chiesi *et al.* (2010) reached similar patterns with a temperature scenario of +2°C, involving a reduction in net forest productivity of 21 and 7 per cent in ecosystems of deciduous oaks and mountain conifers, respectively. However, increased temperature is generally associated with increased NPP in temperate forests (Kirschbaum, 2000; Law *et al.*, 2002). The observed NPP can be explained considering that Mediterranean forests are generally limited by summer water availability (Chiesi *et al.*, 2010), resulting in a decrease in soil moisture (Melillo *et al.*, 1993). Studies have reported that increases in temperature combined with a decrease in water availability could lead to additional drought zones (Christensen *et al.*, 2007) and a decline in biomass growth and primary production (Melillo *et al.*, 1993; Santos *et al.*, 2002; Ogaya *et al.*, 2003; Bogino and Bravo, 2008; Huiqing *et al.*, 2008). In spring and summer, temperature and precipitation induce plants to limit photosynthetic activity in order to reduce water loss by transpiration (Waring and Running, 2007), which support the results of this study: elevated temperatures and a decrease in precipitation leads to reduced primary productivity for both species (up to 14 per cent less productivity in oak and 17 per cent in pine) by decreasing soil moisture and likely enhancing plant respiration (Melillo *et al.*, 1993). This is in accordance with the results found by Maselli *et al.* (2009) and Chiesi *et al.* (2010). Even the scenarios with a decrease in precipitation, maintaining the reference temperature, had a decreased NPP (4 per cent in pine and 3 per cent in oak) due to lower soil moisture. Precipitation levels play a crucial role in forest ecosystems, especially on drier sites (Maselli *et al.*, 2009; Boisvenue and Running, 2010). The growth in the forest species studied was strongly associated with changes in precipitation. This coincides with a previous study in Spain, which suggested that precipitation is the dominant climatic variable in the *P. pinaster* growth (Bogino and Bravo, 2008). Some studies also report a positive effect of summer precipitation on the growth of three pine species (*Pinus sylvestris*, *Pinus nigra* and *Pinus uncinata*) in the Iberian Peninsula (Andreu *et al.*, 2007) and in southern Portugal with *Pinus pinea* (Campelo *et al.*, 2006).

The scenario with changes in both precipitation and atmospheric CO_2 concentration shows lower NPP values for both species compared with the scenarios with changes only in the atmospheric CO_2 concentration. This reaffirms that precipitation is a very important climate variable in growth and the consequent productivity of ecosystems (Huiqing *et al.*, 2008; Maselli *et al.*, 2009). A similar pattern has been observed in a *Pinus schrenkiana* forest (Su *et al.*, 2007). The results also indicated that the interactive effects of climate and CO_2 changes were not a simple addition of the individual responses and provided support to the view that forest response to climatic change also depends on local site conditions.

Conclusion

Ecosystem process-based models have been proposed as a tool to explore ecosystem responses to changes in future environmental and climate features and can be used to generate policy-relevant scenarios or projections of future change (Norby and Luo, 2004; Chiesi *et al.*, 2010). Models of forest ecosystem processes, such as Biome-BGC, are particularly suited to this aim because they rely on conventional ground data descriptive of site, climatology, fertility, vegetation condition and meteorology and can simulate all main functions of forest environments (Running and Hunt, 1993).

The model performed well with good estimations of NPP against data from field measurements of pine and oak species in the Vila Real district, northern Portugal, despite the differences that both species present in management approaches and in terms of climate and edaphic demands.

This study demonstrated the potential consequences of climate change and CO_2 increase on pine and oak forest NPP using the Biome-BGC model. The influence of the diverse climate variables affecting NPP response varies, and it is important to consider the interactions between the different variables on tree growth. Simulations indicated that climate change and elevated atmospheric CO_2 concentration had strongly interactive effects on NPP. Higher temperatures and lower precipitation decreased productivity, but increased CO_2 concentrations led to higher forest productivity. The combined effect of a warmer climate and increasing CO_2 concentration is positive for forest productivity but, when compared with the scenario of increased CO_2 concentration only, the NPP was lower.

The importance of the Biome-BGC model was validated in this study, and it can be used in the future as a diagnostic tool to shed light on productivity and forest growth resulting from global climate change. It will also help to understand how ecosystems react and can be a key tool to forest managers, allowing them to implement scientifically based policies supported on the prediction of future impacts.

Supplementary data

Supplementary data are available at *Forestry* online.

Conflict of interest statement

None declared.

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