

Model-based assessment of ecological adaptations of three forest tree species growing in Italy and impact on carbon and water balance at national scale under current and future climate scenarios

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A semi-empirical model has been used to estimate total net primary productivity, canopy transpiration and the water use efficiency under actual and future climate projections (B1 and A2 IPCC Scenarios) of two deciduous (*Fagus sylvatica*, *Quercus cerris*) and one evergreen tree species (*Quercus ilex*) growing in Italy. In response to changes in the air temperature, the two deciduous species showed a strong reduction of NPP values, whereas the evergreen one showed very limited reductions. Under future warmer conditions, *Q. ilex* proved to be the best adapted species, probably for its drought-tolerant water-saving strategy, while *Q. cerris* suffered a reduction of transpiration, due to stomatal closure which was sensitive to the change of evaporative demand. Water Use Efficiency (WUE) values did not increase in the B1 and A2 scenarios, indicating a non-conservative water-saving strategy, which likely affected the distribution pattern of *Q. cerris* under these conditions. Similar functional behaviour have been noted for *F. sylvatica*, although this species adopted a water spending strategy, typical of species growing in mesic environments, that could represent a risk for survival of beech population under extreme air temperature change. In this respect, the reduced suitable area for this species under the A2 scenario could reduce the possibilities of an upward shift toward higher altitudes.

Keywords: Semi-empirical Model, Climate Change, Mediterranean Region, Net Primary Productivity, Water Use Efficiency

Introduction

Global air temperatures have increased by 0.7 °C during the 20th century and are projected to increase by between 1.1 and 6.4 °C during the 21st century, with the greatest increases expected to occur at more northerly latitudes (IPCC 2007). Furthermore, the outcomes of different climate change scenarios show regional variability of climate change. The changes in average temperatures that forests will have to face over the next 100 years, according to the latest projections (IPCC 2007), will be 2 °C increase in Ireland and the UK, up to about 3 °C increase in central Europe and 4-5 °C increase in northern Boreal and parts of the Mediterranean regions. All global circulation models agree that the warming will be greatest in eastern Europe during winter and in western and southern Europe during summer. In northern Europe the increase in temperature will be similar in all seasons. These increases will also be accompanied by changes in precipitation patterns that are much more difficult to forecast (IPCC 2007). However,

many models predict that summer droughts in some central and southern European regions will become more prevalent (Peñuelas et al. 2005, IPCC-SRES 2007). Climate is therefore expected to become more variable with a greater risk of extreme weather events, such as prolonged drought, storms and floods.

Forests will be exposed to changes in mean climate variables but also to increased variability. The responses of plant productivity and other ecosystem processes to climate change are quite variable and increases, decreases, or no change at all have all been reported (Rustad et al. 2001, Peñuelas et al. 2004). However, an overall positive response of aboveground plant productivity to warming has been reported for colder ecosystems (Rustad et al. 2001). Furthermore, there is a large body of observational, satellite, and atmospheric data regarding plant species and ecosystems that shows clear biological responses to warming such as extended growing seasons and altitudinal and northward movement of species' distribu-

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tions in both northern and southern, cold-wet and warm-dry ecosystems (Myneni et al. 1997, Walther et al. 2002, Parmesan & Yohe 2003, Peñuelas & Boada 2003, Menzel et al. 2006, Parmesan 2007). Ecosystem processes and biological species may respond asymmetrically to climatic changes (Walther et al. 2002) and the overall effect on ecosystem functioning and species richness is, therefore, highly complex and determined by the relative sensitivity of the different processes to climate change.

The accounting of biological carbon sequestration requires adequate knowledge of inter and intra-annual variation in ecosystem carbon exchange with the atmosphere. Large variations in the C sequestration capacities of various forest ecosystems have been reported (Nabuurs & Mohren 1995). These variations depend on climate, species, site productivity and disturbances, including management. Drought represents one of the main source of inter-annual variation in terrestrial carbon sequestration as it causes large reductions in gross primary productivity (GPP) as well as in net ecosystem exchange (NEE) of terrestrial ecosystems (Ciais et al. 2005, Granier et al. 2007, Pereira et al. 2006). Although this is true for most terrestrial biomes, it is especially relevant in seasonally dry climates, where there is often

a large variability in seasonal and annual precipitation. The Mediterranean climate has a marked seasonality with a dry and hot summer, when low precipitation is coupled to high atmospheric evaporative demand, leading to a decrease in moisture availability to plants. If the dry season lasts too long plant water deficits may negatively affect the capacity for carbon assimilation as a result of lower photosynthetic rates and reduced leaf areas (or shorter life span of annual plants) induced by limited water availability. It is generally expected that elevated CO₂ will promote reductions in stomatal conductance (g_s) that can ameliorate the negative effects of drought in many species through decreased water use (Morison & Gifford 1983), and it may have important consequences for forest water dynamics (Betts et al. 2007, Leuzinger & Körner 2010). However, growing experimental evidence suggests that many forest tree species show small or non-significant changes in stomatal conductance under long-term elevated CO₂ (Eamus & Jarvis 1989, Bunce 1992, Curtis 1996, Saxe et al. 1998), suggesting that stomata acclimate in parallel to, and possibly depending on, photosynthetic acclimation (Herrick et al. 2004, Ainsworth & Long 2005).

Carbon (C) pool and fluxes estimations are required at a regional level to assess carbon exchange under the ongoing climatic change in order to establish suitable policies for mitigation and adaptation to climate change. The interest in modelling C exchange reflects the growing attraction in using models as vehicles to integrate knowledge, research activities, experimental results, and to test hypotheses (Goudriaan et al. 1999), and as the most flexible tools to address how climate change (especially for temperature and soil water availability) will affect the process-based forest functionality (Fosberg 1990, Bossel 1996, Kickert et al. 1999). An example of simplification of models applied to the forest systems is the use of the so-called “big leaf” model (Magnani et al. 1998, Vitale et al. 2007), that describes the response of vegetation as a whole (big leaf) in terms of variations of the main environmental factors (Sellers et al. 1992, Amthor et al. 1994). The aim of this paper is to show simulations of total net primary production, transpiration and water use efficiency for tree species as *Fagus sylvatica*, *Quercus cerris* and *Quercus ilex*, forming widely diffused forest-types in the Mediterranean area, under actual climatic scenario and CO₂ concentration “1961-90” and two climatic scenarios representing low and high CO₂ emission trajectories: B1 (stabilization at 550 ppm atmospheric CO₂) and A2 (no stabilization of atmospheric CO₂) storylines (Nakicenovic & Swart 2000), for the temporal frame “2071-2100”. Results will be presented for the Italian territory, with an evaluation

of the consequences on total net primary productivity and distribution patterns of these tree species.

Material and methods

Study area and tree species

The study area includes the Italian Peninsula, an area of 301 338 km², geographically divided from the rest of Europe by the Alps. The forest landscape changes according to latitudinal and altitudinal gradients. Mountains forests - characterized by conifers such as *Abies alba*, *Picea abies*, *Larix decidua* and *Pinus sylvestris* are common in the Alps. Below this belt and along the Apennine chain forests are dominated by *Fagus sylvatica*. Sub-mountain and hill areas are characterized by deciduous species, mainly *Quercus cerris*, *Quercus pubescens*, *Ostrya carpinifolia* and *Fraxinus ornus*. Typical Mediterranean species such as *Quercus suber*, *Quercus ilex*, *Pinus halepensis* and *Pinus pinaster* can be found along the coasts and become more and more common towards the south of the peninsula. In this study, we considered three populations of tree species characterizing the Italian forest ecosystems, from temperate to Sub- and Mediterranean species: *Fagus sylvatica* (European beech), *Quercus cerris* (Turkey oak), and *Quercus ilex* (Holm oak). All three species are widely represented in Italy, forming pure or mixed woods covering extensive areas.

Environmental variables

Current (average of time period lasting from 1961 to 1990) and future (average of time period lasting from 2071 to 2100) climate scenarios are derived by using the HadCM3 model (Mitchell et al. 2004). The HadCM3 model projected the average climate under the two scenarios A2 and B1 storylines (Nakicenovic & Swart 2000) as reported in the Intergovernmental Panel on Climate Change Special Report on Emissions Scenarios (IPCC-SRES 2007). Climatic data are statistically downscaled through a bilinear interpolation so as to obtain raster data with a spatial resolution of 3 km (for a total of 33 432 grid cells over-imposed on Italy), that is corresponding to the grid map of the forest data used in this paper. Only the temperature data are interpolated after detrending at sea level by using a normal lapse rate of 0.6 °C for each 100 m of altitude (Attorre et al. 2007).

Climatic variables are chosen among those believed to be more meaningful for their influence on the physiology of tree species. We used annual mean temperature (*MeanT*, °C), minimum temperature of the coldest month (*MinT*, °C), maximum temperature of the hottest month (*MaxT*, °C), summer (*SP*) and winter (*WP*) precipitations (mm), and total annual precipitation (*PTot*, mm).

The MOCA model

The MOCA (MOdelling for Carbon Assessment) model has been mainly developed to estimate the total net primary production of forest stands (*NPP*, tC ha⁻¹ yr⁻¹) by using climatic and physiological parameters as guide variables. This model has been previously used to calculate the *NPP* variation according to the foreseen temperature change for an evergreen Mediterranean forest (Vitale et al. 2003), and to quantify and simulate the residence of *Phillyrea angustifolia* maquis after a fire event (Vitale et al. 2007). MOCA is based on the big-leaf approach (Kull & Jarvis 1995, Dai et al. 2003, Vitale et al. 2003), which considers the canopy structure as a big leaf that is functionally defined by time-dependent Leaf Area Index (*LAI*, m²_{leaf} m⁻²_{ground}). MOCA can be adapted to different species and vegetation types, basically requiring annual mean air temperature (*MeanT*) and geographical coordinates for each site as input, in order to calculate both daily values of light intensity above canopies [*Q₀(t)*, μmole photons m⁻² s⁻¹] and air temperature [*Tair(t)*]. Additional parameters must be obtained by a set of parameters acquired by laboratory and field data in order to adapt the model to different species.

Daily net photosynthetic rate [*A(t)*, μmol CO₂ m⁻² s⁻¹] is calculated as a response to the mean light radiation inside the canopy at the *t*th day of year [*Q₀(t)*, μmole photons m⁻² s⁻¹], according to De Wit et al. (1978 - eqn. 1):

$$A(t) = (A_{max} - Rd) \cdot \left[1 - e^{-\left(\frac{QY \cdot Q_0(t)}{A_{max}}\right)} \right] + Rd$$

where *A_{max}* is the maximum rate of net photosynthesis at light saturation (μmolCO₂ m⁻² s⁻¹ - Tab. 1), *Rd* is the dark respiration rate (μmolCO₂ m⁻² s⁻¹ - Tab. 1) integrated for the darkness period, and *QY* is the quantum yield efficiency of photosynthesis (μmolCO₂ μmole photons⁻¹ - Tab. 1).

Total net primary productivity (gC m⁻² yr⁻¹) is calculated by an integration with time (from 100th to 281st Julian Day, JD for deciduous species, and the overall JDs for the evergreen species) of *A(t)* as (eqn. 2):

$$NPP = \sum_i [A(t) - Kc(t)] \cdot \left(\frac{12}{10^6} \right)$$

where *Kc(t)* is the maintenance respiration calculated as a function of leaf temperature by the *Q₁₀* temperature coefficient (that is a measure of the rate of change of a biological or chemical system as a consequence of increasing the temperature by 10 °C - eqn. 3):

$$Kc(t) = R_{10} Q_{10}^{\left(\frac{T_{leaf}(t) - 10}{10}\right)}$$

where *R₁₀* is the respiration rate at 10 °C (1.5 μmolCO₂ m⁻² s⁻¹) and *Q₁₀* is 1.7, which was in the range found by Granier et al. (2000) for

Tab. 1 - Input and simulated parameters utilised by the MOCA model. All input parameters except light extinction coefficients and *NPP* repartition coefficient to the leaves come from leaf gas exchange measurements performed plant species; in particular, *F. sylvatica* and *Q. cerris* forests growing in the Italian Central Apennine - Abruzzi and Molise Regions, whereas values concerning *Q. ilex* derived from Manes et al. 1997, Manes et al. 2006, Faria et al. 1998.

Parameter Type	Parameter Name	Symbol	<i>Fagus sylvatica</i>	<i>Quercus cerris</i>	<i>Quercus ilex</i>	Units
Input	Rate of respiration in the dark	<i>Rd</i>	1.03	1.03	0.50	μmol CO ₂ m ⁻² s ⁻¹
	Maximum rate of net photosynthesis at light saturation	<i>A_{max}</i>	20	21	15	μmol CO ₂ m ⁻² s ⁻¹
	<i>NPP</i> repartition coefficient to the leaves	<i>α</i>	0.301	0.280	0.230	-
	Quantum yield efficiency	<i>QY(T)</i>	0.055	0.036	0.044	μmol CO ₂ μmol photons ⁻¹
	Light extinction coefficient	<i>k</i>	0.71	0.60	0.69	Dimensionless
	Simulated	Total net primary productivity	<i>NPP</i>	-	-	-
Daily net photosynthetic rate		<i>A(t)</i>	-	-	-	μmol CO ₂ m ⁻² s ⁻¹
Leaf Area Index		<i>LAI(t)</i>	Initial value: 0	Initial value: 0	Initial value: 2.2	m ² leaf m ⁻² ground

the beech ($1.6 \leq Q_{10} \leq 1.8$), and applied also for *Quercus cerris*. Q_{10} was set to 2.2 for *Q. ilex*.

The foliage emission period has been calculated by analysis of fifteen NDVI images acquired from Terra satellite (from 14 May to 18 December 2005) through the GRASS-GIS software (Zatelli & Neteler 2005), thus deriving the annual NDVI curve, approximated by the Richard's equation, for each plant species.

Light attenuation through the canopy $Q_i(t)$ (μmole photons m⁻² s⁻¹) is assumed to be depending on the $LAI(t)$ according to the Beer-Lambert law (eqn. 4):

$$Q_i(t) = Q_0(t) \cdot e^{-K \cdot LAI(t)}$$

where K (=0.72) is the coefficient of light extinction through the canopy. The LAI_{tot} (m² leaf m⁻² ground) is modelled by the following equations (eqn. 5-6):

$$\frac{dLAI(t)}{dt} = SLA(t) \cdot \beta \cdot A_g(t-1)$$

$$LAI_{tot} = \sum \frac{dLAI(t)}{dt}$$

where $A_g(t-1)$ is the net photosynthetic rate (g_{Dry Weight} m⁻² day⁻¹) of previous year-day (t^{th} -1), β is the leaf partition coefficient of the accumulated biomass (=0.25), and $SLA(t)$ is the specific leaf area at the t^{th} day of the year (m² g⁻¹ Dry Weight) defined by a saturation growth equation fitting empirical data derived from

measurement campaigns in beech and mixed forests of the Apennine mountains (eqn. 7):

$$SLA(t) = \frac{c \cdot \text{time}}{d + \text{time}}$$

where c and d are fitted parameters ($c = 0.0116$ and $d = -52.563$ for *Q. cerris*; $c = 0.0059$ and $d = -95.250$ for *F. sylvatica*). The SLA is kept constant during the year (0.005 m² g⁻¹ Dry Weight) only for *Quercus ilex*.

Daily stomatal conductance to water vapour [$gs(t)$, mol m⁻² s⁻¹] is calculated as function of $A(t)$, ambient CO₂ (C_a , 380 ppm) and relative humidity [$RH(i)$, dimensionless] after Ball et al. (1987) and Harley et al. (1992). Daily canopy transpiration [$E(t)$, g H₂O m⁻² day⁻¹] is then calculated as function of diurnal average leaf temperature, vapour pressure difference [$VPD(i)$, mbar], photoperiod [$ph(t)$, h], and LAI (Jarvis et al. 1981 - eqn. 8):

$$E(t) = \left[gc(t) \cdot \frac{(cp \cdot \rho)}{(\lambda \cdot \gamma)} \cdot VPD(t) \right] \cdot ph(t) \cdot 3600$$

where $VPD(t)$ is the daytime mean atmospheric vapour pressure deficit calculated by air and leaf temperature-based empirical functions (Allen et al. 1998), $gc(t)$ is the diurnal average canopy stomatal conductance (m s⁻¹), cp is the specific heat of air at constant pressure (1.012 J g⁻¹ °C⁻¹), $\rho(T_{air})$ is the air density (g m⁻³), $\lambda(T_{air})$ is the latent heat of vaporisation of water (J g⁻¹), and γ/λ , cp is the psychrometric constant (mbar °C⁻¹)

(Friend & Woodward 1990). Saturation water vapour pressure is calculated according to Dillley (1968). The water vapour conductance of the canopy [$gc(t)$, m s⁻¹] is calculated as function of the stomatal conductance, $gs(t)$, and the $LAI(t)$, for each t^{th} day of year (Jarvis et al. 1981 - eqn. 9):

$$gc(t) = \frac{gs(t) \cdot LAI(t)}{fc \cdot 10^3}$$

where fc transforms the stomatal conductance expressed in molar units (mmol m⁻² s⁻¹) to non-molar units (mm s⁻¹) as function of the leaf temperature (eqn. 10):

$$fc = -10^{-3} \cdot T_{leaf} + 0.045$$

where T_{leaf} is a linear function of T_{air} empirically found by leaf gas exchange measurements.

Total canopy transpiration (Et - tH₂O m⁻² yr⁻¹) is calculated by an integration with time (from 100th to 281st Julian Day, JD for deciduous species, and the overall JDs for the evergreen species) of $E(t)$ as (eqn.11):

$$Et = \sum_i E(t)$$

The water use efficiency (WUE) has been calculated as NPP/Er ratio (tC tH₂O⁻¹) to characterise the differences in the water use under several climate scenarios.

Finally, MOCA implemented a sub-routine generating pseudo-random numbers for each day which fluctuated between 0 and 1. These numbers were used to simulate the daily clouds coverage, adopting an average of 42% for the Italian annual cloudiness, regarding the time-frame 1961-1990 (SCIA 2011), and affecting thus the irradiance above the canopy $Q_0(t)$. It is assumed that the Italian average cloudiness did not change in the future. The randomly assessment of daily cloudiness implied that one run of the model was slightly different to another. For this reason, the NPP values utilised in the paper were average values coming from 10 runs of the MOCA model for each different climatic scenarios.

The MOCA validation

MOCA results have been validated with the NPP data coming from eddy covariance flux towers of the CarboEurope Programme such as Roccarespanpani (42°23' N, 11°51' E, *Q. cerris* forest - Kowalski et al. 2004), Collelongo (41°52' N, 13°38' E, *F. sylvatica* forest - Scartazza et al. 2004), and Castelporziano estate (41°45' N, 12°22' E, *Q. ilex* forest - Tirone et al. 2003) for the 2000-2005 period. The latter two sites are also included in the Italian Long Term Ecosystem Research network (LTER-Italy, <http://www.lteritalia.it/defaultuk.php>).

For site based validation, *NPP* values have been calculated from Gross Primary Production (*GPP*) measured by towers multiplied by: (a) the *NPP/GPP* ratios reported from Mediterranean warm evergreen (0.542) and temperate humid deciduous (0.537) biomes (Luyssaert et al. 2007); and (b) the ratio (*NEP+Rh*)/*GPP* reported in the same paper, where *NEP* is the net ecosystem production and *Rh* is the heterotrophic respiration. In case (b), *Fagus sylvatica* and *Quercus cerris* showed a (*NEP+Rh*)/*GPP* ratio of 0.514, whereas *Q. ilex* value was 0.639. The denominator of ratios (a) and (b) are independent as *NPP* comes from biometric estimates, *NEP* from fluxes and *Rh* from various

measurements techniques (Luyssaert et al. 2007).

MOCA model has been applied for each eddy covariance test site and run for ten times for each year (2000-2005). Averages values of measured and modelled net primary productivity have been reported and compared by the one-way ANOVA test and using a Newman-Keuls test as *post-hoc* test.

Furthermore, the values estimated by MOCA model have been compared to the above-ground net primary production data derived by remote sensing studies carried out on the same plant species formations distributed over the Italian territory (Chirici et al. 2007).

Maps of the total net primary productivity

MOCA model has been applied on a range of latitudinal bands with a width of 0.25°, lasting from forty-two to forty-seven depending on the species specific distribution of plant species analysed here and ranging from north (47°39'12") to south (35°51'54") of Italy (Tab. 2). *NPP*, *Et* and *WUE* values have been calculated for each latitudinal band by using proper climatic and environmental maps characterising each band. In details, climatic parameters used in these simulations were of the "average year" of both "1961-1990" (for current scenario) and "2071-2100" (for B1 and A2 scenarios) tem-

Tab. 2 - Latitudinal ranges for mean annual temperature (*mean T*) and their differences with the mean temperature of the coldest month, used as input for the MOCA model.

<i>F. sylvatica</i>			<i>Q. cerris</i>			<i>Q. ilex</i>		
LAT ranges	MeanT	ΔT	LAT ranges	MeanT	ΔT	LAT ranges	meanT	ΔT
36.89-37.14	15.90	9.70	35.51-35.76	18.10	9.90	35.51-35.76	18.10	9.90
37.14-37.39	15.50	10.30	35.76-36.01	18.10	9.70	35.76-36.01	15.87	10.16
37.39-37.64	15.00	10.50	37.01-37.26	17.00	8.20	36.76-37.01	18.65	9.90
37.64-37.89	12.90	9.90	37.26-37.51	15.30	10.80	37.01-37.26	16.35	10.01
37.89-38.14	12.60	10.00	37.51-37.76	14.30	11.50	37.26-37.51	15.30	9.99
38.14-38.39	11.40	9.50	37.76-38.01	14.20	10.80	37.51-37.76	15.60	10.40
38.39-38.64	11.40	9.50	38.01-38.26	14.30	10.00	37.76-38.01	14.95	10.41
38.64-38.89	11.40	9.60	38.26-38.51	15.80	9.20	38.01-38.26	14.42	9.98
38.89-39.14	11.50	9.60	38.51-38.76	14.30	10.30	38.26-38.51	15.70	9.13
39.14-39.39	11.50	9.60	38.76-39.01	14.30	10.60	38.51-38.76	14.16	10.10
39.39-39.64	11.40	9.60	39.01-39.26	14.50	10.70	38.76-39.01	14.23	10.58
39.64-39.89	11.40	9.60	39.26-39.51	12.30	10.00	39.01-39.26	14.68	10.75
39.89-40.14	11.40	9.50	39.51-39.76	12.60	10.00	39.26-39.51	13.39	10.17
40.14-40.39	11.20	9.50	39.76-40.01	13.50	9.90	39.51-39.76	13.42	10.10
40.39-40.64	11.20	9.50	40.01-40.26	12.10	9.60	39.76-40.01	13.57	9.91
40.64-40.89	11.10	9.50	40.26-40.51	12.90	9.80	40.01-40.26	12.49	9.66
40.89-41.14	11.10	9.50	40.51-40.76	12.86	10.24	40.26-40.51	13.18	9.77
41.14-41.39	11.50	9.70	40.76-41.01	12.81	10.58	40.51-40.76	14.02	10.47
41.39-41.64	10.40	10.50	41.01-41.26	12.48	10.92	40.76-41.01	13.76	10.74
41.64-41.89	10.40	10.50	41.26-41.51	13.08	11.49	41.01-41.26	13.35	10.90
41.89-42.14	10.50	10.50	41.51-41.76	13.16	11.30	41.26-41.51	13.82	11.41
42.14-42.39	9.20	11.30	41.76-42.01	12.81	11.42	41.51-41.76	14.07	11.10
42.39-42.64	9.20	11.30	42.01-42.26	12.68	11.45	41.76-42.01	13.20	11.42
42.64-42.89	9.20	11.20	42.26-42.51	12.92	11.78	42.01-42.26	13.48	11.46
42.89-43.14	10.00	10.50	42.51-42.76	12.96	11.88	42.26-42.51	13.28	11.81
43.14-43.39	8.70	11.00	42.76-43.01	12.60	11.94	42.51-42.76	13.37	11.96
43.39-43.64	10.00	10.50	43.01-43.26	12.80	11.90	42.76-43.01	13.35	12.01
43.64-43.89	10.00	10.50	43.26-43.51	12.89	11.79	43.01-43.26	13.44	11.89
43.89-44.14	8.90	11.00	43.51-43.76	12.78	11.69	43.26-43.51	13.20	11.79
44.14-44.39	8.90	11.00	43.76-44.01	12.64	11.82	43.51-43.76	13.12	11.65
44.39-44.64	8.80	10.90	44.01-44.26	12.14	11.72	43.76-44.01	13.39	11.92
44.64-44.89	8.80	10.90	44.26-44.51	10.81	11.66	44.01-44.26	13.46	11.57
44.89-45.14	8.80	10.90	44.51-44.76	10.72	11.69	44.26-44.51	12.90	11.41
45.14-45.39	8.70	10.90	44.76-45.01	10.94	11.75	44.51-44.76	12.70	11.84
45.39-45.64	6.60	10.50	45.01-45.26	11.54	13.01	44.76-45.01	12.98	12.06
45.64-45.89	6.50	11.50	45.26-45.51	11.22	13.11	45.01-45.26	13.07	13.29
45.89-46.14	5.90	11.50	45.51-45.76	11.31	13.67	45.26-45.51	12.48	13.83
46.14-46.39	6.00	11.50	45.76-46.01	10.66	12.73	45.51-45.76	12.99	13.86
46.39-46.64	7.90	11.00	46.01-46.26	10.80	12.55	45.76-46.01	12.41	13.13
46.64-46.89	7.80	11.00	46.26-46.51	10.20	12.94	46.01-46.26	12.80	13.19
46.89-47.14	5.60	11.50	46.51-46.76	9.75	13.75	46.26-46.51	11.93	13.49
47.14-47.39	5.60	11.50	46.76-47.01	8.96	14.18	46.51-46.76	11.27	14.72
-	-	-	47.01-47.26	8.50	14.61	46.76-47.01	9.88	14.73
-	-	-	-	-	-	47.01-47.26	9.40	15.03

Fig. 1 - Comparisons between modelled and measured *NPP* average values regarding three woody plant species. Eddy covariance flux measurements have been performed in the 2000-2005 time period for Castelporziano (*Q. ilex* forest), Collelongo (*F. sylvatica* forest) and Roccarespampani (*Q. cerris* forest) sites. Different letters denote significant differences between *NPP* values assessed by the Newman-Keuls test performed at $p \leq 0.05$.

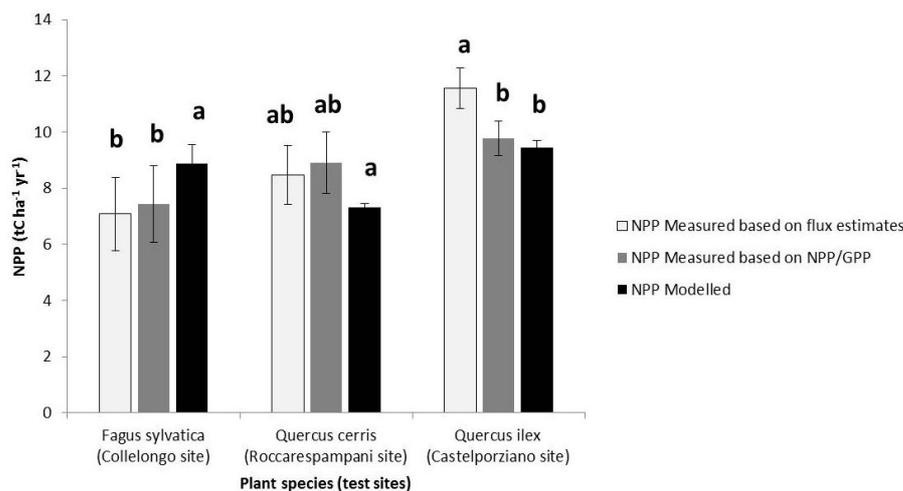
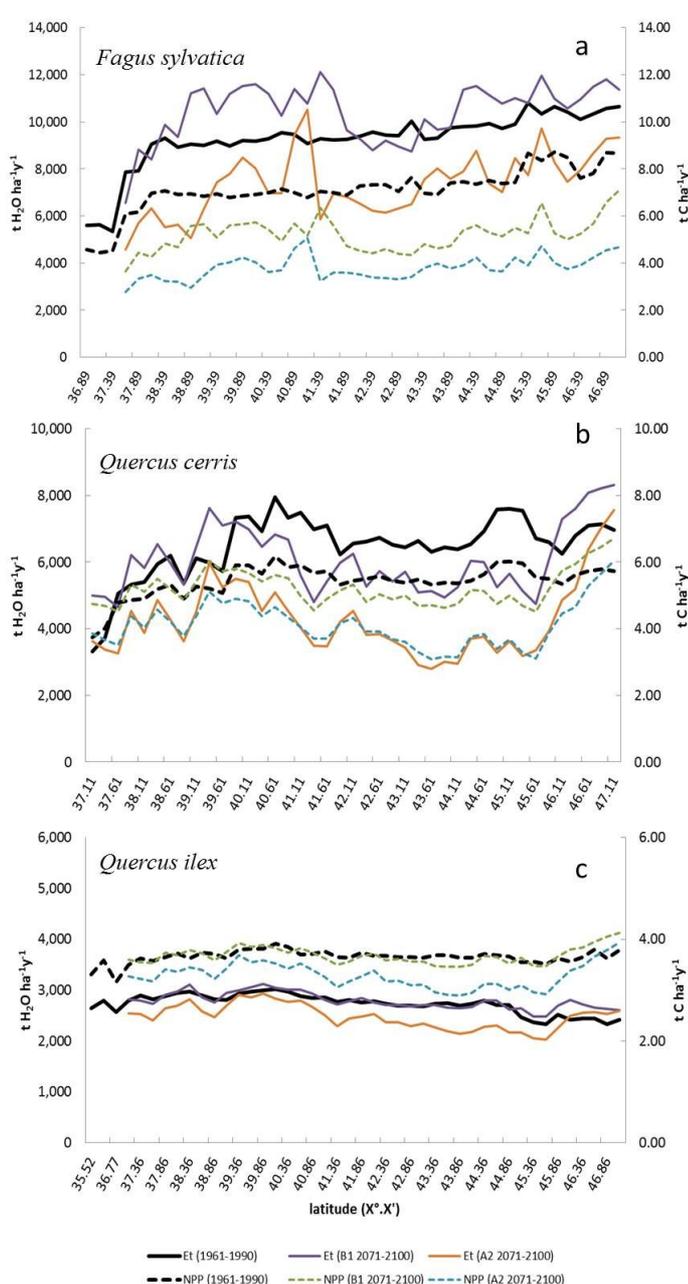


Fig. 2 - Latitudinal trends of net primary productivity (*NPP*, tC ha⁻¹) and transpiration rate (*Et*) estimated under actual (1961-90) and future scenarios (B1 and A2 - 2071-2100) for (a) *Fagus sylvatica*, (b) *Quercus cerris* and (c) *Quercus ilex*.



poral ranges, coming from the downscaled climatic data of the HadCM3 model. MOCA routines run for one full year (365 JD) at a daily time step. Current and future potential distributions of plant species analysed here (Attorre et al. 2008, 2011 - see Di Traglia et al. 2011 for technical details) have been used as template to generate the *NPP* distribution maps. The distribution of plant species is based on the Importance Value (*IV*) which is an indicator of abundance based on the density and dominance of a tree species (Husch et al. 2003). Finally, the *NPP* values have been geographically represented for all cells of the Italian grid at the resolution of 3×3 km.

Results

Validation of the modelled *NPP* outputs

For specific locations where the eddy covariance flux towers are placed, the modelled *NPP* values are in agreement to the calculated ones (Fig. 1). Statistical analysis demonstrates that the modelled *NPP* values are included in range of variation of the measured ones, although it should be taken into account that the climate parameters used by MOCA are based on both current climate scenario “1961-1990” and astronomical algorithms which, in turn, are depending on geographical coordinates of each measuring site, so can be considered independent from the actual climate of the years when the fluxes were measured (2000-2005). Indirect estimations of *NPP* made by remote sensing approach or hybrid methodologies highlight a strong correspondence with average values modelled by MOCA model and represented in the annual *NPP* maps. Chirici et al. (2007) reported modelled *NPP* values by C-Fix model for Italy as $4.26 \text{ tC ha}^{-1} \text{ yr}^{-1}$ for beech forests, compared to $2 \text{ to } 4 \text{ tC ha}^{-1} \text{ yr}^{-1}$ as modelled by MOCA, whereas Mediterranean broad-leaves forests showed an averaged *NPP* value of $4.27 \text{ tC ha}^{-1} \text{ yr}^{-1}$ in C-Fix vs. $5.43 \text{ tC ha}^{-1} \text{ yr}^{-1}$ for MOCA. Finally, values

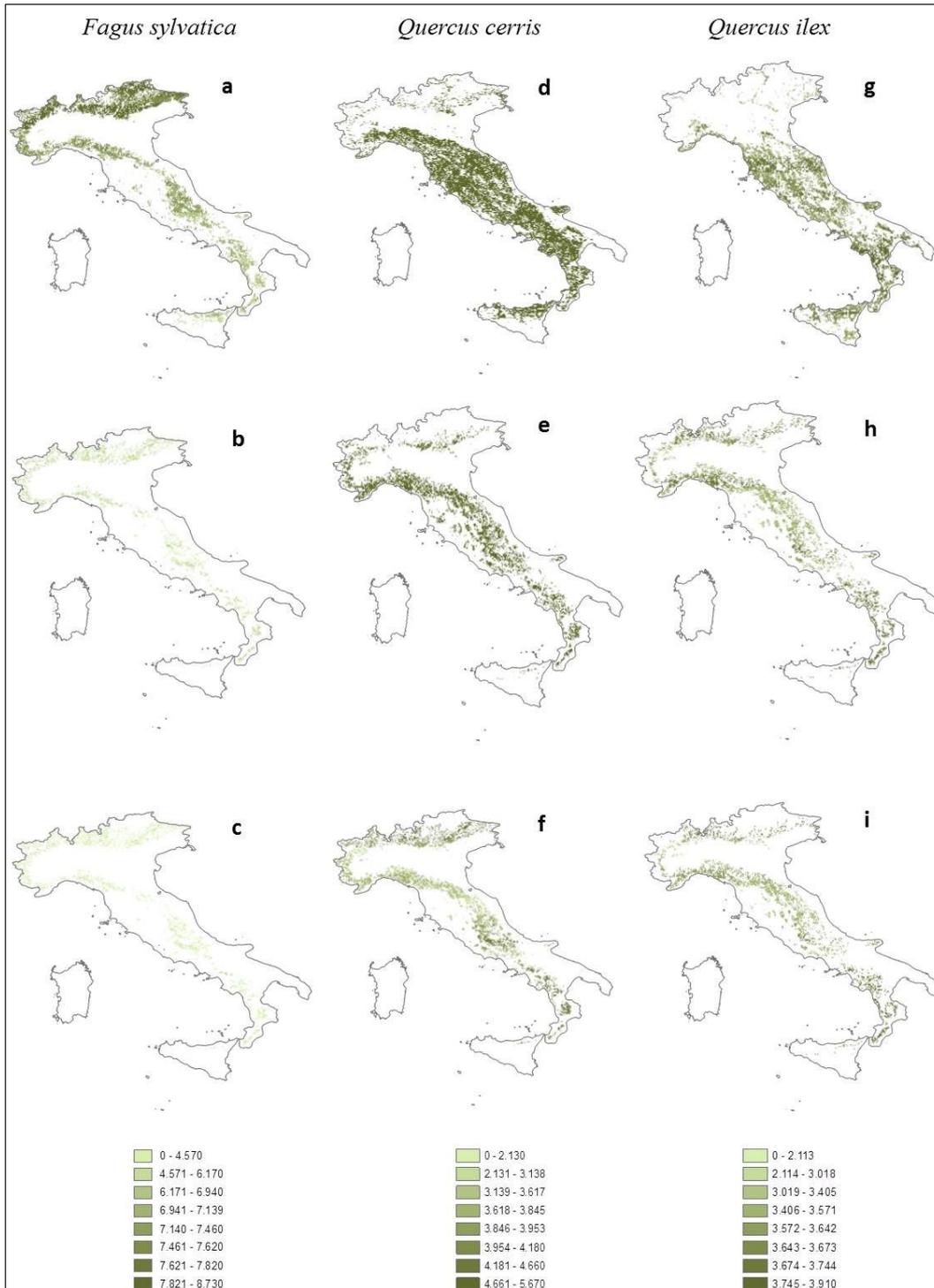


Fig. 3 - Italian distribution of net primary productivity (*NPP*, tC ha⁻¹) under different climatic scenarios. *Fagus sylvatica*: (a) actual climate 1961-90; (b) B1 2071-2100; (c) A2 2071-2100. *Quercus cerris*: (d), (e), (f) as for *F. sylvatica*. *Quercus ilex*: (g), (h), (i) as for *F. sylvatica*.

from the two modelling approaches for the Holm oak forests are very similar (4.96 tC ha⁻¹ yr⁻¹ and 4.97 tC ha⁻¹ yr⁻¹).

Time and latitudinal dynamics

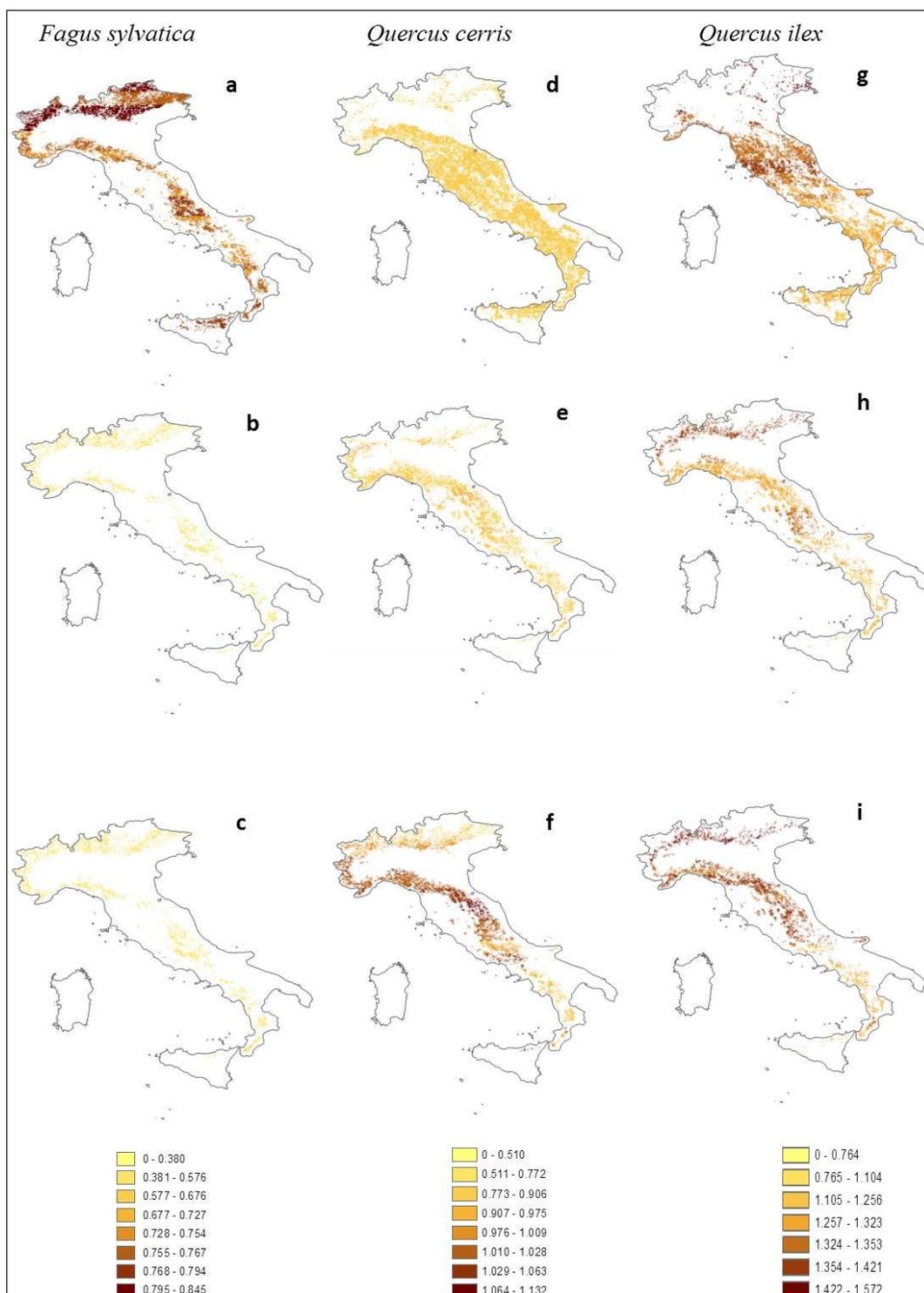
Fig. 2a-c shows the *NPP* and transpiration rates (*Et*) along latitudinal ranges from south to north of Italy. *Fagus sylvatica* (Fig. 2a) has a *NPP* (“1961-90”) trend growing similarly to a power regression model, showing the lowest values for Sicily and the southern

Apennines (4.51 ± 0.06 tC ha⁻¹yr⁻¹), constant values for the beech populations located along the south-central to the northern Apennines (7.11 ± 0.96 tC ha⁻¹), and highest ones for the Alps (8.38 ± 0.43 tC ha⁻¹yr⁻¹). However, *NPP* decreases when climatic scenarios change, which is of about -26% in the “2071-2100” B1 scenario and -40% in the “2071-2100” A2 scenario (Fig. 2a). *Quercus cerris* shows similar trends for the *NPP* values, although it seems to maintain higher

NPP values than *F. sylvatica* under limiting climatic scenarios (Fig. 2b). The *NPP* values of *Quercus ilex* are lower than the other two species, but it keeps its trend and values, also under limiting environmental conditions (Fig. 2c).

On average, *F. sylvatica* shows an increase of canopy transpiration (*Et*) under the “2071-2100” B1 climate scenario (+7.8%) and a reduction in more limiting A2 scenario (-22.9%) with respect to the “1961-90” sce-

Fig. 4 - Italian distribution water use efficiency (*WUE*, kgC tH₂O⁻¹) under different climatic scenarios. *Fagus sylvatica*: (a) actual climate 1961-90; (b) B1 2071-2100; (c) A2 2071-2100. *Quercus cerris*: (d), (e), (f) as for *F. sylvatica*. *Quercus ilex*: (g), (h), (i) as for *F. sylvatica*.



nario (9843 ± 631 tH₂O ha⁻¹ yr⁻¹). Differently, *Q. cerris* shows a progressive reduction of *Et* values (-13.9% and -40.7% for the B1 and A2 scenarios, respectively), compared to the “1961-90” (6758 ± 528 tH₂O ha⁻¹ yr⁻¹), especially for central and northern Italy. *Q. ilex* shows a clear water conservative strategy pointed out by a very slight reduction of the transpiration rates (-0.8% and -6.3% for the B1 and A2 scenario, respectively) compared

to the reference period of “1961-90” (2782 ± 131 tH₂O ha⁻¹ yr⁻¹). It is worth noting that *Q. ilex* has reduced *NPP* between foliage and atmosphere for all locations of its distribution in Italy, resulting thus more tolerant to the increasing drought stress.

Annual net primary productivity maps

Fig. 3a-i reports the geo-spatial representation of the *NPP* values for Italy. The map

represents the distribution of potential *NPP* distribution, that refers to the potential distribution of plant species as defined by Atorre et al. (2011) and determined by the bioclimate envelope in the current and changed climatic conditions. Each pixel represents a cell of 3 x 3 km (900 ha), which is returned to a value of productivity in tC ha⁻¹. Each cell holds the Importance Value (*IV*) index and the territorial suitability. Fig. 3a shows

the primary productivity of beech, according to its current potential distribution. The net primary productivity ranges from 2 to 4 tC ha⁻¹ yr⁻¹, and in some favourable and suitable areas, where the species is dominant, the primary productivity of the beech reaches values of 6-8 tC ha⁻¹ yr⁻¹. However, an overall reduction of the beech's distribution area throughout the country is evident under the climate "2071-2100" B1 scenario (Fig. 3b). The beech coverage tends to become scarce in central and southern Italy, and potentially increases in the Alps. In this climatic scenario, beech reduces the estimated *NPP* values to 3 tC ha⁻¹ yr⁻¹. The reduction in *NPP* would justify the reduction of the potential distribution area, whereas a good productivity is kept in areas which are less affected by the rise of temperature. Under the "2071-2100" A2 scenario (Fig. 3c) beech responds in a negative way, experiencing a strong impact on its potential distribution and, consequently, on primary productivity reducing both their values, mainly due to more limiting climatic conditions, being more critical for the species.

Q. cerris covers large part of central Italy under the "1961-90" climatic scenario with *NPP* values ranging from 3.7 to 6.2 tC ha⁻¹ yr⁻¹ and an average value of 5.57 ± 0.27 tC ha⁻¹ yr⁻¹ (Fig. 3d). The "2071-2100" B1 scenario exerts a negative impact on the potential distribution of *Q. cerris* and the higher productivity areas shift to the Apennines, reaching a maximum value of 6.3 tC ha⁻¹ yr⁻¹ (Fig. 3e). Primary productivity is greatly reduced (3.92 ± 0.55 tC ha⁻¹ yr⁻¹) along with the potential distribution of the species in the A2 scenario (Fig. 3f, -20.3% - Attorre et al. 2011).

Quercus ilex is a Mediterranean sclerophyllous species growing along the Italian coasts and south-facing limestone slopes of the hinterland. In the "1961-90" scenario, *NPP* map points out appreciable values (4 tC ha⁻¹ yr⁻¹) for regions of the central Italy, and a range between 1 and 3 tC ha⁻¹ yr⁻¹ for Italian southern regions (Fig. 3g). Interestingly, under climate change, this species would be able to potentially expand and to establish itself in the northern regions of Italy. Nuclei of *Q. ilex* are evident in several regions of the pre-Alps (Piedmont, Valle d'Aosta, Lombardy, Trentino, Veneto and Friuli Venezia Giulia), where *Q. ilex* has the opportunity to grow, preferring the hottest exposures. In the "2071-2100" B1 scenario, *Q. ilex* moves to the innermost areas of the Italian peninsula (Fig. 3h), where the primary productivity reaches values of 3.64 ± 0.15 tC ha⁻¹ yr⁻¹. Under the "2071-2100" A2 scenario (Fig. 3i), the presence on the Apennine ridge and pre-Alps becomes more evident. The diffusion in the regions of the Po valley, those with the greatest climatic variations in raising the temperature, appears to favour

the occupation of territory by *Q. ilex*. Productivity values are low, but similar to the B1 climate scenario ones (3.58 ± 0.14 tC ha⁻¹ yr⁻¹). Nuclei in the southern regions (Campania and Calabria) are also preserved, showing a primary productivity of about 3.5 tC ha⁻¹ yr⁻¹.

Water use efficiency maps

Water use efficiency (WUE) maps of *Fagus sylvatica* highlight a reduction of values induced by climate changes (Fig. 4a-c). The difference percentages calculated between "1961-90" and "2071-2100" B1 scenarios range from -42% to -26%, showing greater reduction in the pre-Alps areas (-41%) and northern Apennines (-37%). Similar values have been calculated for difference between "1961-90" and "2071-2100" A2 scenarios. Average values of WUE are progressively decreasing from 0.772 ± 0.029 kgC tH₂O⁻¹ ("1961-90" scenario) to 0.486 ± 0.016 kgC tH₂O⁻¹ and 0.507 ± 0.025 kgC tH₂O⁻¹ ("2071-2100" B1 and A2 scenarios, respectively). *Quercus cerris* shows increasing difference percentages of WUE in the "2071-2100" B1 scenario compared to the reference "1961-90" one (Fig. 4d-f). The most representative frequency class of percentage change ranges between 7% and 15%, characterizing the northern and central Apennines, whereas these difference percentages range from -5% to 3% in the southernmost part of Apennines. The increasing trend in percentage differences appears also under the "2071-2100" A2 scenario with the most representative frequency class ranging from 25% to 30% and similar geographical localizations to the B1 climatic scenario. Average values of WUE are higher than beech ones, being 0.825 ± 0.026 kgC tH₂O⁻¹, 0.875 ± 0.039 kgC tH₂O⁻¹ and 0.991 ± 0.065 kgC tH₂O⁻¹ for the "1961-90", "2071-2100" B1 and A2 scenarios, respectively. The difference percentages calculated for *Quercus ilex* between "1961-90" and "2071-2100" B1 scenarios are more limited, ranging from -7.9% to -1.7%, showing greater reduction in the central and southern Apennines (Fig. 4g-i) than in the northerners. However, these differences remain at similar values for the "2071-2100" A2 scenario, although they are higher than the difference between "2071-2100" B1 and "1961-90" scenarios, ranging between -3.8% and 5.6%. As a consequence, the average values of WUE for *Q. ilex* are rather constant as 1.326 ± 0.053 kgC tH₂O⁻¹, 1.318 ± 0.046 kgC tH₂O⁻¹ and 1.375 ± 0.061 kgC tH₂O⁻¹ for "1961-90", "2071-2100" B1 and A2 scenarios, respectively. This increase of WUE is parallel to the reduction of geographical distribution of *Q. ilex*, where only the 13% of current potential distribution (1961-90) is maintained (Attorre et al. 2011). Overall, it is worth noting that the

more drought-tolerant and adapted species is also the one showing the highest WUE in all scenarios.

Discussion

Ecological considerations on the dynamics and physiology of the species

Climate change projections indicate an increased likelihood of droughts (Kerr 2005) and variability of precipitation - in time, space, and intensity - that would directly influence water resource availability. The combination of long-term changes (e.g., warmer average temperatures) and greater extremes (e.g., droughts) can have decisive impacts on water demand, with further impact on the ecosystems. An increase in air temperatures and a slight decrease in precipitations are forecast for the Mediterranean area by General Circulation Models (GCMs, Fourth Assessment Report - IPCC 2007). Lower water availability is also projected for this region by eco-physiological models such as GOTILWA (Sabaté et al. 2002, Peñuelas et al. 2005). In fact, increased temperatures and lower water availability have been already experienced in the last decades (Le Houérou 1996, Piñol et al. 1998, De Luis et al. 2001, Peñuelas & Boada 2003, Peñuelas et al. 2005). Several studies have described reduced plant performance in the Mediterranean area during summer months due to heat and drought stress (Filella et al. 1998, Yordanov et al. 2000, Ogaya & Peñuelas 2003a, Peñuelas et al. 2007).

Ecosystem responses to climate change are driven by complex multifactor influences (Norby & Luo 2004). In the Mediterranean area, the future presence of a species is thus likely determined by the complex balance of temperature change, soil water availability, species-specific photosynthetic capacity, seasonal fires, air-free pollutants and land use changes. Moreover, species-specific responses may affect the structure and functioning of ecosystems through altered relationships with other plant-competitors on mineral resources and vital spaces. Comprehensive analysis of gas exchanges of each species can be made on the basis of data simulated by MOCA model. Two deciduous species show a strong reduction of *NPP* values as responding to the climate change, whereas evergreen Mediterranean oak shows a much lower *NPP* reduction. These responses may be affected by the non-consideration of the possible different impact of the increase of CO₂ atmospheric concentration on the three studied species in the future scenarios. As reported by Keenan et al. (2010), the increase of CO₂ may counteract the reduction of *NPP* due to the climatic limitations induced by alteration of species-specific climate envelopes. Furthermore, a decreased suitability for a pixel (niche-based) to host a species was

reflected in less *NPP* for the same site, if no CO_2 effect was taken into account (semi-empirical modelling). *NPP* simulations made by a process-based model, GOTILWA+ showed that *NPP* increased as CO_2 raised in the future climatic scenario, although the root mean squared error (RMSE) increased by a factor of three between GOTILWA+ simulations considering atmospheric CO_2 as constant and those considering a CO_2 increment (Keenan et al. 2010). However, studies have also identified interspecies variability in responses to increasing atmospheric CO_2 concentrations, and importantly have highlighted the possibility of species-specific response saturation rates. For these reasons, we have maintained the air CO_2 concentration at 380 ppm also in the future climate changing scenarios and compared the response of the three species. As a consequence, the reduction of *NPP* values observed in all tree species examined here is due mainly to the influence of the bioclimatic envelope (distribution of the species) and changed climate.

Also transpiration rates and water use efficiency differed among tree species under climate change scenarios. *Q. ilex* was the best adapted to drought stress among plant species considered here. The higher drought resistance of *Q. ilex* is based on a drought-tolerant water-saving strategy (Levitt 1980), due to the morpho-anatomic characteristics of the sclerophyllous leaves and their longer physiological functioning in time (Manes et al. 2006), on generally low transpiration rates, and on the root system which is able to adapt and to resist to dehydrated soils (Manes et al. 2006). Furthermore, the higher WUE values of *Q. ilex* under limiting climatic scenarios with respect to the other two species point out a well-adapted functional mechanisms to maintain a positive carbon gain by the activation of “alternative ways” to dissipate the excess of incoming radiant energy (Zaragoza-Castells et al. 2008, Rennenberg et al. 2006). Increases in WUE have also been found in rainfall exclusion experiments (Ogaya & Peñuelas 2003b, Lloret et al. 2004, Fischer et al. 2007), although uncertainty remains in terms of how long such increases can be sustained. *Q. cerris* showed a progressive reduction of *NPP* and transpiration rates under limiting scenarios, due to the closure of stomata which are sensitive to change of evaporative demand between plant and atmosphere. However, under water stress the stomatal closure could be justified by the reduction of the stem/root hydraulic conductance and to the variation of soil water availability (Cochard et al. 1996, 2000, Nardini et al. 1999) for oaks. An integrated mechanism seems to be involved for the limitation of water loss when soil water dehydration becomes more intense; high evaporative demand becomes just as important as the state of dehydration of the soil, which

directly affects the root ability to water uptake (Manes et al. 2006). Nevertheless, WUE values do not increase in the 2071-2100 B1 and A2 scenarios, pointing out a non-conservative water strategy under limiting climate conditions for this species. This could affect the distribution pattern of *Quercus cerris* and, in turn, its ability to fix carbon under these conditions. *Q. cerris* has potentially the possibility to shift to higher altitudes (Attorre et al. 2011), towards cooler conditions and closer to its favourable climatic niche, although it may be limited by the presence of *F. sylvatica*. Functional similarities with *Q. cerris* have been noted in *F. sylvatica*, although beech shows different adaptive abilities to counteract the climate change, adopting a water spender strategy, that is typical for species growing in mesophilous environments. This strategy could represent a risk for survival of plant populations when environmental conditions extremely change. However, it has been reported that beech can show inter-annual and seasonal adaptation and relatively flexible changes in WUE, allowing the maintenance of carbon gain in relatively dry years (Matteucci, personal communication, Scartazza et al. submitted). It is worth noting that the remaining beech suitable surface area under the 2071-2100 A2 scenario is 65% compared to the reference “1961-90” period (Attorre et al. 2011), pointing out a scarce possibility to shift to higher altitudes. As a consequence, *F. sylvatica* may be seriously threatened by climate change in Italy, being also subjected to a strong reduction of *NPP*.

However, it seems that in a warmer and drier environment, as the one projected for the Mediterranean areas for the following decades, the performance of the dominant species could be less competitive with respect to the other more drought and heat resistant species such as the co-dominant *Phillyrea latifolia* for *Q. ilex* (see Ogaya et al. 2011); as a general rule, the temporal dynamics of progressive physiological adjustments counteracting the environmental limiting factors (high temperature and drought increase) seem to play a fundamental role for determining competitive abilities against other co-occurring plant species under Mediterranean limiting conditions, conditioning thus the final distribution patterns of plant species.

Finally, it is also important to stress that our results are restricted to tree species in Italy, and thus we cannot be certain to what extent any patterns or results observed here may be either affected by species (co-)occurrences in other regions, or extrapolated to other topo-climatic scenarios.

Conclusions

The resulting spatial representation of the net primary productivity under two climatic

scenarios was consistent with what is known about the eco-physiological response to environmental stresses (high temperature, drought) of the species analysed here. The use of multivariate statistical models to assess the different distribution areas of the species under different climatic conditions (Attorre et al. 2011) has been very important to address the geo-referring of the MOCA's output. This combined approach allowed also to deduce some aspects on the use environmental resources (water, solar radiation) in relation to north-south latitudinal gradient and two different climate scenarios. These suggestions may be helpful to identify priority areas to be managed in an adaptive way, so as to preserve the actual forest resource and mitigate or minimize the effects of climate change.

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References

- Ainsworth EA, Long SP (2005). 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 Phytologist* 165: 351-372. - doi: [10.1111/j.1469-8137.2004.01224.x](https://doi.org/10.1111/j.1469-8137.2004.01224.x)
- Allen RG, Pereira LS, Raes D, Smith M (1998). Crop evapotranspiration: guidelines for computing crop water requirements. Irrigation and Drainage Paper No. 56, UN-FAO, Rome.
- Amthor JS, Goulden ML, Munger JW, Wofsy SC (1994). Testing a mechanistic model of forest-canopy mass and energy exchange using eddy correlation: carbon dioxide and ozone uptake by a mixed oak-maple stand. *Australian Journal of Plant Physiology* 21: 623-651. - doi: [10.1071/PP9940623](https://doi.org/10.1071/PP9940623)
- Attorre F, Alfò M, De Sanctis M, Francesconi F, Bruno F (2007). Comparison of interpolation methods for mapping climatic and bioclimatic variables at regional scale. *International Journal of Climatology* 27:1825-1843. - doi: [10.1002/joc.1495](https://doi.org/10.1002/joc.1495)
- Attorre F, Francesconi F, Scarnati L, De Sanctis M, Alfò M, Bruno F (2008). Predicting the effect of climate change on tree species abundance and

- distribution at a regional scale. *iForest* 1: 132-139. - doi: [10.3832/ifor0467-0010132](https://doi.org/10.3832/ifor0467-0010132)
- Attorre F, Francesconi F, Valenti R, Vitale M, Alfò M, Bruno F (2011). Evaluating the effects of climate change on tree species abundance and distribution in the Italian peninsula. *Applied Vegetation Science* 14:242-255. - doi: [10.1111/j.1654-109X.2010.01114.x](https://doi.org/10.1111/j.1654-109X.2010.01114.x)
- Ball JT, Woodrow IE, Berry JA (1987). A model predicting stomatal conductance and its contribution to the control of photosynthesis under different environmental conditions. In: "Progress in photosynthesis research" (Biggins I ed). Vol. IV, Martinus Nijhoff, Dordrecht, The Netherlands, pp. 221-224.
- Betts RA, Boucher O, Collins M, Cox PM, Falloon PD, Gedney N, Hemming DL, Huntingford C, Jones CD, Sexton D, Webb MJ (2007). Projected increase in continental runoff due to plant responses to increasing carbon dioxide. *Nature* 448: 1037-1041. - doi: [10.1038/nature06045](https://doi.org/10.1038/nature06045)
- Bossel H (1996). TREEDYN3 forest simulation model. *Ecological Modelling* 90:187-227. - doi: [10.1016/0304-3800\(95\)00139-5](https://doi.org/10.1016/0304-3800(95)00139-5)
- Bunce JA (1992). Stomatal conductance, photosynthesis and respiration of temperate deciduous tree seedlings grown outdoors at an elevated concentration of carbon dioxide. *Plant Cell and Environment* 15: 541-549. - doi: [10.1111/j.1365-3040.1992.tb01487.x](https://doi.org/10.1111/j.1365-3040.1992.tb01487.x)
- Chirici G, Barbati A, Maselli F (2007). Modelling of Italian forest net primary productivity by the integration of remotely sensed and GIS data. *Forest Ecology and Management* 246: 285-295. - doi: [10.1016/j.foreco.2007.04.033](https://doi.org/10.1016/j.foreco.2007.04.033)
- Ciais P, Reichstein M, Viovy N, Granier A, Ogee J, Allard V, et al. (2005). Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature* 437:529-533. - doi: [10.1038/nature03972](https://doi.org/10.1038/nature03972)
- Cochard H, Bréda N, Granier A (1996). Whole tree hydraulic conductance and water loss regulation in *Quercus* during drought: evidence for stomatal control of embolism? *Annals of Science Forest* 53:197-206. - doi: [10.1051/forest:19960203](https://doi.org/10.1051/forest:19960203)
- Cochard H, Martin R, Gross P, Bogeat-Triboulot MB (2000). Temperature effects on hydraulic conductance and water relations of *Quercus robur* L. *Journal of Experimental Botany* 51: 1255-1259. - doi: [10.1093/jexbot/51.348.1255](https://doi.org/10.1093/jexbot/51.348.1255)
- Curtis PS (1996). A meta-analysis of leaf gas exchange and nitrogen in trees grown under elevated CO₂ in situ. *Plant Cell and Environment* 19: 127-137. - doi: [10.1111/j.1365-3040.1996.tb00234.x](https://doi.org/10.1111/j.1365-3040.1996.tb00234.x)
- Dai Y, Zeng X, Dickinson RE, Baker I, Bonan GB, Bosilovich MG, Denning AS, et al. (2003). The Common Land Model (CLM). *Bulletin of the American Meteorological Society* 84:1013-1023. - doi: [10.1175/BAMS-84-8-1013](https://doi.org/10.1175/BAMS-84-8-1013)
- De Luis M, Garcia-Cano MP, Cortina J, Raventós J, González-Hidalgo JC, Sánchez JR (2001). Climatic trends, disturbances and short-term vegetation dynamics in a Mediterranean shrubland. *Forest Ecology and Management* 147: 25-37. - doi: [10.1016/S0378-1127\(00\)00438-2](https://doi.org/10.1016/S0378-1127(00)00438-2)
- de Wit CT, Goudriaan J, van Laar HH, Penning de Vries FWT, Rabbinge R, van Keulen H, Louwerse W, Sibma L, de Jonge C (1978). Simulation of assimilation, respiration and transpiration of crops. *Simulation Monographs*, PUDOC, Wageningen, The Netherlands.
- Di Traglia M, Attorre F, Francesconi F, Valenti R, Vitale M (2011). Is cellular automata algorithm able to predict the future dynamical shifts of tree species in Italy under climate change scenarios? A methodological approach. *Ecological Modelling* 222 (4): 925-934. - doi: [10.1016/j.ecolmodel.2010.12.009](https://doi.org/10.1016/j.ecolmodel.2010.12.009)
- Dilley AC (1968). On the computer calculation of vapor pressure and specific humidity gradients from psychrometric data. *Journal of Applied Meteorology* 7: 717-718. - doi: [10.1175/1520-0450\(1968\)007<0717:OTCCOV>2.0.CO;2](https://doi.org/10.1175/1520-0450(1968)007<0717:OTCCOV>2.0.CO;2)
- Faria T, Silvério D, Breia E, Cabral R, Abadia A, Abadia J, Pereira JS, Chaves MM (1998). Differences in the response of carbon assimilation to summer stress (water deficits, high light and temperature) in four Mediterranean tree species. *Physiologia Plantarum* 102: 419-428. - doi: [10.1034/j.1399-3054.1998.1020310.x](https://doi.org/10.1034/j.1399-3054.1998.1020310.x)
- Eamus D, Jarvis PG (1989). The direct effects of increase in the global atmospheric CO₂ concentration on natural and commercial temperate trees and forests. *Advances in Ecological Research* 19: 1-55. - doi: [10.1016/S0065-2504\(08\)60156-7](https://doi.org/10.1016/S0065-2504(08)60156-7)
- Filella I, Llusia J, Piñol J, Peñuelas J (1998). Leaf gas exchange and fluorescence of *Phillyrea latifolia*, *Pistacia lentiscus* and *Quercus ilex* saplings in severe drought and high temperature conditions. *Environmental and Experimental Botany* 39: 213-220. - doi: [10.1016/S0098-8472\(97\)00045-2](https://doi.org/10.1016/S0098-8472(97)00045-2)
- Fischer RA, Williams M, Lola da Costa A, Malhi RF, da Costa RF, Almeida S, Meir P (2007). The response of an Eastern Amazonian rain forest to drought stress: results and modelling analyses from a throughfall exclusion experiment. *Global Change and Biology* 13: 2361-2378. - doi: [10.1111/j.1365-2486.2007.01417.x](https://doi.org/10.1111/j.1365-2486.2007.01417.x)
- Fosberg MA (1990). Global change - a challenge to modeling. In: "Process modelling of forest growth responses to environmental stress" (Dixon RK, Mehl Dahl MS, Ruark GA, Warren WG eds). Timber Press, Portland, OR, USA.
- Friend AD, Woodward FI (1990). Evolutionary and ecophysiological responses of mountain plants to the growing season environment. *Advances in Ecological Research* 20: 59-124. - doi: [10.1016/S0065-2504\(08\)60053-7](https://doi.org/10.1016/S0065-2504(08)60053-7)
- Goudriaan J, Shugart HH, Bugmann H, Cramer W, Bondeau A, Gardner RH, et al. (1999). Use of models in global change studies. In: "The terrestrial biosphere and global change" (Walker B, Steffen W, Canadell J, Ingram J eds). Cambridge University Press, Cambridge, UK.
- Granier A, Ceschia E, Damesin C, Dufréne E, Epron D, Gross P, Lebaube S, et al. (2000). The carbon balance of a young beech forest. *Functional Ecology* 14: 312-325. - doi: [1365-2435.2000.00434.x](https://doi.org/10.1046/j.1365-2435.2000.00434.x)
- Granier A, Reichstein M, Breda N, Janssens IA, Falge E, Ciais P, et al. (2007). Evidence for soil water control on carbon and water dynamics in European forests during the extremely dry year: 2003. *Agricultural and Forest Meteorology* 143: 123-145. - doi: [10.1016/j.agrformet.2006.12.004](https://doi.org/10.1016/j.agrformet.2006.12.004)
- Harley PC, Thomas RB, Reynolds JF, Strain BR (1992). Modelling photosynthesis of cotton grown in elevated CO₂. *Plant, Cell and Environment* 15: 271-282. - doi: [10.1111/j.1365-3040.1992.tb00974.x](https://doi.org/10.1111/j.1365-3040.1992.tb00974.x)
- Herrick JD, Maherali H, Thomas RB (2004). Reduced stomatal conductance in sweetgum (*Liquidambar styraciflua*) sustained over long-term CO₂ enrichment. *The New Phytologist* 162: 387-396. - doi: [10.1111/j.1469-8137.2004.01045.x](https://doi.org/10.1111/j.1469-8137.2004.01045.x)
- Husch B, Beers TW, Kershaw JA (2003). *Forest Mensuration*. Wiley, New York, USA, pp. 465.
- IPCC (2007). Fourth Assessment Report (Walser ML, Nodvin SC eds). Intergovernmental panel on climate change, Fourth Assessment Report 2007. [online] URL: http://www.ipcc.ch/pdf/assessment-report/ar4/syr/ar4_syr.pdf
- IPCC-SRES (2007). Climate change 2007: the physical science basis. Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change (Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL eds). Cambridge University Press, Cambridge, UK and New York, USA, pp. 996.
- Jarvis PG, Edwards WRN, Talbot H (1981). Models of plant and crop water use. In: "Mathematical and Plant Physiology" (Rose DA, Charles-Edwards CW eds). Academic Press, London, UK, pp. 151-194.
- Keenan T, Sabate S, Gracia C (2010). Soil water stress and coupled photosynthesis-conductance models: bridging the gap between conflicting reports on the relative roles of stomatal, mesophyll conductance and biochemical limitations to photosynthesis. *Agricultural and Forest Meteorology* 150: 443-453. - doi: [10.1016/j.agrformet.2010.01.008](https://doi.org/10.1016/j.agrformet.2010.01.008)
- Kerr RA (2005). Confronting the bogeyman of the climate system. *Science* 310:432-433. - doi: [10.1126/science.310.5747.432](https://doi.org/10.1126/science.310.5747.432)
- Kickert RN, Tonella G, Simonov A, Krupa A (1999). Predictive modeling effects under global change. *Environmental Pollution* 100 (1-3): 87-132. - doi: [10.1016/S0269-7491\(99\)00089-5](https://doi.org/10.1016/S0269-7491(99)00089-5)
- Kowalski A, Loustau D, Berbigier P, Manca G, Tedeschi V, Borghetti M, Valentini R, Kolari P, Berninger F, Rannik U, Hari P, Rayment M, Mencuccini M, Moncrieff J, Grace J (2004). Paired comparison of carbon exchange between undisturbed and regenerating stands in four managed forests in Europe. *Global Change Biology* 10: 1707-1723 - doi: [10.1111/j.1365-2486.2004.00846.x](https://doi.org/10.1111/j.1365-2486.2004.00846.x)
- Kull O, Jarvis PG (1995). The role of nitrogen in a simple scheme to scale up photosynthesis from leaf to canopy. *Plant, Cell and Environment* 18: 1174-1182. - doi: [10.1111/j.1365-3040.1995.tb00627.x](https://doi.org/10.1111/j.1365-3040.1995.tb00627.x)

- Le Houérou HN (1996). Climate change, drought and desertification. *Journal of Arid Environment* 34: 133-185. - doi: [10.1006/jare.1996.0099](https://doi.org/10.1006/jare.1996.0099)
- Leuzinger S, Körner C (2010). Rainfall distribution is the main driver of runoff under future CO₂-concentration in a temperate deciduous forest. *Global Change and Biology* 16: 246-254. - doi: [10.1111/j.1365-2486.2009.01937.x](https://doi.org/10.1111/j.1365-2486.2009.01937.x)
- Levitt J (1980). Responses of plants to environmental stresses. Vol. II, Academic Press, London, UK.
- Lloret F, Peñuelas J, Ogaya R (2004). Seedling versus sprout recruitment of two Mediterranean trees (*Phillyrea latifolia* and *Quercus ilex*) under drought conditions. *Journal of Vegetation Science* 15: 237-244. - doi: [10.1111/j.1654-1103.2004.tb02258.x](https://doi.org/10.1111/j.1654-1103.2004.tb02258.x)
- Luyssaert S, Inglisma I, Jung M, Richardson AD, Reichstein M, Papale D, Piao SL, Schulze ED, Wingate L, Matteucci G, et al. (2007). CO₂ balance of boreal, temperate, and tropical forests derived from a global database. *Global Change Biology* 13: 1-29. - doi: [10.1111/j.1365-2486.2006.01280.x](https://doi.org/10.1111/j.1365-2486.2006.01280.x)
- Magnani F, Leonardi S, Tognetti R, Grace J, Borghetti M (1998). Modelling the surface conductance of a broad-leaf canopy: effects of partial decoupling from the atmosphere. *Plant, Cell and Environment* 21: 867-879. - doi: [10.1046/j.1365-3040.1998.00328.x](https://doi.org/10.1046/j.1365-3040.1998.00328.x)
- Manes F, Vitale M, Donato E, Giannini M, Puppi G (2006). Different ability of three Mediterranean oak species to tolerate progressive dehydration stress. *Photosynthetica* 44 (3): 387-393. - doi: [10.1007/s11099-006-0040-7](https://doi.org/10.1007/s11099-006-0040-7)
- Manes F, Seufert G, Vitale M (1997). Ecophysiological studies of Mediterranean plant species at the Castelporziano Estate. *Atmospheric Environment* 31 (SI): 51-60. - doi: [10.1016/S1352-2310\(97\)00073-3](https://doi.org/10.1016/S1352-2310(97)00073-3)
- Menzel A, Sparks TH, Estrella N, Elisabeth Koch E, et al. (2006). European phenological response to climate change matches the warming pattern. *Global Change and Biology* 12: 1969-1976. - doi: [10.1111/j.1365-2486.2006.01193.x](https://doi.org/10.1111/j.1365-2486.2006.01193.x)
- Mitchell T, Carter TR, Jones P, Hulme M, New M (2004). A comprehensive set of high-resolution grids of monthly climate for Europe and the globe: observed record (1901-2000) and 16 scenarios (2001-2100). Working Paper no. 55, Tyndall Centre for Climate Change Research, University of East Anglia, UK.
- Morison JIL, Gifford RM (1983). Stomatal sensitivity to carbon dioxide and humidity. A comparison of two C3 and C4 grass species. *Plant Physiology* 71: 789-796. - doi: [10.1104/pp.71.4.789](https://doi.org/10.1104/pp.71.4.789)
- Myneni RB, Keeling CD, Tucker CJ, Asrar G, Nemani RR (1997). Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature* 386: 698-702. - doi: [10.1038/386698a0](https://doi.org/10.1038/386698a0)
- Nabuurs GJ, Mohren GMJ (1995). Modelling analysis of potential carbon sequestration in selected forest types. *Canadian Journal of Forest Research* 25: 1157-1172. - doi: [10.1139/x95-128](https://doi.org/10.1139/x95-128)
- Nakicenovic N, Swart R (2000). Special report on emissions scenarios. A special report of working group III of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK and New York, USA, pp. 570. [online] URL: <http://www.ipcc.ch/ipccreports/sres/emission/index.htm>
- Nardini A, LoGullo MA, Salleo S (1999). Competitive strategies for water availability in two Mediterranean *Quercus* species. *Plant, Cell and Environment* 22: 109-116. - doi: [10.1046/j.1365-3040.1999.00382.x](https://doi.org/10.1046/j.1365-3040.1999.00382.x)
- Norby RJ, Luo Y (2004). Evaluating ecosystem responses to rising atmospheric CO₂ and global warming in a multi-factor world. *New Phytologist* 162: 281-293. - doi: [10.1111/j.1469-8137.2004.01047.x](https://doi.org/10.1111/j.1469-8137.2004.01047.x)
- Ogaya R, Peñuelas J (2003a). Comparative field study of *Quercus ilex* and *Phillyrea latifolia*: photosynthetic response to experimental drought conditions. *Environmental and Experimental Botany* 50: 137-148. - doi: [10.1016/S0098-8472\(03\)00019-4](https://doi.org/10.1016/S0098-8472(03)00019-4)
- Ogaya R, Peñuelas J (2003b). Comparative seasonal gas exchange and chlorophyll fluorescence of two dominant woody species in a Holm Oak Forest. *Flora* 198: 132-141. - doi: [10.1078/0367-2530-00085](https://doi.org/10.1078/0367-2530-00085)
- Ogaya R, Peñuelas J, Asensio D, Llusà J (2011). Chlorophyll fluorescence responses to temperature and water availability in two co-dominant Mediterranean shrub and tree species in a long-term field experiment simulating climate change. *Environmental and Experimental Botany* 71: 123-127. - doi: [10.1016/j.envexpbot.2010.10.016](https://doi.org/10.1016/j.envexpbot.2010.10.016)
- Parnesan C (2007). Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Global Change and Biology* 13: 1860-1872. - doi: [10.1111/j.1365-2486.2007.01404.x](https://doi.org/10.1111/j.1365-2486.2007.01404.x)
- Parnesan C, Yohe G (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421: 37-42. - doi: [10.1038/nature01286](https://doi.org/10.1038/nature01286)
- Peñuelas J, Boada M (2003). A global distribution of biodiversity inferred from climatic constraints: results from a process-based modelling study. *Global Change and Biology* 9:131-140. - doi: [10.1046/j.1365-2486.2003.00566.x](https://doi.org/10.1046/j.1365-2486.2003.00566.x)
- Peñuelas J, Filella I, Sabate S, Gracia C (2005). Natural systems: terrestrial ecosystems. In: "Report on climate change in Catalonia" (Llebot JE ed). Institut d'Estudis Catalans, Barcelona, Spain, pp. 517-553.
- Peñuelas J, Gordon C, Llorens L, Nielsen T, Tietema A, Beier C, Bruna P, Emmet BA, Estiarte M, Gorissen T (2004). Non-invasive field experiments show different plant responses to warming and drought among sites seasons and species in a North-South European gradient. *Ecosystems* 7: 598-612. - doi: [10.1007/s10021-004-0179-7](https://doi.org/10.1007/s10021-004-0179-7)
- Peñuelas J, Prieto P, Beier C, Cesaraccio C, De Angelis P, De Dato G, Emmett B, Estiarte M, et al. (2007). Response of plant species richness and primary productivity in shrublands along a north-south gradient in Europe to seven years of experimental warming and drought. Reductions in primary productivity in the heat and drought year of 2003. *Global Change and Biology* 13: 2563-2581. - doi: [10.1111/j.1365-2486.2007.01464.x](https://doi.org/10.1111/j.1365-2486.2007.01464.x)
- Pereira JS, Chaves MM, Caldeira MC, Correia AV (2006). Water availability and productivity. In: "Plant growth and climate change" (Morrison JIL, Morecroft D eds). Blackwell Publishers, London, UK, pp. 118-145.
- Piñol J, Terradas J, Lloret F (1998). Climate warming, wildfire Hazard, and wildfire occurrence in coastal eastern Spain. *Climatic Change* 38: 345-357. - doi: [10.1023/A:1005316632105](https://doi.org/10.1023/A:1005316632105)
- Rennenberg H, Loreto F, Polle A, Brillì F, Fares S, Beniwal RS, Gessler A (2006). Physiological responses of forest trees to heat and drought. *Plant Biology* 8: 556-571. - doi: [10.1055/s-2006-924084](https://doi.org/10.1055/s-2006-924084)
- Rustad L, Campbell J, Marion G, Norby R, Mitchell M, Hartley A, Cornelissen J, Gurevitch J, GCTE-NEWS (2001). A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia* 126:543-562. - doi: [10.1007/s004420000544](https://doi.org/10.1007/s004420000544)
- Sabaté S, Gracia CA, Sánchez A (2002). Likely effects of climate change on growth of *Quercus ilex*, *Pinus halepensis*, *Pinus pinaster*, *Pinus sylvestris* and *Fagus sylvatica* forests in the Mediterranean region. *Forest Ecology and Management* 162: 23-37. - doi: [10.1016/S0378-1127\(02\)00048-8](https://doi.org/10.1016/S0378-1127(02)00048-8)
- Saxe H, Ellsworth DS, Heath J (1998). Tree and forest functioning in an enriched CO₂ atmosphere. *New Phytologist* 139: 395-436. - doi: [10.1046/j.1469-8137.1998.00221.x](https://doi.org/10.1046/j.1469-8137.1998.00221.x)
- Scartazza A, Mata C, Matteucci G, Yakir D, Moscatello S., Brugnoli E (2004). Comparisons of δ¹³C of photosynthetic products and ecosystem respiratory CO₂ and their responses to seasonal climate variability. *Oecologia* 140: 340-351. - doi: [10.1007/s00442-004-1588-1](https://doi.org/10.1007/s00442-004-1588-1)
- SCIA (2011). National system for collecting, processing and dissemination of climatological data of environmental interest. [online] URL: http://www.scia.sinanet.apat.it/sciaweb/scia_valori_mappe.html
- Sellers PJ, Berry JA, Collatz GJ, Field CB, Hall FG (1992). Canopy reflectance, photosynthesis, and transpiration. III. A reanalysing using improved leaf models and a new canopy integration scheme. *Remote Sensing and Environment* 42: 187-216. - doi: [10.1016/0034-4257\(92\)90102-P](https://doi.org/10.1016/0034-4257(92)90102-P)
- Tirone G, Dore S, Matteucci G, Greco S, Valentini R (2003). Evergreen Mediterranean forests: carbon and water fluxes, balances, ecological and ecophysiological determinants. In: "Fluxes of carbon, water and energy of european forests" (Valentini R ed). Ecological Studies 163, Springer-Verlag, Berlin, Heidelberg, pp. 125-149.
- Vitale M, Capogna F, Manes F (2007). Resilience assessment on *Phillyrea angustifolia* L. maquis undergone to experimental fire. *Ecological Mo-*

- delling 203: 387-394. - doi: [10.1016/j.ecolmodel.2006.12.004](https://doi.org/10.1016/j.ecolmodel.2006.12.004)
- Vitale M, Scimone M, Feoli E, Manes F (2003). Modelling leaf gas exchanges as a function of temperature increase to predict trends of functional processes in Mediterranean *Quercus ilex* forest under climatic changes. *Ecological Modelling* 166: 123-134. - doi: [10.1016/S0304-3800\(03\)00129-7](https://doi.org/10.1016/S0304-3800(03)00129-7)
- Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin J-M, Hoegh-Gudberg O, Bairlein F (2002). Ecological responses to recent climate change. *Nature* 416: 389-395. - doi: [10.1038/416389a](https://doi.org/10.1038/416389a)
- Yordanov I, Velikova V, Tsonev T (2000). Plant responses to drought, acclimation, and stress tolerance. *Photosynthetica* 38: 171-186. - doi: [10.1023/A:1007201411474](https://doi.org/10.1023/A:1007201411474)
- Zaragoza-Castells J, Sánchez-Gómez D, Hartley IP, Matesanz S, Valladares F, Lloyd J, Atkin OK (2008). Climate-dependent variations in leaf respiration in a dry-land, low productivity Mediterranean forest: the importance of acclimation in both high-light and shaded habitats. *Functional Ecology* 22:172-184.
- Zatelli P, Neteler M (2005). GRASS status and future development. *The Geomatics Workbooks* 5, Milan, Italy. [online] URL: <http://geomatica-como.polimi.it/workbooks>