

# Likely effects of climate change on growth of *Quercus ilex*, *Pinus halepensis*, *Pinus pinaster*, *Pinus sylvestris* and *Fagus sylvatica* forests in the Mediterranean region

Santiago Sabaté<sup>a,b,\*</sup>, Carlos A. Gracia<sup>a,b</sup>, Anabel Sánchez<sup>a</sup>

<sup>a</sup>Centre for Ecological Research and Forestry Applications (CREAF), Universitat Autònoma de Barcelona,  
08193 Bellaterra, Barcelona, Spain

<sup>b</sup>Departament d'Ecologia, Facultat de Biologia, Universitat de Barcelona, Diagonal 645, 08028 Barcelona, Spain

## Abstract

Mediterranean forest growth is constrained by drought and high temperatures during summer. Effects of climate change on these forests depend on how changes in water availability and temperature will take place. A process-based forest growth model, growth of trees is limited by water in the Mediterranean (GOTILWA+), was applied in the Mediterranean region on *Quercus ilex*, *Pinus halepensis*, *P. pinaster*, *P. sylvestris* and *Fagus sylvatica* forests. The effects of climate change on growth were analysed, as well as the effect of thinning cycle length, combined with the assumption of different soil depths. Thinning cycle lengths was included because it can affect the response of stands to climatic conditions, and soil depth because this is positively related to soil water-holding capacity and consequently may change the effects of drought. The simulation period covered 140 years (1961–2100). Model results show that leaf area index (LAI) may increase, favoured by the increase of atmospheric CO<sub>2</sub>, particularly at sites where rainfall is relatively high and climatic conditions not too warm. The predicted increase in temperature significantly influenced mean leaf life span (MLLS). MLLS of *F. sylvatica* would increase with climate change, implying a longer growing period. Conversely, MLLS of evergreen species would be reduced, accelerating leaf turnover. In general, our results showed a higher production promoted by projected climate change in response to the increasing atmospheric CO<sub>2</sub> concentration and rainfall in the region. Temperature increase would have different consequences for production. In *F. sylvatica*, the longer growing period would promote higher production, particularly when water is not limiting. On the other hand, *Q. ilex* and *Pinus* species would expend more carbon in maintaining and producing leaves to replace those lost in increased turnover rate. As expected, access of roots to deeper soil results in an increased final wood yield (FWY) due to an improved water balance that promotes higher transpiration, photosynthesis and growth. In general, the shorter the harvest cycle, the larger the FWY, because of less tree mortality between harvesting events. According to our results, temperature and rainfall may constrain growth during certain periods but if rainfall increases in the future, a positive effect on growth is likely. © 2002 Elsevier Science B.V. All rights reserved.

**Keywords:** Holm oak; Aleppo pine; Maritime pine; Scots pine; Beech; Forest growth modelling; Climate change

## 1. Introduction

At present, Mediterranean forests are highly constrained by dry conditions and to a lesser extent by nutrient deficiency (N in siliceous soils—Mayor and

\* Corresponding author. Tel.: +34-93-5811920;  
fax: +34-93-5811312.  
E-mail address: santi.sabate@uab.es (S. Sabaté).

Rodà, 1992, 1994; Sabaté and Gracia, 1994 and P in calcareous soils—Sardans, 1997). Solar radiation is not in short supply but combined with summer drought, it increases vegetation stress and raises fire probability. Current annual potential evapotranspiration (PET) is often nearly twice the size of rainfall, although precipitation is highly variable within and between years. In fact, summer drought has been recognised as the major stress, limiting plant species distribution and growth in all Mediterranean regions of the world (Mooney, 1983). In the context of climate change, it is desirable to know whether drought will occur more often in the future, increasing physiological stress, and whether the present forest can adapt to such conditions, along with the projected increase in temperatures and atmospheric CO<sub>2</sub> concentration. Additionally, harvesting schedules and silvicultural practices should be considered because they could affect the response of stands to climatic conditions. The impact of extreme drought can be reduced by forest management, as has been shown by thinning in *Quercus ilex* forests. Thus, forest management policies may play an important role in adjusting to new climatic conditions (Gracia et al., 1999a, see also Lindner, 2000). In addition, soil depth also would play an important role in determining where it is possible for plants to overcome increased drought since it is positively related with soil water-holding capacity.

In the framework of long-term regional effects of climate change on European forests (LTEEF): impact assessment and consequences for carbon budgets, several process-based models were applied to assess the impacts of climate change on European forests, in terms of water and carbon fluxes, regional differences of the impacts, long-term effects, and the overall carbon budget for forests in Europe (Mohren and Kramer, 1997; Mohren et al., 2000; Kramer and Mohren, 2001; Kramer et al., in press). Following a thorough model evaluation, regional impact studies were carried out to assess potential impacts of climate change on a range of forests throughout Europe. There has been very little knowledge to date about long-term species responses in the Mediterranean region to climate change.

In this paper, the process-based forest growth model, growth of trees is limited by water in the Mediterranean (GOTILWA+), was applied to analyse the effects of climate change in the Mediterranean

region, as projected by Erhard et al. (2001). The analysis focused on forests dominated by one of the following species: *Q. ilex*, *Pinus halepensis*, *P. pinaster*, *P. sylvestris* and *Fagus sylvatica*. The effects on wood yield at the end of a rotation are also evaluated assuming trees have either shallow or deep roots at different soil depths.

## 2. Material and methods

### 2.1. Climate change scenarios and sites

To quantify the climate situation over the specified period, we used transient climate scenarios generated by the Potsdam Institute for Climate Impact Research (PIK) following the model prediction derived from the Hadley Centre Global Circulation Model (GCM) *HadCM2* (see Erhard et al., 2001). The GCM simulations were based on a transient run including the cooling effects of sulphate aerosols on climate. The *HadCM2* has a spatial resolution of  $2.5^\circ \times 3.75^\circ$  (latitude by longitude) that was refined to a grid of  $0.5^\circ \times 0.5^\circ$  by PIK. For the time period 1901–1990 the monthly  $0.5^\circ \times 0.5^\circ$  climate data set of Climatic Research Unit (CRU, University of East Anglia, Norwich; see Hulme et al., 1995; Mitchel et al., 1995; New et al., 2000) was available. The *HadCM2* run used was based on the ‘business as usual’ emission scenario IS92a (Houghton et al., 1995; Mitchel et al., 1995). The GCM results were downscaled to the sites by calculating the difference for each parameter between the time period 1990–2100 and the average values of the reference period 1931–1960 using monthly time steps. The time series of these anomalies were then added to the average values of CRU data for the same period. The historic period of climate data was extended. PIK generated climate data for the period 1831–2100 for a number of sites, assuming an exponential increase in atmospheric CO<sub>2</sub> concentration from the years 1990 to 2100, when concentrations were expected to reach approximately  $700 \mu\text{mol mol}^{-1}$ . Relative humidity and radiation were not affected by the scenarios. The monthly climate data were disaggregated with the C2W weather generator (Bürger, 1997), which was fitted with climatic station data set to the conditions at the modelling sites. Further details of the climate scenarios used in this study can be found

Table 1  
Locations where climate change impacts have been analysed

Country (site name)	Longitude	Latitude	Altitude (m)	Tree species
Italy (S11-hi)	7.25	44.75	1160	<i>F. sylvatica</i>
Italy (S12-hi)	13.25	42.25	1133	<i>F. sylvatica</i>
Italy (S12-lo)	16.25	40.75	437	<i>Q. ilex</i>
Italy (Ginosa)	16.87	40.42	2	<i>P. halepensis</i>
Spain (S13-hi)	−3.75	41.75	917	<i>P. sylvestris</i>
Spain (Prades)	0.92	41.21	500	<i>Q. ilex</i>
Spain (S14)	−4.25	38.25	643	<i>P. halepensis</i> , <i>P. pinaster</i> , <i>Q. ilex</i>

in Erhard et al. (2001). The sub-period of 1961–2100 was then used for detailed analysis.

Our study investigated impacts of climate change at seven Mediterranean sites (four in Italy and three in Spain). These sites have different environmental conditions reflecting a wide range in elevation, latitude, rainfall and temperature patterns (see Table 1). The species included in this analysis presently occur around the area of the representative sites. Both *Q. ilex* (Holm oak, which is an evergreen broad-leaved species) and *P. halepensis* (Aleppo pine) typically occur in Mediterranean climate conditions. *P. pinaster* (Maritime pine) can also occur in areas with Mediterranean climatic conditions, although it grows better in areas with an Atlantic influence, which are still warm but wetter than typical Mediterranean conditions. The remaining two species, namely *F. sylvatica* (beech) and *P. sylvestris* (Scots pine), are widely spread over Europe. The first is common in temperate conditions and the second has the broadest distribution over Europe and beyond (Euro-Siberian). Both of them may occur in the mountains of the Mediterranean region where conditions are cooler and water is more readily available as compared to the Mediterranean climate. In addition to the increase of atmospheric CO<sub>2</sub> concentration, the projected climates suggest an increase in temperature and rainfall over the period 1961–2100. To illustrate the magnitude of change at the seven sites, mean annual values of these variables averaged over three decades are shown in Table 2. The general trend is that rainfall is expected to be stable between 2040 and 2049 and to rise afterwards. However, the climate scenarios do not show significant changes with regard to intra-annual distribution patterns of precipitation (data not shown). Despite such long-term projected increase, a decrease is expected

between 2040 and 2050 at S11-hi and S13-hi with respect to current values. In all cases, temperatures are projected to increase continuously. In addition to climate change, the implications of different harvest schedules, every 20, 40 years and none until the end of the period, 140 years, are considered with fixed initial plantation. Finally, the effect of differential rooting was considered by setting soil depth at 20 and 40 cm (see Table 3).

## 2.2. GOTILWA+ model

GOTILWA+ is a forest growth model that has been implemented to simulate forest growth processes and to explore how these are influenced by climate, tree and stand structure, management techniques, soil properties and climate change. GOTILWA+ is an improved version of GOTILWA+ described in Gracia et al. (1999b). GOTILWA+ is built on a Visual Basic platform and simulates carbon and water balance and fluxes through forests in different environments (from boreal northern Europe to Mediterranean), for different single tree species stands (coniferous or broad-leaved, evergreen or deciduous) and in changing environmental conditions, due either to climate or to management. A general scheme on how the processes are interrelated in the model is provided in Fig. 1. Descriptions of the model can be found in Gracia et al. (2001) and Kramer (2001).

In summary, this version of the model has a daily time step. Stands are assumed to be homogeneous but two canopy layers are distinguished (sun and shade conditions). Broad DBH size classes are defined and all individuals are considered identical in each of them. Light extinction coefficient is estimated using Campbell's equation (Campbell, 1986).

Table 2

Mean annual values of atmospheric CO<sub>2</sub>, temperature and rainfall, averaged over three decades: 1990–1999, 2040–2049 and 2090–2099, from the simulated period 1961–2100 at each site<sup>a</sup>

	Period		
	1990–1999	2040–2049	2090–2099
Ambient CO <sub>2</sub> (ppm)	360.1 ± 6.9	493.5 ± 9.4 (1.4)	679.2 ± 12.9 (1.9)
Italy (S11-hi)			
<i>T</i> (°C)	10.5 ± 1.1	12.1 ± 0.7 (1.2)	14.3 ± 0.6 (1.4)
Rainfall (mm per year)	1109 ± 314	996 ± 238 (0.9)	1456 ± 354 (1.3)
Italy (S12-hi)			
<i>T</i> (°C)	10.8 ± 1.1	13.5 ± 2.0 (1.2)	16.9 ± 1.1 (1.6)
Rainfall (mm per year)	804 ± 176	806 ± 137 (1.0)	1143 ± 254 (1.4)
Italy (S12-lo)			
<i>T</i> (°C)	15.6 ± 1.1	18.3 ± 2.0 (1.2)	21.7 ± 1.1 (1.4)
Rainfall (mm per year)	621 ± 135	619 ± 116 (1.0)	902 ± 188 (1.5)
Italy (Ginosa)			
<i>T</i> (°C)	18.2 ± 1.1	21.0 ± 2.0 (1.1)	24.5 ± 1.2 (1.3)
Rainfall (mm per year)	614 ± 128	616 ± 121 (1.0)	894 ± 182 (1.5)
Spain (S13-hi)			
<i>T</i> (°C)	12.4 ± 0.9	14.9 ± 1.7 (1.2)	17.9 ± 4.4 (1.4)
Rainfall (mm per year)	509 ± 134	472 ± 99 (0.9)	660 ± 125 (1.3)
Spain (Prades)			
<i>T</i> (°C)	16.3 ± 0.9	18.8 ± 1.8 (1.2)	21.9 ± 0.9 (1.3)
Rainfall (mm per year)	489 ± 130	471 ± 99 (1.0)	639 ± 122 (1.3)
Spain (S14)			
<i>T</i> (°C)	16.8 ± 1.0	19.5 ± 0.5 (1.2)	23.1 ± 1.0 (1.4)
Rainfall (mm per year)	459 ± 78	475 ± 104 (1.0)	724 ± 136 (1.6)

<sup>a</sup> Mean annual values ± S.D. of the period. The values shown in the parenthesis represent the ratio with respect to current values (1990–1999).

Photosynthesis is estimated with Farquhar's equations (Farquhar and Von Caemmerer, 1982). Stomatal conductance uses Leuning's approach which assumes that an equilibrium is reached with photosynthetic capacity and light availability (Leuning, 1995). Leaf temperature is determined based on leaf energy balance (Gates, 1980) and transpiration estimations use the Penman–Monteith equation (Monteith, 1965; Jarvis and McNaughton, 1986).

Phenology, i.e. seasonal plant activity driven by environmental factors, results from a combination of two components. The first is the stage of annual development, which is modulated by the effect of the increase in temperatures on frost dehardening (according to the temperature sum approach, see Leinonen, 1997), and the decrease in temperatures on hardening, i.e. assuming that frost temperatures reduce or reverse

the development. In addition, seasonal photosynthetic capacity incorporates the Pelkonen and Hari (1980) approach, which introduces a factor *K* (ranging from 0 to 1 depending of the stage of annual development). This factor multiplies the value of *V*<sub>cmax</sub> and *J*<sub>max</sub> used in Farquhar's equations (Leinonen, 1997). The second component acts under drought conditions: when water availability is lower, which in Mediterranean conditions usually coincides with a rise in temperatures. Under such circumstances stomatal conductance is reduced according to Leuning's equation, and consequently gas exchange. At this point, when leaf respiration is higher than photosynthesis and mobile carbon exhausted, a number of leaves are shed until the negative value of the carbon balance is offset. Both deciduous and evergreen trees have the two components. Evergreen trees produce new leaves when

Table 3

Management criteria by fixing stand density (stems  $\text{ha}^{-1}$ ) at different stand ages (years) with the thinning interventions (I) according to the performed management schedule (MS)<sup>a</sup>

Stand age when (I) (years)	Standing trees left after (I) (stems $\text{ha}^{-1}$ )			
	<i>Pinus</i> ssp.		<i>Q. ilex</i> and <i>F. sylvatica</i>	
	MS of 20 years	MS of 40 years	MS of 20 years	MS of 40 years
20			6500	6500
30	2750	2750		
40			5500	
50	2250			
60			4500	4500
70	1750	1750		
80			3500	
90	1225			
100			2500	2500
110	750	750		
120			1500	
130	750			
140			750	750

<sup>a</sup> Initial stem densities were 3000 stems  $\text{ha}^{-1}$  in *Pinus* stands and 8000 stems  $\text{ha}^{-1}$  in *Fagus* and *Quercus* stands.

photosynthesis has recharged mobile carbon expended in winter to maintain the living biomass. Deciduous trees unfold leaves when the stage of development imposes conditions for photosynthesis at 90% of optimal (i.e.  $K > 0.9$ ), then leaf unfolding occurs in 10 days (arbitrary value, but matching observed time for unfolding). Then stored mobile carbon is, as in evergreens, used to build up new leaves. As in evergreens, new flushes may occur when mobile carbon pools are replenished. Leaf fall occurs gradually when day length is decreasing and the stage of development imposes values of photosynthesis lower than 95% of optimal conditions ( $K < 0.95$ ). As the stage of development decreases, leaf fall rate is increased.

Autotrophic respiration is separated into maintenance and growth respiration. Maintenance respiration rates depend on temperature according to a  $Q_{10}$  approach (which is estimated in each site from available data). Growth respiration is assumed to be 32% of the fraction of available carbohydrates for growth (i.e. a constant efficiency of 0.68 g of new tissue  $\text{g}^{-1}$  of carbohydrate, based on Penning de Vries data,

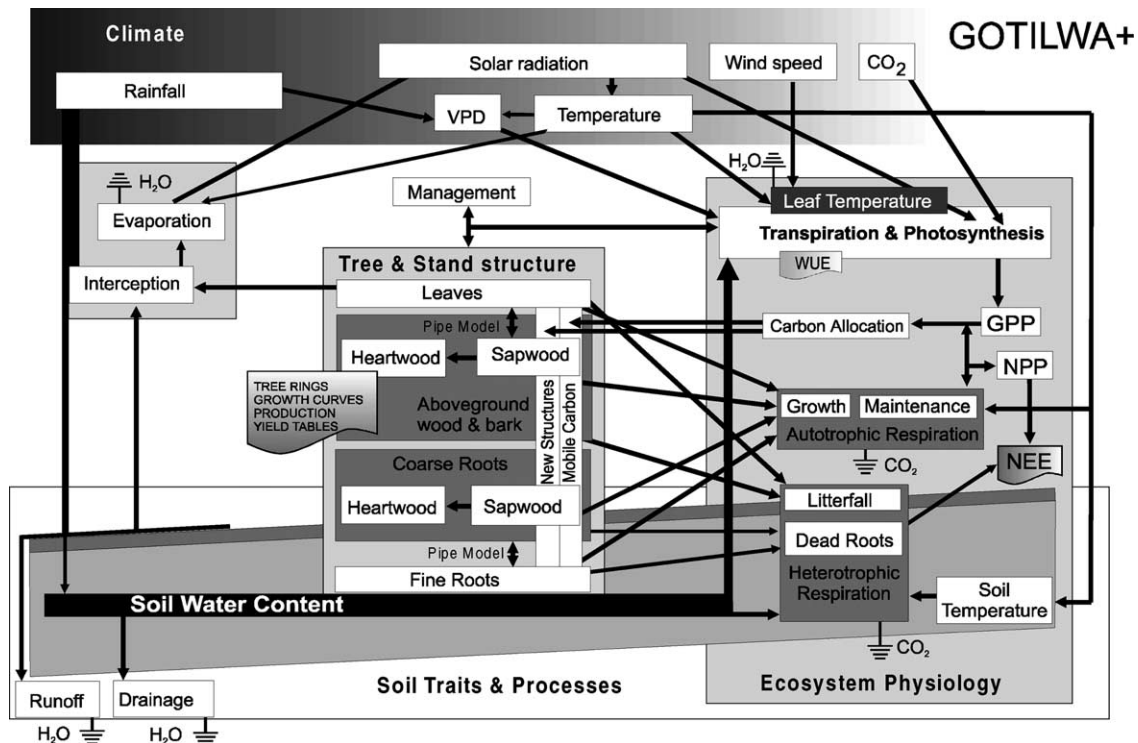


Fig. 1. General scheme on how the processes are interrelated in the GOTILWA+ model.

unpublished). NPP is allocated first to the formation of new leaves and fine roots to compensate their turnover. The remainder is allocated to the pool of mobile carbon in leaves and woody tissues. Any surplus is invested in new tissues (leaves, fine roots and sapwood) according to the pipe model (Shinozaki et al., 1964). Soil is divided into two layers, namely an organic and an inorganic horizon. Soil organic matter (SOM) is recognised to originate from leaves, branches, stems and reproductive organs aboveground, and from coarse and fine roots belowground. SOM decomposition is dependent on soil temperature and soil moisture. Tree mortality occurs when carbon balance is negative and the mobile carbon of the tree is exhausted. All calculations are performed for each DBH size class. Model parameterisation was done in close collaboration with the EUROFLUX project (Valentini, 1999; Aubinet et al., 2000), supplemented with more recent experimental data (López et al., 1997; Medlyn and Jarvis, 1997; Jarvis, 1998; Rodà et al., 1999; Kramer et al., in press). Comparison of model predictions were made with flux data (to evaluate seasonal predictions) and long-term growth obtained from permanent plots. This checking was performed at EUROFLUX sites as part of the model evaluation in LTEEF-II (see Kramer et al., 2001, in press), similarly to other model evaluations found in the literature (see for instance Aber et al., 1996; Law et al., 2000; Williams et al., 2001). Since no EUROFLUX site was available for *Q. ilex*, measured data from experimental plots in Prades (NE Spain) was used for this species. In this case, leaf fall model predictions were checked using aggregated monthly leaf litterfall data (1982–1989 period) as well as wood increment based on repeated measurements on stem diameter (see Gracia et al., 1999b).

### 2.3. Evaluated variables

The model outputs were integrated on yearly time steps since the aim of this analysis was to look at long-term effects of climate change. We focused the results on outputs of the following model variables: maximum projected leaf area index (LAI,  $\text{m}^2 \text{m}^{-2}$ ), mean leaf life span (MLLS, average duration of leaves in years and days for evergreen and deciduous species, respectively), gross primary production (GPP, Mg DW biomass  $\text{ha}^{-1}$  per year), net primary production (NPP,

Mg DW biomass  $\text{ha}^{-1}$  per year, i.e. net carbon assimilation rate per unit ground area), wood production (Wood P, Mg DW wood biomass  $\text{ha}^{-1}$ , i.e. the net carbon assimilation rate per unit of ground area allocated into wood) and final wood yield (FWY, Mg DW wood biomass  $\text{ha}^{-1}$ , i.e. the amount of aboveground wood biomass that would be harvested at the end of the simulated period (140 years) in different soil conditions and management criteria).

## 3. Results

### 3.1. Leaf compartment

The effects of climate change scenarios on the leaf compartment are presented in Table 4. Results of GOTILWA+ show that maximum LAI tends to increase favoured by the increase of atmospheric  $\text{CO}_2$  concentration, particularly in sites where rainfall is relatively high. This tendency vanishes by reaching steady values or even lower values in warmer sites as is shown by *P. halepensis* in S14 and Ginosa, where the highest temperatures are projected. The increase in temperature strongly influences MLLS. This effect is the opposite in deciduous trees, i.e. *F. sylvatica* in this study, as compared to evergreen trees, for both *Q. ilex* and *Pinus* species. According to the model projection, MLLS of *F. sylvatica* increases with climate change, i.e. LLS and, thus, the duration of the growing season becomes longer. This longer growing season is promoted by the effect of the increase in temperature on the stage of development during the year (see explanations on model phenology described earlier), which generates an earlier leaf unfolding but also a delay of leaf fall. In S11-hi, the average values of *F. sylvatica* leaf unfolding is advanced from Julian days 74 (1990–1999 period, current) to 36 and 40 in the periods 2040–2049 and 2090–2099, respectively. Leaf fall is predicted to move from Julian days 324 to 338 and 340 (period 2040–2049 and 2090–2099, respectively). In S12-hi, these values showed even more differences. *F. sylvatica* leaf unfolding at this site is shifted from Julian days 42 (current) to 27 and 7 (period 2040–2049 and 2090–2099, respectively) and leaf fall from Julian days 328 (current) to 348 and 359 (period 2040–2049 and 2090–2099, respectively).

Table 4

Mean of maximum annual values of simulated LAI and MLLS, averaged over three decades: 1990–1999, 2040–2049 and 2090–2099, from the simulated period 1961–2100 at each site, using a soil depth of 40 cm<sup>a</sup>

	1990–1999	2040–2049	2090–2099
<i>F. sylvatica</i> (S11-hi)			
LAI (m <sup>2</sup> m <sup>-2</sup> )	4.7 ± 1.1	7.0 ± 1.5 (1.5)	8.6 ± 1.3 (1.8)
MLLS (days)	251 ± 40	303 ± 45 (1.2)	301 ± 41 (1.2)
<i>F. sylvatica</i> (S12-hi)			
LAI (m <sup>2</sup> m <sup>-2</sup> )	4.7 ± 1.5	6.8 ± 1.3 (1.4)	8.8 ± 0.9 (1.9)
MLLS (days)	287 ± 58	323 ± 38 (1.1)	353 ± 25 (1.2)
<i>Q. ilex</i> (S12-lo)			
LAI (m <sup>2</sup> m <sup>-2</sup> )	3.7 ± 0.4	4.2 ± 0.1 (1.1)	4.8 ± 0.2 (1.3)
MLLS (year)	2.0 ± 0.2	1.7 ± 0.2 (0.8)	1.4 ± 0.1 (0.7)
<i>Q. ilex</i> (Prades)			
LAI (m <sup>2</sup> m <sup>-2</sup> )	3.5 ± 0.3	4.1 ± 0.1 (1.2)	4.6 ± 0.1 (1.3)
MLLS (year)	2.0 ± 0.2	1.7 ± 0.1 (0.9)	1.4 ± 0.1 (0.7)
<i>Q. ilex</i> (S14)			
LAI (m <sup>2</sup> m <sup>-2</sup> )	3.1 ± 0.2	4.3 ± 0.1 (1.4)	4.9 ± 0.2 (1.5)
MLLS (year)	1.8 ± 0.2	1.5 ± 0.1 (0.9)	1.3 ± 0.1 (0.7)
<i>P. pinaster</i> (S14)			
LAI (m <sup>2</sup> m <sup>-2</sup> )	2.0 ± 0.1	3.3 ± 0.1 (1.7)	4.4 ± 0.1 (2.2)
MLLS (year)	2.0 ± 0.1	1.8 ± 0.1 (0.9)	1.4 ± 0.1 (0.7)
<i>P. halepensis</i> (S14)			
LAI (m <sup>2</sup> m <sup>-2</sup> )	3.2 ± 0.3	5.5 ± 0.2 (1.7)	5.3 ± 0.2 (1.7)
MLLS (year)	2.8 ± 0.2	2.4 ± 0.1 (0.8)	1.8 ± 0.2 (0.6)
<i>P. halepensis</i> (Ginosa)			
LAI (m <sup>2</sup> m <sup>-2</sup> )	4.4 ± 0.3	4.1 ± 0.2 (0.9)	3.9 ± 0.2 (0.9)
MLLS (year)	2.5 ± 0.3	2.1 ± 0.3 (0.8)	1.5 ± 0.1 (0.6)
<i>P. sylvestris</i> (S13-hi)			
LAI (m <sup>2</sup> m <sup>-2</sup> )	2.5 ± 0.2	3.2 ± 0.2 (1.3)	4.1 ± 0.3 (1.7)
MLLS (year)	1.9 ± 0.1	1.6 ± 0.2 (0.8)	1.2 ± 0.1 (0.6)

<sup>a</sup> No management is applied. Mean annual values ± S.D. of the period. The values shown in the parenthesis represent the ratio with respect to current values (1990–1999).

Contrastingly, the increase in temperature has an opposite effect on evergreen species according to the model projections. MLLS of *Q. ilex* and *Pinus* species are reduced in accordance with the projected increase in temperature at each site provided by climate scenarios. The increase of leaf biomass combined with the decrease of MLLS signifies that leaf biomass turnover is accelerated and, thus, carbon is invested into this compartment.

### 3.2. Production

The effects of climate change scenarios on production are presented in Table 5. In all sites and climate

scenarios, species show an increase in GPP, NPP as well as in most of the cases, of Wood P. These increased values reflect the positive effect of increasing atmospheric CO<sub>2</sub> concentration but are also influenced by temperature and rainfall. Rainfall tends to increase in most cases (see ratios in Table 2), thus, increasing soil water content and then also stomatal conductance, therefore, contributing to the positive effect on production. This is not the case for *P. sylvestris* Wood P at S13-hi in the middle of the simulated period due to the decrease in rainfall at this time. When drought takes place soil water content is reduced, as is stomatal conductance and then carbon uptake. Temperature increase has different

Table 5

Mean annual values of simulated GPP, NPP and Wood P averaged over three decades: 1990–1999, 2040–2049 and 2090–2099, from the simulated period 1961–2100 at each site<sup>a</sup>

	1990–1999 (Mg ha <sup>-1</sup> per year)	2040–2049 (Mg ha <sup>-1</sup> per year)	2090–2099 (Mg ha <sup>-1</sup> per year)
<i>F. sylvatica</i> (S11-hi)			
GPP	39.2 ± 3.5	44.8 ± 3.1 (1.1)	48.9 ± 3.2 (1.2)
NPP	13.9 ± 2.0	17.1 ± 2.0 (1.2)	18.8 ± 1.7 (1.4)
Wood P	0.4 ± 0.5	1.1 ± 1.2 (2.8)	2.1 ± 1.5 (5.5)
<i>F. sylvatica</i> (S12-hi)			
GPP	35.1 ± 6.6	49.4 ± 6.8 (1.4)	61.5 ± 2.8 (1.8)
NPP	12.1 ± 4.5	17.9 ± 4.4 (1.5)	21.2 ± 3.6 (1.7)
Wood P	1.3 ± 1.1	2.3 ± 0.9 (1.8)	5.0 ± 1.8 (4.0)
<i>Q. ilex</i> (S12-lo)			
GPP	37.6 ± 6.2	50.5 ± 5.4 (1.3)	68.1 ± 5.3 (1.8)
NPP	8.0 ± 5.1	10.5 ± 4.0 (1.3)	11.9 ± 5.9 (1.5)
Wood P	2.3 ± 1.1	3.1 ± 1.7 (1.3)	2.5 ± 1.9 (1.1)
<i>Q. ilex</i> (Prades)			
GPP	39.8 ± 7.2	53.3 ± 6.7 (1.3)	73.0 ± 5.7 (1.8)
NPP	10.2 ± 5.5	11.4 ± 5.1 (1.1)	15.5 ± 5.6 (1.4)
Wood P	3.1 ± 1.4	3.2 ± 1.3 (1.0)	4.3 ± 2.1 (1.4)
<i>Q. ilex</i> (S14)			
GPP	32.0 ± 4.0	51.0 ± 3.5 (1.6)	68.3 ± 1.6 (2.1)
NPP	9.1 ± 4.1	12.1 ± 4.0 (1.3)	12.9 ± 3.8 (1.4)
Wood P	2.7 ± 0.9	2.8 ± 1.0 (1.1)	3.2 ± 1.3 (1.2)
<i>P. pinaster</i> (S14)			
GPP	18.2 ± 2.5	32.8 ± 3.5 (1.8)	60.0 ± 3.4 (3.3)
NPP	9.3 ± 2.0	16.3 ± 2.3 (1.7)	29.5 ± 2.2 (3.2)
Wood P	3.3 ± 1.1	5.8 ± 1.6 (1.8)	8.8 ± 2.1 (2.7)
<i>P. halepensis</i> (S14)			
GPP	21.2 ± 3.1	45.6 ± 2.9 (2.1)	57.7 ± 1.8 (2.7)
NPP	7.5 ± 2.7	14.1 ± 2.5 (1.9)	15.8 ± 3.2 (2.1)
Wood P	2.6 ± 1.0	3.5 ± 1.3 (1.3)	4.2 ± 1.9 (1.6)
<i>P. halepensis</i> (Ginosa)			
GPP	27.6 ± 3.6	37.3 ± 3.5 (1.4)	49.7 ± 2.8 (1.8)
NPP	5.5 ± 2.6	10.3 ± 2.5 (1.9)	12.4 ± 3.1 (2.3)
Wood P	0.9 ± 0.9	3.1 ± 1.5 (3.6)	2.7 ± 1.8 (3.1)
<i>P. sylvestris</i> (S13-hi)			
GPP	21.9 ± 5.1	32.4 ± 4.7 (1.5)	54.5 ± 5.6 (2.5)
NPP	8.6 ± 3.5	12.2 ± 3.0 (1.4)	20.2 ± 3.9 (2.3)
Wood P	2.4 ± 1.6	2.3 ± 1.55 (0.9)	5.0 ± 2.3 (2.1)

<sup>a</sup> Soil depth: 40 cm. No management is applied. Mean annual values ± S.D. of the period. The values shown in the parenthesis represent the ratio with respect to current values (1990–1999).

consequences for production. In *F. sylvatica*, a longer growing period favours a higher production, particularly when water is not limiting. On the other hand, as mentioned above, *Q. ilex* and *Pinus* species spent more carbon in maintaining and producing leaves to replace those lost in more rapid turnover. Such a replacement of leaves increases growth respiration,

in addition increasing temperatures results in higher maintenance respiration. Nevertheless, the final production–respiration balance appears positive according to these projections. The ratios NPP/GPP (data not shown in Table 5) are relatively low, ranging from 0.51 for *P. pinaster* in S14 to 0.20 for *P. halepensis* in Ginosa.



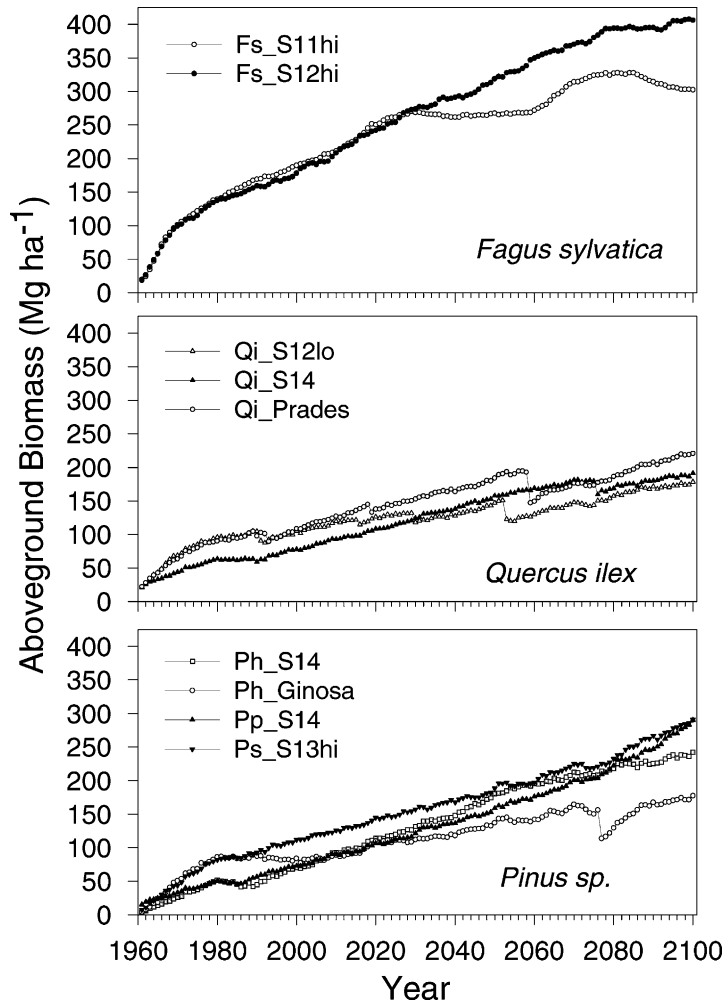


Fig. 2. Standing aboveground biomass (Mg ha<sup>-1</sup>) over the simulated period 1961–2100. Upper panel shows *F. sylvatica* (Fs) at sites S11-hi and S12-hi; central panel shows *Q. ilex* (Qi) at sites S12-lo, S14 and Prades; and lower panel shows *Pinus* sp. (Ph: *P. halepensis*, Pp: *P. pinaster* and Ps: *P. sylvestris*) at sites S13-hi, S14 and Ginosa. Soil depth 40 cm. No management is applied.

### 3.3. Aboveground biomass

Fig. 2 shows the evolution of aboveground biomass over the simulated period for the different species and site conditions when no management is applied. Results of the simulations for *F. sylvatica* show the higher standing biomass. The sustained increase of standing biomass is in agreement with the results of production discussed earlier. Standing biomass in site S12-hi is favoured by the increased CO<sub>2</sub> concentration and temperature, as well as rainfall, and so is soil water content and stomatal conductance at the end of the

period. The simulation at site S11-hi is slightly different. In this case decreased rainfall in the middle of the simulated period constrains the increase of standing biomass during the second half of the period. Standing biomass of *Q. ilex* is clearly smaller than the one of *F. sylvatica*. *Q. ilex* forests are located in sites where rainfall distribution and amounts are typically Mediterranean and, thus, their present growth is already constrained by water. During the first half of the simulation period, the driest site, S14, supports a smaller amount of biomass. It is worth noting that the climate scenarios used for this species (S12-lo, S14,

and Prades) presented an extreme drought throughout 1980–1990 that is clearly reflected by aboveground biomass. During this decade standing biomass reached a relative plateau or even showed slightly decreasing values due to tree mortality. Tree mortality occurred when respiration became higher than GPP and reserves of mobile carbon were exhausted (i.e. negative carbon balance cannot be compensated by reserves). Later on, *Q. ilex* standing biomass continued to grow in all cases, but this was sometimes reduced by tree mortality events. *Q. ilex* standing biomass at site S14 became more similar to the other two sites because of the relative increase in rainfall. Current climatic conditions strongly constrain growth there.

According to simulations for pine species (lower panel, Fig. 2), *P. halepensis* growth appears very constrained by the climate change scenario in Ginosa. This site has the highest temperature of all sites and it is the only place where simulation results give a reduction of LAI and MLLS. Therefore, it is not surprising that *P. halepensis* standing biomass shows lower values after the middle part of the simulated period. Its biomass increase over the simulated period was very slow. In S14, aboveground biomass of *P. halepensis* and *P. pinaster* showed a similar plateau as mentioned above for *Q. ilex*, but later on the increase in rainfall was reflected by sustained growth until the end of the simulation. Simulation results for *P. sylvestris* in S13-hi showed an increase in standing biomass favoured by relatively lower temperatures than at the other sites.

### 3.4. Effects of thinning cycle and soil depth on final wood yield

The effect of thinning cycle length and soil depth on FWY is shown in Table 6. In general, as expected, under the assumption of deeper soils FWY is increased. Deeper soils lead to an improved water balance that promotes higher stomatal conductance and, thus, transpiration, photosynthesis and growth. Therefore, deeper soils may speed up growth. When this happens, a reduction of stored mobile carbon in larger trees may occur, and they may show slightly lower values of standing biomass in deeper soils at that moment. On the other hand, as the harvest cycle is shortened the FWY becomes larger because a larger

Table 6

Simulated FWY ( $\text{Mg ha}^{-1}$ ) after the 1961–2100 period, growing the forest at two soil depth (20 and 40 cm) and three management cycles (20, 40 years and no management until the end of the period, 140 years)

Site and tree species	Soil depth (cm)	Management cycle (years; FWY ( $\text{Mg ha}^{-1}$ ))		
		20	40	140
Italy (S11-hi)	20	459	384	241
<i>F. sylvatica</i>	40	468	380	227
Italy (S12-hi)	20	503	426	290
<i>F. sylvatica</i>	40	600	449	305
Italy (S12-lo)	20	205	174	117
<i>Q. ilex</i>	40	259	225	134
Spain (Prades)	20	249	238	161
<i>Q. ilex</i>	40	298	270	166
Spain (S14)	20	224	197	134
<i>Q. ilex</i>	40	243	212	143
Spain (S14)	20	236	155	197
<i>P. pinaster</i>	40	260	174	218
Spain (S14)	20	216	148	177
<i>P. halepensis</i>	40	245	170	182
Italy (Ginosa)	20	172	130	116
<i>P. halepensis</i>	40	202	143	133
Spain (S13-hi)	20	283	163	207
<i>P. sylvestris</i>	40	303	210	218

fraction of the dying trees can be salvage and, thus, less woody debris is decomposed on the site due to tree mortality. This mortality occurs after stressful periods, either because of high temperatures or because of drought.

## 4. Discussion

The climate change scenarios analysed in this study have a general positive effect on forest growth. It can be stated that this positive effect obtained by GOTILWA+ is explained by the increased atmospheric  $\text{CO}_2$  concentration combined with the increased rainfall amount in the region. Thus, according to the model results, the positive effects of higher atmospheric  $\text{CO}_2$  concentration and rainfall would be sufficient to compensate for the increased respiration costs and the increased investment on leaves and fine

roots turnover, which are driven by the projected rise of ambient temperature, providing that nutrients are available and do not limit tree growth.

It is well known that temperature has a strong effect on plant respiration. Carey et al. (1997) did not find evidence of respiratory acclimation in arid zones. They suggested that the potential increase in aboveground carbon gain due to enhanced photosynthetic rates may be partially offset by increases in maintenance respiration in large trees growing in CO<sub>2</sub> enriched atmospheres but under predicted increases in temperature and aridity. Direct effects of rising atmospheric CO<sub>2</sub> concentration on down-regulating respiration rates are not included in this model analysis, but if they exist, they may be small (see Amthor, 2000).

Positive effects of increased atmospheric CO<sub>2</sub> concentration on growth have been found in experimental studies (e.g. Lin et al., 1999), and reported in some meta-analysis compilations (see Curtis and Wang, 1998; Medlyn et al., 1999). Curtis and Wang (1998) did not find any consistent evidence of photosynthetic acclimation to CO<sub>2</sub> enrichment and no significant effect on stomatal conductance. Medlyn et al. (1999) found some evidence of down-regulation on photosynthesis, accounting for 10–20% reduction, mainly explained by leaf nitrogen concentration decrease and its decreased use efficiency. However, the stimulatory effect of CO<sub>2</sub> enrichment was shown to be very important in any case. When considering such long-term simulations, perhaps nitrogen will play a more important role in the future by down-regulating the photosynthetic response of trees. Since GOTILWA+ does not include nutrient dynamics in the present version (i.e. does not take into account these potential limitations to forest growth), model predictions must be regarded as valid only for forest stands growing in a steady state of nutrient availability. Nutrient limitations and particularly nitrogen will reduce photosynthesis, as well as will limit the maximum LAI, which was simulated rather high in this study for *F. sylvatica* at the end of the projected period (see Table 2). Consequently, by including nutrient limitations, and particularly nitrogen, our predictions would likely improve as shown in other models (see for instance forest-BGC, Running, 1994). However, at present nutrients do not limit growth (Mayor and Rodà, 1992) as water does in the Mediterranean region. Furthermore, experimental work in controlled environment chambers have shown

that positive effects on *Q. ilex* growth promoted by increased CO<sub>2</sub> concentration tend to vanish when water stress is increased, or that it only compensates for the negative effects of decreased water (López et al., 1997). Hence, rainfall regimes other than those projected with the climate scenarios applied may alter the magnitude of the positive effects of climate change foreseen in the present analysis.

GOTILWA+ does not assume a constant ratio of NPP/GPP as it has been suggested in other analysis (see Gifford, 1994; Landsberg and Waring, 1997; Waring et al., 1998). Furthermore, the ratios in our predictions are rather low compared to the ratios suggested by Waring et al. (1998), with values around 0.47 ( $\pm 0.04$ S.D.), mainly obtained under temperate climatic conditions. The lower values of the ratio predicted by GOTILWA+ model in this study can be explained by the high maintenance respiration rates due to high temperatures along the time series of the scenario, as well as to high growth respiration rates promoted by turnover of leaves and fine roots. In general, summer drought induces a dramatic mortality of fine roots and subsequently a high renovation when conditions become more humid. These model predictions are in agreement with field measurements on fine root dynamics under Mediterranean conditions (López et al., 2001, in press).

It is important to note that no single climate change scenario for a site/area is likely to be definitive, and other situations may change completely the picture. For instance, changing the seasonal patterns of rainfall distribution may have a crucial importance in the Mediterranean type climate and even a higher total annual rainfall does not always mean a better water status during summer. From that point of view, it is worth pointing out that the climate scenarios used in the present analysis did not predict changes in the relative distribution of precipitation between summer and winter over the projected period. However, according to the scenarios used, our results show that temperature and rainfall constrain growth within certain periods. If rainfall increases in the future, a positive effect on growth is very likely. Conversely, if rainfall becomes less, these positive effects of climate change on forest eco-physiological functioning may be offset. *P. sylvestris* shows structural adaptations rather than water conservation strategies over a latitudinal gradient, ranging from wet to dry climates

(Palmroth et al., 1999). This may imply that *P. sylvestris* trees currently living in the region would simply acclimate their structure according to new conditions, rather than promote a more efficient use of water. This result suggests some structural plasticity according to environmental conditions. On the other hand, the ability of plants to tolerate extremely high temperatures is remarkable, provided that enough water is available (Kirschbaum, 2000). Thus, future rainfall patterns are crucial in assessing climate change induced stress and disturbance impact analyses. Furthermore, if temperature increase is not matched by an increase in water availability, in the long-term its negative effects may not even be compensated by an increase in CO<sub>2</sub>.

The increase in temperature promotes an increase in the duration of the growing season of *F. sylvatica* forests and a decrease in LLS for evergreen ones. The dramatic change in the duration of *F. sylvatica*'s growing season may be arguable, as there is no restriction applied to the plasticity of this species in the model. Previous analyses have shown that trees have a certain amount of plasticity to accommodate such a change (Kramer, 1995). According to Kramer's analysis (Kramer, 1995, 1996) *F. sylvatica* may advance its leaf unfolding, while leaf fall remains essentially the same. In S11-hi this advance accounts at the end of the simulation for slightly more than 1 month, and leaf fall is delayed around 15 days. S12-hi shows an even higher plasticity, which may need further checking with the model parameters and the genotypes living in this southern European latitude. The pattern of these changes in leaf phenology of *F. sylvatica* seems logical, but the absolute values themselves need further analysis. Menzel and Fabian (1999) showed how the growing season was lengthened in Europe from 1959 to 1993, by 10.8 days on average—advanced spring of 6 days and delayed autumn of 4.8 days. They related this change with the increase in temperature. However, most of the observational data were obtained in temperate and cold environmental conditions. In another study, under warmer conditions and lower latitudes, Peñuelas et al. (in press) also found significant changes in leaf unfolding and fall of several deciduous species in Cardadeu field station (Catalonia NE Spain). In this study, they analysed a long-term data set, from 1952 to 2000, of phenological observations on several plant

and animal species from the area. Concerning deciduous plants, on average leaves unfold 20 days earlier and fall 13 days later at the end of the period. At the same time they show how temperature has become 1.4 °C warmer over the period in the area, and how phenological changes are highly correlated with these changes in temperature. These data show impressive biological effects of climate warming in the Mediterranean plants and despite *F. sylvatica* was not present in Peñuelas et al. analysis, their results are consistent with our projections in the area. Furthermore, the scenarios used in our analysis predicted much higher temperature increase (see average values shown in Table 2).

In relation to evergreen species, there is empirical evidence that lower values of *Q. ilex* MLLS occur in warmer areas, as shown in the Iberic Peninsula (Gracia et al., 2001). This type of response may lead to a larger investment of carbon allocation to the canopy with increasing temperatures, which would be more important when a larger amount of leaf biomass is sustained. Investment of primary production in leaf turnover represents an important proportion in Mediterranean ecosystems. For instance, in stands of *Q. ilex* from Montseny (NE Spain) litter fall accounts for about 57% of NPP, and only 43% of NPP is allocated to stem growth (Mayor and Rodà, 1994). Forest management strategies will play an important role in the future to achieve objectives such as maximising forest CO<sub>2</sub> uptake from the atmosphere. This is suggested by our results as well as by other studies (see Lindner, 2000). This author highlighted the influence of management strategies on forest growth, and the need to adapt management strategies to expected changes in climate. Furthermore, management may be very important to sustain Mediterranean forest ecosystems. It may reduce respiring biomass and, thus, increase the water available to each tree, which could be important to sustain the functioning of forest ecosystems, especially to overcome severe periods of drought and high temperatures (Gracia et al., 1999a).

## 5. Conclusions

These simulations suggest that Mediterranean species may be positively affected by climate change if future conditions provide better conditions of rainfall

than current ones. If this was not the case, the negative effect of the increase in temperature may become stronger, and not compensated for the positive effects promoted by increasing atmospheric CO<sub>2</sub> concentration. Leaf phenology may be strongly modified by climate change (Kramer, 1995; Peñuelas et al., in press). Deciduous species may increase the duration of their growing season (*F. sylvatica* in our analysis). Nevertheless, further analysis of the plasticity of such species is needed to evaluate the actual ability of living trees to modify their growth performance. In this analysis, it is also shown that evergreen trees will increase their leaf turnover rate. Thus, it is important to pay closer attention to the effect of climate change on canopy functioning in terms of primary production invested in maintaining such a forest compartment, i.e. sustained leaf biomass and its turnover. New conditions may constrain the viability of some forest types if they need to invest too much carbon amounts into this compartment. Management could be a key tool to improve growing conditions when facing new climatic conditions.

## Acknowledgements

The LTEEF-II project is funded under the 4th Framework Programme of the Environment and Climate Research Programme of the European Union (ENV4-CT-97-0577). Additional funding has been provided by the Spanish Ministry of Education and Culture. We thank Marcus Erhard from Potsdam Institute for Climate Impact Research (PIK) for providing the climate scenarios, and the other colleagues of the LTEEF project for sharing the interest on this project as well as for exchanging experience and information. We are grateful to Julie Bygraves for checking the English as well as to Jorge Meave, Koen Kramer and two anonymous referees who provided useful comments on the manuscript.

## References

- Aber, J.D., Reich, P.B., Goulden, M.L., 1996. Extrapolating leaf CO<sub>2</sub> exchange to the canopy: a generalized model of forest photosynthesis compared with measurements by eddy correlation. *Oecologia* 106, 257–265.
- Amthor, J.S., 2000. Direct effect of elevated CO<sub>2</sub> on nocturnal in situ leaf respiration in nine temperate deciduous tree species is small. *Tree Physiol.* 20, 139–144.
- Aubinet, M., Grelle, A., Ibrom, A., Rannik, Ü., Moncrieff, J., Foken, T., Kowalski, A.S., Martin, P.H., Berbigier, P., Bernhofer, C., Clement, R., Elbers, J., Granier, A., Grünwald, T., Morgenstern, K., Pilegaard, K., Rebmann, C., Snijders, W., Valentini, R., Vesala, T., 2000. Estimates of the annual net carbon and water exchange of European forests: the EURO-FLUX methodology. *Adv. Ecol. Res.* 30, 113–175.
- Bürger, G., 1997. On the disaggregation of climatological means and anomalies. *Climate Res.* 8, 183–194.
- Campbell, G.S., 1986. Extinction coefficients for radiation in plan canopies calculated using an ellipsoidal inclination angle distribution. *Agric. For. Meteorol.* 36, 317–321.
- Carey, E.V., Callaway, R.M., DeLucia, E.H., 1997. Stem respiration of ponderosa pines grown in contrasting climates: implications for global change. *Oecologia* 111, 19–25.
- Curtis, P.S., Wang, X., 1998. A meta-analysis of elevated CO<sub>2</sub> effects on woody plant mass, form, and physiology. *Oecologia* 113, 299–313.
- Erhard, M., Lindner, M., Cramer, W., 2001. Climate data. In: Kramer, K., Mohren, G.M.J. (Eds.), Long-term Effects of Climate Change on Carbon Budgets of Forests in Europe. ALTErrA Report 194, ALTErrA, Wageningen, The Netherlands, pp. 151–161.
- Farquhar, G.D., Von Caemmerer, S., 1982. Modeling of photosynthetic response to environment. In: Lange, O.L., Nobel, P.S., Osmond, C.B., Ziegler, H. (Eds.), *Encyclopedia of Plant Physiology: Physiological Plant Ecology II, Water Relations and Carbon Assimilation*, Vol. 12B. Springer, Berlin, pp. 549–587.
- Gates D.M., 1980. *Biophysical Ecology*. Springer, New York.
- Gifford, R.M., 1994. The global carbon cycle: a viewpoint on the missing sink. *Aust. J. Plant Physiol.* 21, 1–15.
- Gracia, C.A., Sabaté, S., Martínez, J.M., Albeza, E., 1999a. Functional responses to thinning. In: Rodà, F., Retana, J., Gracia, C.A., Bellot, J. (Eds.), *Ecology of Mediterranean Evergreen Oak Forests: Ecological Studies*, Vol. 137. Springer, Berlin, pp. 229–338.
- Gracia, C.A., Tello, E., Sabaté, S., Bellot, J., 1999b. GOTILWA+: an integrated model of water dynamics and forest growth. In: Rodà, F., Retana, J., Gracia, C.A. and Bellot, J. (Eds.), *Ecology of Mediterranean Evergreen Oak Forests: Ecological Studies*, Vol. 137. Springer, Berlin, pp. 163–178.
- Gracia, C.A., Sabaté, S., López, B., Sánchez, A., 2001. Presente y futuro del bosque mediterráneo: balance de carbono, gestión forestal y cambio global. In: Zamora, R., Pugnaire, F.I. (Eds.), *Ecosistemas Mediterráneos. Análisis funcional. Colección textos universitarios* 32. CSIC, AEET, Spain, pp. 351–372.
- Houghton, J.T., Meira Filho, L.G., Bruce, J., Hoesung, L., Callander, B.A., Haites, E., Harris, N., Maskell, K., 1995. *Climate Change 1994: Radiative Forcing of Climate Change and an Evaluation of the IPCC IS92a Emission Scenarios*. Cambridge University Press, Cambridge, UK, 339 p.
- Hulme, M., Conway, D., Jones, P.D., Jiang, T., Barrow, E.M., Turney, C., 1995. Construction of a 1961–1990 European

- climatology for climate change modelling and impacts applications. *Int. J. Climatol.* 15, 1333–1363.
- Jarvis, P.G., 1998. European Forests and Global Change. The Likely Impacts of Rising CO<sub>2</sub> and Temperature. Cambridge University Press, Cambridge, UK.
- Jarvis, P.G., McNaughton, K.G., 1986. Stomatal control of transpiration: scaling up from leaf to region. *Adv. Ecol. Res.* 15, 1–49.
- Kirschbaum, M.U.F., 2000. Forest growth and species distribution in a changing climate. *Tree Physiol.* 20, 309–322.
- Kramer, K., 1995. Phenotypic plasticity of the phenology of seven European tree species in relation to climatic warming. *Plant Cell Environ.* 18, 93–104.
- Kramer, K., 1996. Phenology and Growth of European Trees in Relation to Climate Change. Thesis, Wageningen Agricultural University, The Netherlands, 210 pp.
- Kramer, K., 2001. Process-based models for scaling up to tree and stand level. In: Kramer, K., Mohren, G.M.J. (Eds.), Long-term Effects of Climate Change on Carbon Budgets of Forests in Europe. ALTErrA Report 194, ALTErrA, Wageningen, The Netherlands, pp. 61–78.
- Kramer, K., Mohren, G.M.J., 2001. Long-term Effects of Climate Change on Carbon Budgets of Forests in Europe. ALTErrA Report 194, Green World Research, Wageningen, The Netherlands, 290 pp.
- Kramer, K., Leinonen, I., Sabaté, S., 2001. Model evaluation. In: Kramer, K., Mohren, G.M.J. (Eds.), Long-term Effects of Climate Change on Carbon Budgets of Forests in Europe. ALTErrA Report 194, ALTErrA, Wageningen, The Netherlands, pp. 79–110.
- Kramer, K., Leinonen, I., Bartelink, H.H., Cienciala, E., Froer, O., Gracia, C.A., Hari, P., Kellomäki, S., Loustau, D., Magnani, F., Matteucci, G., Nissinen, A., Sabaté, S., Sánchez, A., Sonntag, M., Berbigier, P., Bernhofer, C., Dolman, A.J., Moors, E., Jans, W., Granier, A., Grünwald, T., Matteucci, G., Valentini, R., Vesala, T., Mohren, G.M.J., in press. Evaluation of six process-based forest growth models based on eddy-covariance measurements of CO<sub>2</sub> and H<sub>2</sub>O fluxes at six forest sites in Europe. *Global Change Biol.*
- Landsberg, J.J., Waring, R.H., 1997. A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. *For. Ecol. Manage.* 95, 209–228.
- Law, B.E., Waring, R.H., Anthoni, P.M., Aber, J.D., 2000. Measurements of gross and net ecosystem productivity and water vapour exchange of a *P. ponderosa* ecosystem, and an evaluation of two generalized models, and an evaluation of two generalized models. *Global Change Biol.* 6, 155–168.
- Leinonen, I., 1997. Frost Hardiness and Annual Development of Forest Trees Under Changing Climate. Ph.D. Thesis, Research Notes, Faculty of Forestry, University of Joensuu, 42 p.
- Leuning, R., 1995. A critical appraisal of a combined stomatal-photosynthesis model for C<sub>3</sub> plants. *Plant Cell Environ.* 18, 339–355.
- Lin, G., Adams, J., Farnsworth, B., Wei, Y., Marino, B.D.V., Berry, J.A., 1999. Ecosystem carbon exchange in two terrestrial ecosystem mesocosms under changing atmospheric CO<sub>2</sub> concentrations. *Oecologia* 119, 97–108.
- Lindner, M., 2000. Developing adaptive forest management strategies to cope with climate change. *Tree Physiol.* 20, 299–307.
- López, B., Sabaté, S., Ruiz, I., Gracia, C.A., 1997. Effects of elevated CO<sub>2</sub> and decreased water availability on Holm oak seedlings in controlled environment chambers. In: Mohren, G.M.J., Kramer, K., Sabaté, S. (Eds.), Impacts of Global Change on Tree Physiology and Forest Ecosystems: Forestry Sciences, Vol. 52, Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 125–133.
- López, B., Sabaté, S., Gracia, C.A., 2001. Annual and seasonal changes in fine root biomass of a *Quercus ilex* L. forest. *Plant and Soil* 230, 125–134.
- López, B., Sabaté, S., Gracia, C.A., 2001. Fine root longevity of *Quercus ilex*. *New Phytol.* 151, 437–441.
- Mayor, X., Rodà, F., 1992. Is primary production in Holm oak forests nutrient limited? A correlational approach. *Vegetatio* 99/100, 209–217.
- Mayor, X., Rodà, F., 1994. Effects of irrigation and fertilization on stem diameter growth in a Mediterranean Holm oak forest. *For. Ecol. Manage.* 68, 119–126.
- Medlyn, B.E., Jarvis, P.G., 1997. Integration of results from elevated-CO<sub>2</sub> experiments on European forest species: the ECOCRAFT project. In: Mohren, G.M.J., Kramer, K., Sabaté, S. (Eds.), Impacts of Global Change on tree Physiology and Forest Ecosystems: Forestry Sciences, Vol. 52, Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 273–279.
- Medlyn, B.E., Badeck, F.W., De Pury, D.G.G., Barton, C.V.M., Broadmeadow, M., De Angelis, P., Forstreuter, M., Jach, M.E., Kellomäki, S., Laitat, E., Marek, M., Philippot, S., Rey, A., Strassmeyer, J., Laitinen, K., Liozon, R., Portier, B., Roberntz, P., Wang, K., Jarvis, P., 1999. Effects of elevated [CO<sub>2</sub>] on photosynthesis in European forest species: a meta-analysis of model parameters. *Plant Cell Environ.* 22, 1475–1495.
- Menzel, A., Fabian, P., 1999. Growing season extended in Europe. *Nature* 397, 659.
- Mitchel, J.F.B., Johns, T.C., Gregory, J.M., Tett, S.F.B., 1995. Climate response to increasing levels of greenhouse gases and sulphate aerosols. *Nature* 376, 501–504.
- Mohren, G.M.J., Kramer, K., 1997. Simulation of direct effects of CO<sub>2</sub> and temperature increase on forest growth: the LTEEF project. In: Mohren, G.M.J., Kramer, K., Sabaté, S. (Eds.), Impacts of Global Change on Tree Physiology and Forest Ecosystems: Forestry Sciences, Vol. 52, Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 307–317.
- Mohren, G.M.J., Bartelink, H.H., Kramer, K., Magnani, F., Sabaté, S., Loustau, D., 2000. Modelling long-term effects of CO<sub>2</sub> increase and climate change on European forests, with emphasis on ecosystem carbon budgets. In: Ceulemans, R.J.M., Veroustraete, F., Gond, V., Van Rensbergen, J.B.H.F. (Eds.), Forest Ecosystem Modeling, Upscaling and Remote Sensing. SPB Academic Publishing BV, The Hague, The Netherlands, pp. 179–192.
- Monteith, J.L., 1965. Evaporation and environment. *Symp. Soc. Exp. Biol.* 19, 205–234.
- Mooney, H.A., 1983. Carbon-gaining capacity and allocation patterns of Mediterranean climate plants. In: Kruger, F.J.,

- Mitchel, D.T., Jarvis, J.U.M. (Eds.), Mediterranean Type Ecosystems: The Role of Nutrients. Springer, Berlin, pp. 103–119.
- New, M., Hulme, M., Jones, P.D., 2000. Representing twentieth century space–time climate variability. Part 2. Development of 1901–1996 monthly grids of terrestrial surface climate. *J. Climate* 13, 2217–2238.
- Palmroth, S., Berninger, F., Nikinmaa, E., Lloyd, J., Pulkkinen, P., Hari, P., 1999. Structural adaptation rather than water conservation was observed in Scots pine over a range of wet to dry climates. *Oecologia* 121, 302–309.
- Pelkonen, P., Hari, P., 1980. The dependence of the springtime recovery of CO<sub>2</sub> uptake in Scots pine on temperature and internal factors. *Flora* 169, 398–404.
- Peñuelas, J., Filella, I., Comas, P., in press. Changed plant and animal life cycles from 1952 to 2000 in the Mediterranean region. *Global Change Biol.*
- Rodà, F., Retana, J., Gracia, C.A., Bellot, J. (Eds.), 1999. Ecology of Mediterranean Evergreen Oak Forests: Ecological Studies, Vol. 137. Springer, Berlin.
- Running, S.W., 1994. Testing forest-BGC ecosystem process simulations across a climatic gradient in Oregon. *Ecol. Appl.* 4, 238–247.
- Sabaté, S., Gracia, C., 1994. Canopy nutrient content of a *Quercus ilex* L. forest: fertilization and irrigation effects. *For. Ecol. Manage.* 68, 31–37.
- Sardans, J., 1997. Resposta de quatre espècies llenyoses mediterrànies a diferent disponibilitat d'aigua i nutrients. Ph.D. Thesis, Autonomous University of Barcelona, Bellaterra, Barcelona.
- Shinozaki, K., Yoda, K., Hozumi, K., Kira, T., 1964. A quantitative analysis of plant form pipe model theory. I. Basic analyses. *Jpn. J. Ecol.* 14, 97–105.
- Valentini, R., 1999. The role of flux monitoring networks in carbon dioxide source/sinks estimation in terrestrial ecosystems. In: Valentini, R., Brüning, C. (Eds.), *Greenhouse Gases and Their Role in Climate Change: The Status of Research in Europe*. European Commission DG XII/B.I EUR (19085 EN), pp. 1–6.
- Waring, R.H., Landsberg, J.J., Williams, M., 1998. Net primary production of forests: a constant fraction of gross primary production. *Tree Physiol.* 18, 129–134.
- Williams, M., Beverly, E., Anthoni, P.M., Unsworth, M.H., 2001. Use of a simulation model and ecosystem flux data to examine carbon–water interactions in ponderosa pine. *Tree Physiol.* 21, 287–298.