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Modelling the recent historical impacts of atmospheric CO₂ and climate change on Mediterranean vegetation

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Abstract

During the past century, annual mean temperature has increased by 0.75°C and precipitation has shown marked variation throughout the Mediterranean basin. These historical climate changes may have had significant, but presently undefined, impacts on the productivity and structure of sclerophyllous shrubland, an important vegetation type in the region. We used a vegetation model for this functional type to examine climate change impacts, and their interaction with the concurrent historical rise in atmospheric CO₂. Using only climate and soil texture as data inputs, model predictions showed good agreement with observations of seasonal and regional variation in leaf and canopy physiology, net primary productivity (NPP), leaf area index (LAI) and soil water. Model simulations for shrubland sites indicated that potential NPP has risen by 25% and LAI by 7% during the past century, although the absolute increase in LAI was small. Sensitivity analysis suggested that the increase in atmospheric CO₂ since 1900 was the primary cause of these changes, and that simulated climate change alone had negative impacts on both NPP and LAI. Effects of rising CO₂ were mediated by significant increases in the efficiency of water-use in NPP throughout the region, as a consequence of the direct effect of CO₂ on leaf gas exchange. This increase in efficiency compensated for limitation of NPP by drought, except in areas where drought was most severe. However, while water was used more efficiently, total canopy water loss rose slightly or remained unaffected in model simulations, because increases in LAI with CO₂ counteracted the effects of reduced stomatal conductance on transpiration. Model simulations for the Mediterranean region indicate that the recent rise in atmospheric CO₂ may already have had significant impacts on productivity, structure and water relations of sclerophyllous shrub vegetation, which tended to offset the detrimental effects of climate change in the region.

Keywords: climate change, drought, Mediterranean vegetation, modelling, rising atmospheric CO₂, water-use efficiency

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Introduction

Climate in the Mediterranean basin is characterized by cool, wet winters and hot, dry summers (Henderson-Sellers & Robinson 1991). Evergreen shrubland is an important and widespread vegetation type throughout the region (Olson *et al.* 1983), and is dominated by sclerophyllous species, such as *Quercus coccifera* and *Pistacia lentiscus*, which are adapted well for surviving the summer drought. Leaf structure and physiology in

this group minimize water-loss and thermal damage, and deep root systems increase access to water (Specht 1988; Archibold 1995), allowing them to remain physiologically active throughout the drought period. However, the majority of growth occurs during the cool, wet spring, being limited by high temperatures and low soil water availability during the summer, and by low temperatures during the winter (Archibold 1995). In addition, although the leaf canopy is evergreen, its size is regulated strongly by summer water availability (Rambal 1993). Temperature and precipitation therefore play key roles in governing the primary productivity and structure of Mediterranean shrublands, and recent historical

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changes in climate are likely to have had significant impacts on this vegetation type.

Global mean temperature has risen by around 0.5 °C during the last century (Jones *et al.* 1998), a change consistent with radiative forcing of climate by increasing greenhouse gas concentrations (Mann *et al.* 1998). Temperature in the Mediterranean region has deviated somewhat from the global picture (Metaxas *et al.* 1991), but has shown an overall warming trend (Kutiel & Maheras 1998). Rising temperature is likely to have promoted the spring growth of sclerophyllous vegetation, but reduced productivity through high summer temperatures. Precipitation in the region has oscillated throughout the past century, with minima around 50 years ago and since 1980, and there has been a long-term downward trend in some areas (Maheras 1988; Kutiel *et al.* 1996; Palutikof *et al.* 1996; Esteban-Parra *et al.* 1998). However, there seem to have been no general trends in the seasonality of precipitation. In conjunction with warming, reductions in precipitation will have subjected vegetation to significant increases in the duration and severity of drought, potentially limiting both primary productivity and canopy structure. Recent changes in climate, particularly reduced precipitation, are therefore likely to have had complex effects on Mediterranean shrub vegetation, but the net impact of these remains uncertain.

Atmospheric CO₂ concentration has risen from around 295 ppm to more than 360 ppm during the past century (Friedli *et al.* 1986; Keeling & Whorf 1998), and is likely to have modified both temperature responses and water relations of Mediterranean vegetation. The stimulation of photosynthesis and growth with temperature, and the temperature optimum for these processes, increase with CO₂ concentration in C₃ plants (Idso *et al.* 1987; Long 1991). However, CO₂ enrichment leads to a more rapid decline in photosynthesis at supraoptimal temperatures (Long 1991). Increasing CO₂ also tends to lower leaf stomatal conductance in Mediterranean shrubs, and this may reduce canopy transpiration rates, improving plant and soil water relations and slowing the rate of soil water loss during drought (Jones *et al.* 1995; Tognetti *et al.* 1998). Recent historical changes in CO₂ may therefore have compensated for reduced water availability in the Mediterranean. However, these benefits for plant and soil water status may have been offset by reduced stomatal sensitivity to CO₂ during periods of drought, and increases in canopy size with CO₂ concentration (Field *et al.* 1995; Tognetti *et al.* 1998).

In this paper, we use a mechanistic model of Mediterranean shrub vegetation to address two questions. First, how has recent historical climate change, particularly increased drought severity, influenced the primary productivity and structure of Mediterranean

shrublands? Secondly, how has the concurrent increase in atmospheric CO₂ concentration modified these impacts?

Materials and methods

Model overview

The model simulates productivity, structure and water relations of patches of Mediterranean vegetation at scales of approximately 10²–10⁴ m², and is designed for application throughout the Mediterranean basin. Plant species are grouped into functional types, and a generic model is applied to each by varying key inputs. This approach is the only practicable way of modelling vegetation at the landscape scale, since it reduces model complexity, and avoids the problem that comprehensive data are lacking for most individual species (Smith *et al.* 1993). Species are grouped into functional types according to their adaptations for coping with water shortage, by considering life history, structural and functional adaptations. Here, the model was applied to simulate evergreen sclerophyllous shrub vegetation, locally known as 'maquis', 'macchia' or 'matorral'.

A document containing a full description of the model is available from our Web site at: <http://www.shef.ac.uk/uni/academic/A-C/aps/medveg.pdf>. Supplementary information is provided at: <http://www.shef.ac.uk/uni/academic/A-C/aps/med1.html>, and an overview of model functions and their interrelations is shown in Fig. 1. Model sensitivity to climate and CO₂ is explored by Osborne & Woodward (2000).

Briefly, canopy CO₂-uptake is simulated by scaling a biochemically based model of photosynthesis, coupled with an empirical model of stomatal conductance, from leaves to the canopy (Farquhar *et al.* 1980; Leuning 1995; de Pury & Farquhar 1997). Fixed CO₂ is added to a temporary pool of carbohydrates which meets maintenance respiration demands and is subsequently used in storage and growth, accounting for growth respiration (Thornley 1970). Growth and litter production are each partitioned between plant organs in fixed proportions, which vary according to phenology and determine net primary productivity (NPP) and biomass. Leaf litter production increases in response to drought and after depletion of stores during long periods with low productivity, and leaf area index (LAI) is thereby regulated by the dynamic balance between leaf growth and abscission. Model predictions of NPP and LAI should be considered as upper estimates, since nutrient limitation and disturbance by fire, herbivory and exploitation by humans are not yet considered.

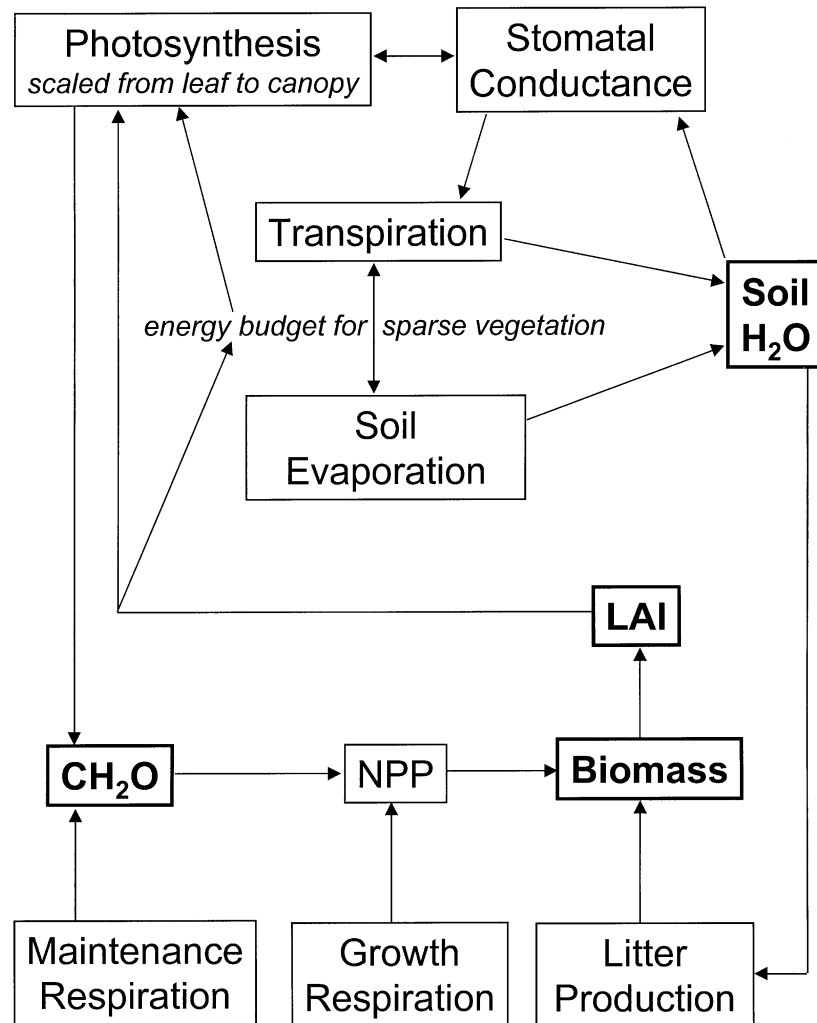


Fig. 1 Model overview, highlighting interactions between processes (normal text), and state variables (bold text). The direction of these interactions is shown using arrows. NPP, Net primary productivity; LAI, Leaf area index; CH₂O, Carbohydrate pool.

Energy and water fluxes are partitioned between canopy transpiration and soil surface evaporation using a derivation of the Penman–Monteith equation which was developed for sparse vegetation (Shuttleworth & Wallace 1985; Shuttleworth & Gurney 1989). Because sparse canopies tend to have a clumped distribution, the vegetated fraction of the land surface depends on LAI after Betts *et al.* (1997). Soil water content is calculated using water balances for a shallow surface layer and a deeper soil layer, accounting for evapotranspiration, infiltration, percolation between layers and deep drainage.

In contrast with a previously published, global vegetation model (DOLY; VEMAP Members 1995), which uses a generic approach to simulate LAI and vegetation function, our regional model simulates key structural and functional features of each plant functional type using a 'bottom-up' approach. It also considers seasonal changes in phenology, physiology,

vegetation structure and water balance in more detail. Given the central importance of water availability for Mediterranean vegetation, simulation of water balance is among the more complex aspects of the model. However, its smaller scope than global models allows model runs to be made at high spatial ($0.5^\circ \times 0.5^\circ$) and temporal (hourly) resolutions.

Model testing

The model was parameterized for evergreen sclerophyllous vegetation using mean observations for as many species as possible, with the aim of making it generally applicable for the functional type. It was tested by comparison with observations for a range of sclerophyllous species, located at sites throughout the Mediterranean region. Most of these are widely distributed in the region (Dallman 1998), and are typical of the functional type in terms of physiognomy and

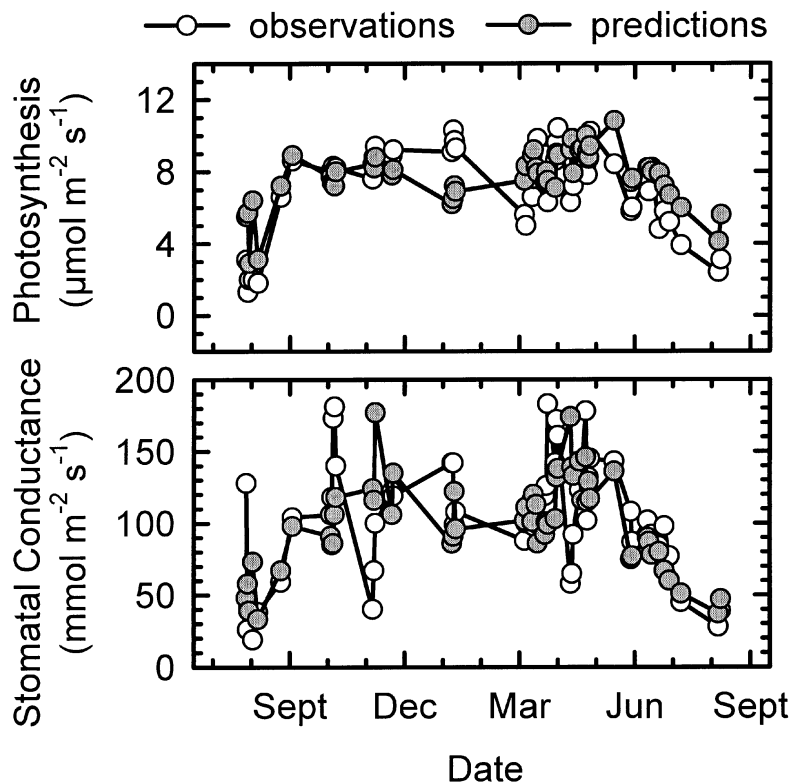


Fig. 2 Comparison of predictions made by the leaf photosynthesis model with independent observations for Mediterranean sclerophyllous shrub vegetation. Observations are daily maxima for sunlit leaves of *Arbutus unedo*, and were obtained using measurements of leaf gas exchange made throughout the year in 1982–83 (Beyschlag *et al.* 1987). Model predictions of net leaf photosynthetic CO_2 -uptake ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and stomatal conductance ($\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$) were based on environmental data recorded at the time of these measurements (Beyschlag *et al.* 1986, 1987).

physiology (Archibold 1995). Observations were independent of those used to parameterize the model and, in each case, comparisons demonstrated that key model processes and outputs showed realistic responses to seasonal and regional variation in climate.

The photosynthetic properties of sunlit leaves in our model are governed by the dependence of Rubisco carboxylation capacity on leaf nitrogen concentration, specific leaf area and longevity. Model predictions of leaf nitrogen and carboxylation capacity agree closely with numerous observations for sunlit leaves of sclerophyllous shrub species made throughout the Mediterranean region (Table 1). The predicted profile of carboxylation capacity through the canopy is consistent with estimates inferred from leaf gas exchange in *Quercus coccifera*, which were $58 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in the uppermost leaves, declining to $26 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ beneath a leaf area index of $3.5 \text{ m}^2 \text{ m}^{-2}$ (Tenhunen *et al.* 1990). Corresponding model predictions were 56 and $26 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, respectively.

Leaf photosynthesis varies during the year according to changes in weather and soil water availability (Fig. 2). Modelled responses of leaf photosynthesis and stomatal conductance to seasonal variation in climate and soil water closely matched observations of leaf gas exchange

reported for *Arbutus unedo* in Portugal (Fig. 2). Given only climatic data and leaf longevity as inputs therefore, the model provides good estimates of seasonal variation in leaf gas exchange.

Model estimates of above- and below-ground biomass, NPP and LAI were made using climate data recorded at El Ardal in south-east Spain (Fig. 3). These very closely matched observations in *Rosmarinus officinalis* shrubland made at the same site (Fig. 3). Model predictions of NPP and LAI were also made for shrubland sites throughout the Mediterranean region (Fig. 4), using soil texture inputs and climate data which were interpolated from historical observations to a 0.5° resolution by New *et al.* (1999a, b). Predictions provided a realistic estimation of the regional variation in these properties (Fig. 4), although they were generally less accurate than predictions based on climate data recorded at the same site as observations (Fig. 3).

Predictions of soil water content generally matched measurements made throughout two years under *R. officinalis* vegetation at El Ardal in Spain (Fig. 3). In addition, predictions of evapotranspiration made using climate data recorded at a site in Central Italy generally showed good agreement with measurements of water fluxes over *Quercus ilex* vegetation at the same location

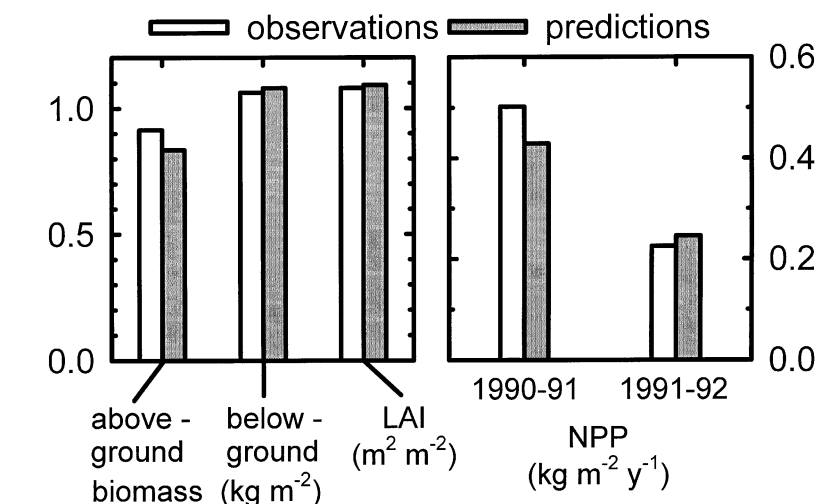
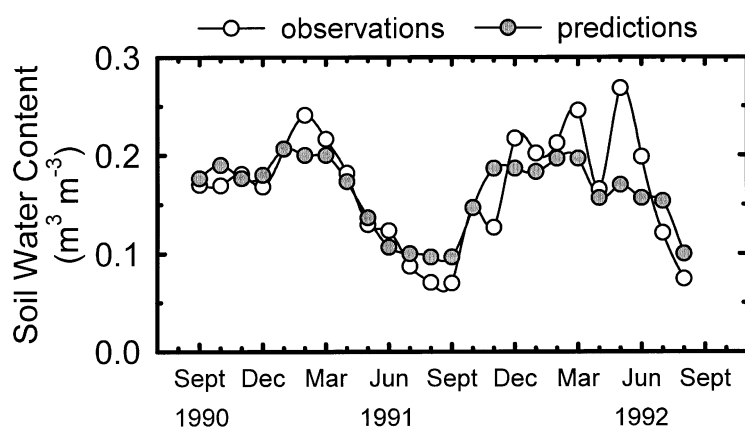


Fig. 3 Comparison of model predictions of biomass (kg dry-matter m⁻²), net above-ground primary productivity (NPP, kg dry-matter m⁻² y⁻¹), leaf area index (LAI; top panels) and volumetric soil water content in the upper soil layer (m³ m⁻³; bottom panel) with independent observations for Mediterranean sclerophyllous vegetation. Observations were made in *Rosmarinus officinalis* shrubland at El Ardal in south-east Spain (López-Bermúdez *et al.* 1996). Model predictions were made using a 30-y climate record from Alcantarilla, a nearby meteorological station, followed by climate data recorded at the site during the period of measurements.



(data not shown). Given only inputs of climate and soil texture, therefore, the model provides reasonable simulations of evapotranspiration and soil water, both key components of the water balance.

Impacts of climate change and rising CO₂

The model was first run to equilibrium by repeated use of 10 years' climate data for the period 1901–10, and the mean CO₂ concentration for this decade, which was approximately 297 ppm (Friedli *et al.* 1986). Equilibrium was reached after around 100 years, and defined as the point when biomass and soil water approached constant values. The model was subsequently run for the period 1901–95 using historical climate data interpolated to a 0.5° resolution (see Model testing). Climatic inputs were total monthly precipitation, and monthly means for the number of days with precipitation, temperature, daily temperature range and atmospheric vapour pressure. The model was run only for those grid cells in the

Mediterranean basin dominated by scrub vegetation (Olson *et al.* 1983). Soil textures from Zobler (1986) were used to derive soil hydraulic properties following Cosby *et al.* (1984).

Two model runs were made: first, with CO₂ held at its 1900 concentration of 297 ppm, to determine the impacts on vegetation of historical changes in climate alone (Fig. 5); and secondly, with a concurrent rise in CO₂, following historical records obtained from an Antarctic ice core and direct observations at the Mauna Loa Observatory (Fig. 5; Friedli *et al.* 1986; Keeling & Whorf 1998). This latter run determined the extent to which historical increases in atmospheric CO₂ have modified the responses of vegetation to recent climatic change.

Temperature and precipitation showed significant long-term trends at the Mediterranean shrubland sites where model runs were made. On average, temperature rose by approximately 0.6°C during the first half of the century, but oscillated during the second half, with a net warming trend of less than 0.2°C, giving a total increase

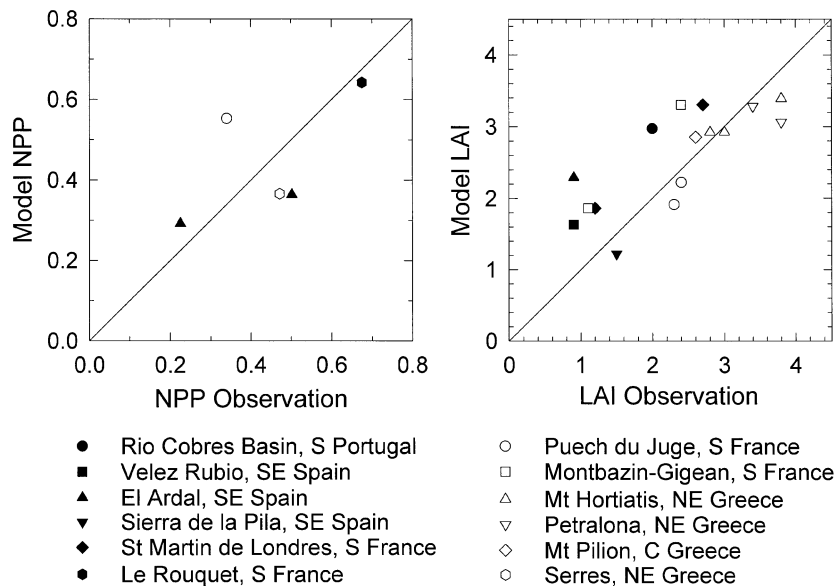


Fig. 4 Comparison of modelled net above-ground primary productivity (NPP, kg dry-matter m⁻² y⁻¹) and canopy leaf area index (LAI) with independent observations for Mediterranean sclerophyllous vegetation. Model predictions were made using climate data which were interpolated from historical observations to a 0.5° resolution by New *et al.* (1999a, b). Soil hydraulic properties for each site were derived from soil texture data (Zobler 1986), following Cosby *et al.* (1984). Observations were made throughout the Mediterranean basin, and therefore differ according to regional variation in climate and soils (Sources: Lossaint 1973; Rambal & Leterme 1987; Malanson & Trabaud 1988; Tsiouvaras 1988; Diamantopoulos *et al.* 1993; Harrison *et al.* 1993; Rambal 1993; Paraskevopoulos *et al.* 1994; López-Bermúdez *et al.* 1996; Rambal *et al.* 1996; Hawkes 1998).

Table 1 Comparison of the leaf nitrogen and carboxylation capacity models with independent observations. Leaf nitrogen concentration and the carboxylation capacity of sunlit leaves at 25°C are derived from a typical value of leaf longevity for sunlit leaves of Mediterranean sclerophyllous shrubs (18.5 months). Observations are for sclerophyllous shrubs at sites located throughout the Mediterranean region (SD=one standard deviation, and SE=one standard error of the mean). In the case of carboxylation capacity, these were estimated by Wullschleger (1993) using curves fitted to responses of leaf photosynthesis to substomatal CO₂ partial pressure

Leaf nitrogen concentration (mmol N g ⁻¹)	Value	Source
Model prediction	1.1	
Annual mean for <i>Pistacia lentiscus</i> in Portugal	1.1	Specht (1988)
Mean (± SD) for 7 species in N. Italy	1.0 ± 0.26	de Lillis & Fontanella (1992)
Mean (± SD) for 8 species in S. France	0.9 ± 0.23	Specht (1988)
Mean (± SD) for 11 species in Greece	0.9 ± 0.23	Specht (1988)
Mean (± SD) for 5 species in S. France	0.9 ± 0.14	Specht (1988)
Rubisco carboxylation capacity (μmol CO ₂ m ⁻² s ⁻¹)		
Model prediction	56	
Mean (± SE) from a survey of seven studies	53 ± 6	Wullschleger (1993)

of approximately 0.75°C (Fig. 5). Conversely, precipitation declined over the same period, dropping by around 15 mm in the first half of the century, and by a further 18 mm in the second half (Fig. 5), a total decrease of approximately 34 mm, or 6% of the annual mean. Decreases in precipitation were particularly pronounced in the late 1940s and the 1980s–1990s (Fig. 5). In the 1940s, precipitation was reduced throughout the year, except during winter, but in the latter period, decreases in precipitation were mainly confined to the winter and spring.

Results

Regional average trends in NPP and LAI

Model simulations for Mediterranean shrub vegetation indicated that NPP has risen by approximately 25% and LAI by 7% during the past century of increasing CO₂ and climate change (Fig. 5). Sensitivity analysis showed that this stimulation was the consequence of changes in atmospheric CO₂ since, when CO₂ was held constant, climate change alone caused net decreases of 3% in NPP

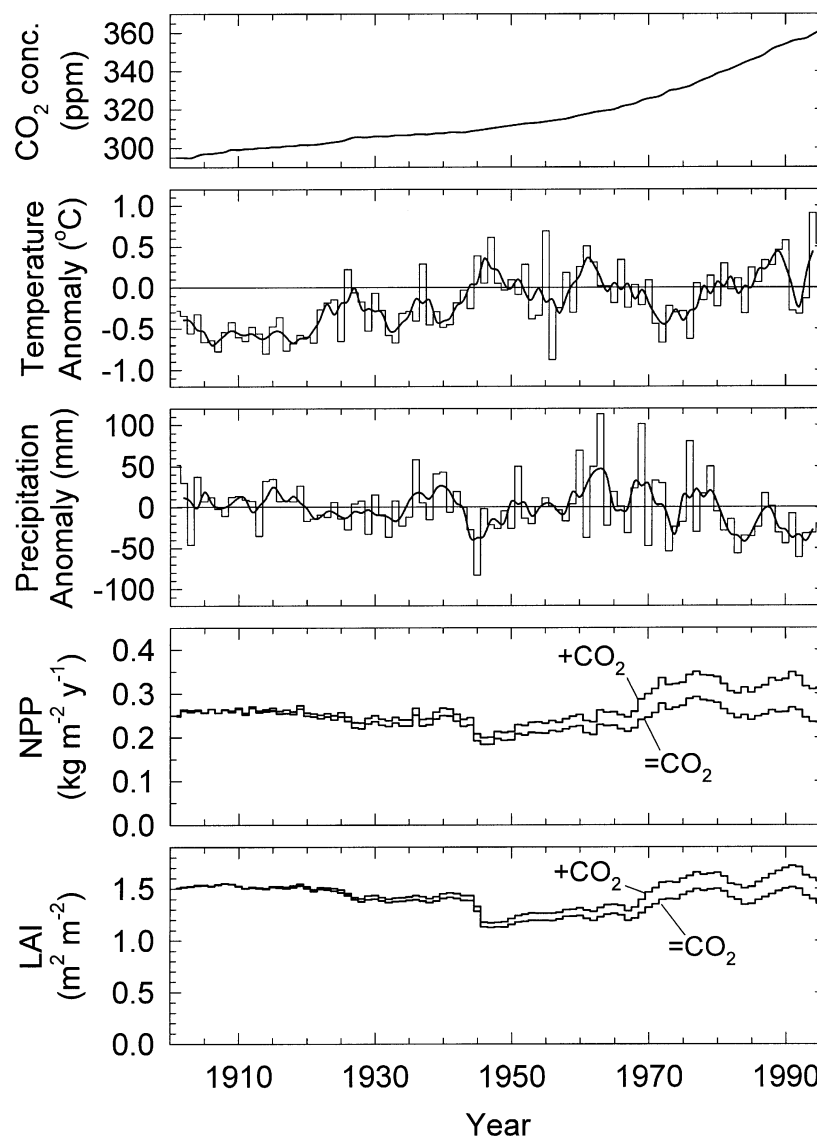


Fig. 5 Mean trends in atmospheric CO₂, climate, model predictions of net primary productivity (NPP) and leaf area index (LAI) for Mediterranean shrubland sites during the past century. Mean annual atmospheric CO₂ concentration was obtained from Friedli *et al.* (1986) and Keeling & Whorf (1998). Annual mean temperature and total precipitation anomalies are for land sites covered predominantly by Mediterranean shrub vegetation, and were calculated using area-weighted climate data relative to mean values for the 1961–90 reference period, following Jones (1994). Data smoothed using a 3-y running mean are also shown. Area-weighted mean above-ground NPP ($\text{kg dry-matter m}^{-2} \text{y}^{-1}$) and LAI ($\text{m}^2 \text{m}^{-2}$) were obtained using model runs where CO₂ was either kept constant at its 1900 level (=CO₂), or allowed to rise following historical data (+CO₂).

and 6% in LAI between the first and last decades of the model run (Fig. 5). Absolute changes in LAI were small, the 7% increase with CO₂ and climate change corresponding to a rise of only $0.1 \text{ m}^2 \text{ m}^{-2}$.

For the model run where atmospheric CO₂ concentration was fixed at 297 ppm, predicted NPP gradually declined from the beginning of the century, with a sharp drop to a minimum in the late 1940s (Fig. 5). The observed CO₂ concentration increased only by around 15 ppm during this period, and had little impact on NPP (Fig. 5). In contrast, rising CO₂ had a considerably greater effect in the latter half of the century, when concentrations rose exponentially by 50 ppm. When CO₂ was held constant, NPP followed an upward trend between 1945 and 1995, which increased significantly with CO₂ enrichment (Fig. 5). During the last decade of the model run, this

increase led to a 29% stimulation of NPP under high CO₂ in comparison with the constant CO₂ run. Major effects of atmospheric CO₂ on NPP are therefore comparatively recent, mostly occurring within the past 50 years (Fig. 5).

Model simulations of LAI for Mediterranean shrub canopies showed similar trends to NPP in response to climate and CO₂ concentration, but the impact of CO₂ was smaller. During the first 50 years, CO₂ had little effect on LAI, which gradually declined until the mid-1940s, when it showed a sharp drop (Fig. 5). LAI subsequently rose throughout the latter half of the century, and CO₂ enrichment increased the rate of this change (Fig. 5). On average, LAI during the last decade was 14% greater with CO₂ enrichment than when CO₂ was held constant at its 1900 level, an absolute increase of $0.2 \text{ m}^2 \text{ m}^{-2}$.

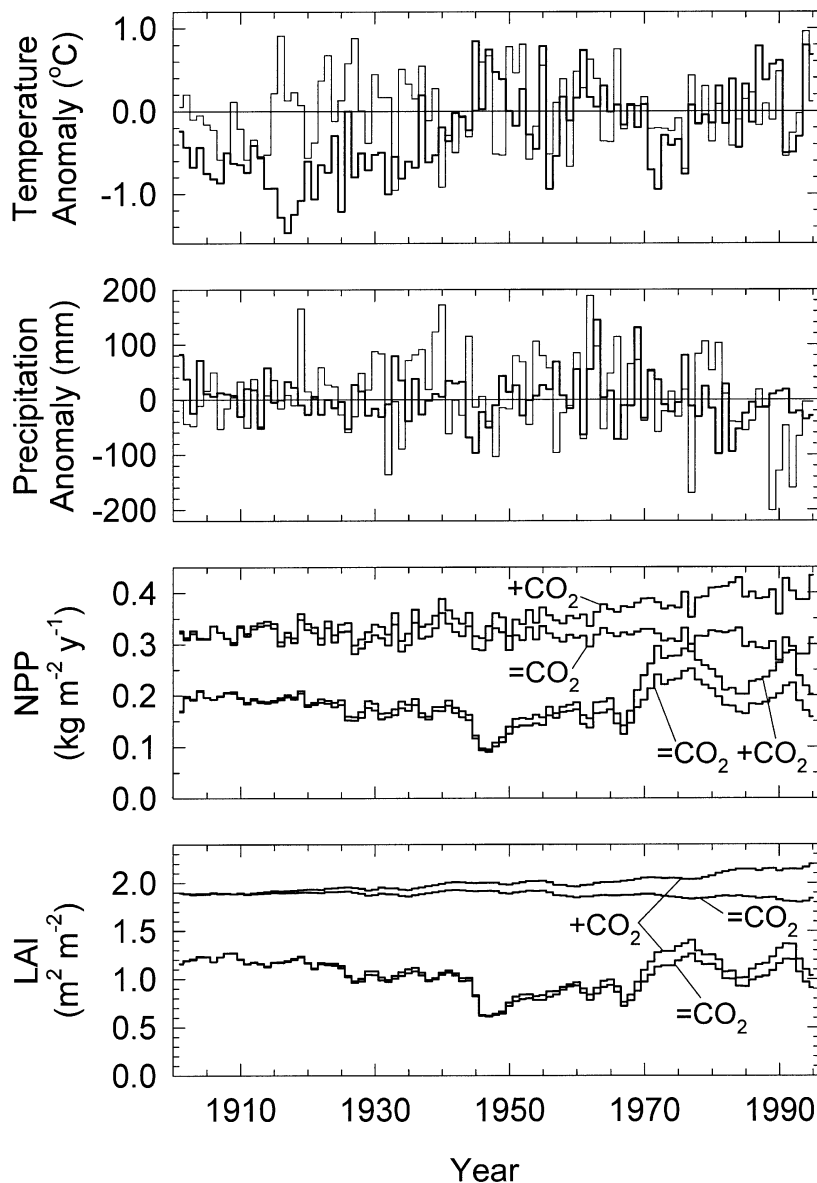


Fig. 6 Regional variation in climate trends and model predictions of net primary productivity (NPP) and leaf area index (LAI) for Mediterranean shrubland sites during the past century. Results are a subset of those shown in Fig. 5: for Greece and western Turkey (36°N–41.5°N, 19°E–30.5°E), and the Mahgreb area of North Africa (31°N–36°N, 10°W–11°E). Thin lines in the top two panels are climate anomalies for Greece, and bold lines are anomalies for the Mahgreb. The lower two panels show NPP and LAI for the ‘=CO₂’ and ‘+CO₂’ cases (see Fig. 5).

In general, decreases in NPP and LAI tended to be most pronounced when declining precipitation occurred in conjunction with rising temperature (Fig. 5), particularly during the late 1940s and mid-1980s (Fig. 5). The following section explores regional variation in the magnitude of these drought-induced decreases, and the mitigating effects of rising CO₂. It focuses on two areas within the Mediterranean where NPP and LAI showed contrasting responses to climate: Greece and western Turkey, and the Mahgreb area of North Africa (Morocco, northern Algeria and Tunisia), hereafter referred to as Greece and the Mahgreb, respectively. In general, vegetation in the coastal areas of eastern Spain, southern France and Italy showed similar climatic responses to vegetation in Greece, while responses to climate in south-

western Spain and Portugal tended to be closer to those of the Mahgreb.

Regional variation in NPP and LAI

In common with general regional trends, mean NPP and LAI decreased in both Greece and the Mahgreb during the late 1940s and mid-1980s as a consequence of drought, which was caused by rapid increases in temperature and declining precipitation (Fig. 6). Decreases in NPP and LAI were more pronounced in the Mahgreb, where precipitation is approximately half of that in Greece (Fig. 6), and precipitation anomalies therefore account for a larger proportion of annual precipitation.

Rising CO₂ during the first half of the century had little impact on NPP and LAI in the severely droughted Mahgreb, but tended to reduce the magnitude of drought-induced decreases in NPP and LAI in Greece (Fig. 6). In contrast, the rapid increase in CO₂ during the latter half of the century had significant impacts. With CO₂ constant, drought in the mid-1980s led to decreases in NPP and LAI in both Greece and the Mahgreb (Fig. 6). Increasing CO₂ completely offset these drought-induced decreases in Greece, resulting in a rising trend in both in NPP and LAI (Fig. 6). However, effects of CO₂ in the Mahgreb were less pronounced, and only partially compensated for the severe effects of drought on vegetation (Fig. 6).

Water-use efficiency and transpiration

Rising CO₂ offset the negative impacts of drought on NPP via an increase in the efficiency of water-use, and not a reduction in total water loss through transpiration. CO₂ enrichment led to an approximately uniform increase in the predicted transpiration efficiency throughout most of the region. During the period 1986–95, transpiration efficiency was around 0.1–0.2 mmol C mol⁻¹ H₂O greater with CO₂ enrichment, in comparison with that under constant CO₂. Mean values of transpiration efficiency varied between approximately 0.2 and 1.0 mmol C mol⁻¹ H₂O.

Transpiration efficiency is the quantity of carbon produced in NPP per unit water lost in transpiration, and a measure of the water-use efficiency of vegetation (Farquhar *et al.* 1989). It increased because of a stimulation in photosynthesis at elevated CO₂, causing higher rates of net canopy CO₂-fixation in relation to water loss. Greater transpiration efficiency was sufficient to offset the negative impacts of mild, but not severe, drought episodes on modelled NPP (Fig. 6).

In contrast to transpiration efficiency, responses of total transpiration to CO₂ enrichment could not explain the mitigation of drought effects on NPP predicted by the model. Higher CO₂ concentrations generally led to small increases in predicted transpiration throughout the northern Mediterranean, and annual mean soil water status generally did not improve. Except in isolated sites, CO₂ enrichment had very little impact on transpiration across much of the southern Mediterranean. However, reductions did occur at a small number of sites, slightly increasing mean soil water content predicted by the model. Mean increases in canopy transpiration due to CO₂ enrichment in the period 1986–95 were 2% (~10 mm) and <1% (~2 mm) for the northern and southern Mediterranean, respectively (north and south of the latitude 36°N).

Improvements in modelled transpiration efficiency with CO₂ enrichment were due principally to sustained increases in the instantaneous water-use efficiency of leaf gas exchange (IWUE). These historical improvements in IWUE inferred from our model were tested using measurements of the discrimination of stable carbon isotopes ($\Delta^{13}\text{C}$) in herbarium leaves, which provide a record of IWUE integrated for the period of leaf growth (Farquhar *et al.* 1982). Values of leaf $\Delta^{13}\text{C}$ derived from our model results showed good agreement with the magnitude of values and trends measured in herbarium specimens of four sclerophyllous shrub species collected throughout the past century in Catalonia, north-east Spain (Fig. 7; Peñuelas & Azcón-Bieto 1992; Peñuelas & Estiarte 1997). The overall slight decreasing trend in $\Delta^{13}\text{C}$ corresponded to an increase in IWUE during the latter part of the century (Fig. 7).

Discussion

Mechanism of historical CO₂ effects on NPP

Our model indicates that rising CO₂ has already led to significant stimulation of NPP and LAI in Mediterranean shrubland during the past century, despite the tendency for long-term trends in climate to reduce both through increasing aridity (Fig. 5). Both the current study, and results from a global vegetation model (Cao & Woodward 1998), suggest that the major effects of atmospheric CO₂ are comparatively recent, occurring mostly within the past 50 years (Fig. 5). However, the impact of CO₂ on NPP for Mediterranean shrub vegetation in this period is around twice that estimated for the global total (Cao & Woodward 1998), perhaps because of the importance of CO₂ in raising the efficiency of water-use in this water-limited ecosystem. Other modelling studies indicate that vegetation types in dry regions may show among the greatest sensitivities of NPP to rising atmospheric CO₂ (Pan *et al.* 1998).

Increases in transpiration efficiency with CO₂ completely offset the widespread negative effects of increasing aridity on NPP in the northern and eastern Mediterranean, as in Greece, and tended to lessen the effects of extreme drought events in the southern and western Mediterranean, as in the Mahgreb (Fig. 6). Greater transpiration efficiency resulted from the direct effects of CO₂ on leaf physiology (Drake *et al.* 1997): first, stimulation of CO₂-uptake through higher carboxylation rates and a rise in the ratio of carboxylation to oxygenation at Rubisco; and secondly, reduction in the rate of water loss through partial stomatal closure. The stimulation of photosynthesis with increasing CO₂ may be partially or wholly offset by acclimation of the photosynthetic system (Gunderson & Wullschlegel

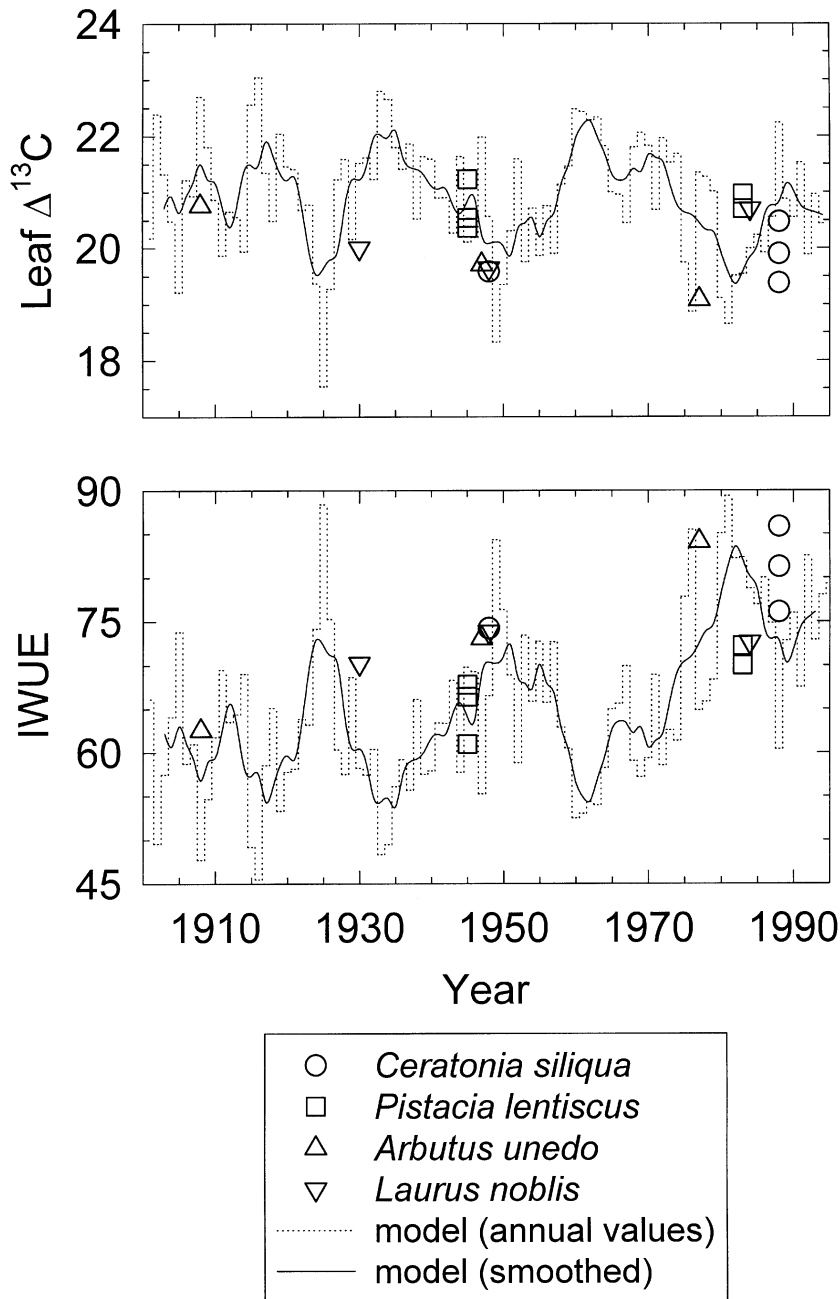


Fig. 7 Stable carbon isotope discrimination ($\Delta^{13}\text{C}$) in leaves of sclerophyllous species during the past century and the corresponding instantaneous water-use efficiency of gas exchange (IWUE). Symbols indicate values of $\Delta^{13}\text{C}$ measured in individual herbarium leaves of four sclerophyllous species collected in Catalonia, north-east Spain (raw data used by Peñuelas & Azcón-Bieto 1992 and Peñuelas & Estiarte 1997). The IWUE was calculated from these measurements following Farquhar & Richards (1984). Lines indicate values calculated using model outputs for Catalonia (Farquhar *et al.* 1982), and weighted for both photosynthetic and leaf growth rates. Data were smoothed using a 5-y running mean.

1994). However, two independent experiments on natural stands of sclerophyllous vegetation growing in elevated CO_2 found no evidence for acclimation (Jones *et al.* 1995; Scarascia-Mugnozza *et al.* 1996), in support of our model assumptions. In addition, evidence of a sustained increase in IWUE was obtained from values of leaf $\Delta^{13}\text{C}$ for herbarium specimens of several Mediterranean sclerophyllous species (Fig. 7).

A linear relationship between the IWUE and atmospheric CO_2 was also indicated by $\Delta^{13}\text{C}$ for four C3 annuals and a steppe shrub grown experimentally at a range of CO_2 concentrations from 200 ppm to the

present-day value (Polley *et al.* 1993a; Polley *et al.* 1995). As in our model study, this rise in CO_2 from historical levels led to increased photosynthesis and growth rate, and was accompanied by a reduction in stomatal conductance (Polley *et al.* 1993a,b, 1995). Also in keeping with our model findings, the IWUE more than doubled in leaves of three sclerophyllous species grown and measured at 700 ppm CO_2 in comparison with their counterparts grown at the current ambient concentration (Scarascia-Mugnozza *et al.* 1996).

Greater transpiration efficiency resulting from CO_2 enrichment seems to have been insufficient to counteract

the impacts of severe drought on NPP and LAI, particularly in the Mahgreb, the western Iberian peninsula and the Middle East (Fig. 6). While high CO₂ concentration may have delayed the onset of drought through a reduction in transpiration rate, the effectiveness of this mechanism would have been limited during severe drought. In addition, gas exchange measurements in *Q. ilex* indicate that the sensitivity of leaf stomatal conductance to CO₂ declines with soil water potential and increasing vapour pressure deficit (Tognetti *et al.* 1998), both encountered during drought. These physiological responses are reproduced well by the model, and mediate the impacts of severe drought.

The area of sclerophyllous vegetation has increased during recent decades in the northern Mediterranean, due to agricultural land abandonment; however, its area in the African Mediterranean has shrunk, at least partly because of firewood harvesting (Puigdefábregas & Medizabal 1998). Our results suggest that historical climate change may have contributed to this latter decline at some localities, increasing the vulnerability of sclerophyllous vegetation to human impacts by reducing potential wood production during extreme drought.

Evidence for an historical increase in NPP

Model results for NPP are consistent with a number of lines of evidence: from observations of Mediterranean sclerophyllous vegetation under CO₂ enrichment; and measurements of tree rings and forest stock inventories in Europe.

The effects of rising CO₂ in the 300–360 ppm historical range have not been examined directly in Mediterranean sclerophyllous vegetation, but experiments have been conducted at 360–700 ppm. This latter increase is approximately five times the historical change examined here, but vegetation productivity is likely to have been more sensitive to past increases in CO₂ because of nonlinearity in the CO₂ response (Luo *et al.* 1998). After 3 years at 700 ppm CO₂, annual wood production per branch in a natural stand of *Q. ilex* was 222% greater than the control (Scarascia-Mugnozza *et al.* 1996). Similarly, the rate of trunk basal area growth increased by 20–80% at 700 ppm CO₂ in comparison with controls in *Q. ilex* trees growing close to a natural CO₂ spring (Hättenschwiler *et al.* 1997). The difference was especially pronounced in years when the spring season was dry (Hättenschwiler *et al.* 1997), supporting our model findings that recent historical increases in CO₂ may have offset some of the negative impacts of drought on NPP (Fig. 5). Wood growth in sclerophyllous vegetation therefore tends to show greater sensitivity to CO₂ enrichment

than our model indicates for NPP in the past, in keeping with expectations for the smaller historical rise in CO₂.

Evidence from tree-rings indicates a marked increase in stem radial growth during recent decades in Europe, strongly suggestive of a rise in productivity (Briffa *et al.* 1998). For example, the annual growth increment in central European forests rose by around 25% between 1961 and the early 1990s (Schadeur 1996; Zingg 1996), similar to the change simulated for Mediterranean shrublands (Fig. 5). Estimates of forest stocks in the Mediterranean suggest that the stem volume of living trees rose by more than 50% between 1950 and 1980, a change which cannot be attributed to afforestation, and which is in keeping with our model results (Kauppi *et al.* 1992). Although the causes of increases in European forest growth are uncertain, they are at least consistent with our findings of a strong CO₂ effect on productivity in the Mediterranean.

Mechanisms and evidence of historical CO₂ effects on LAI

Model results suggested that small increases in LAI have occurred as a consequence of recent historical changes in atmospheric CO₂, particularly during the past 50 years (Figs 5,6). Canopy leaf area tends to be limited by water availability because soil water losses via transpiration and drainage must balance the infiltration of precipitation into the soil (Woodward 1987). Modelled reductions in stomatal conductance and the rate of leaf transpiration with rising CO₂ therefore allowed a small increase in LAI (Figs 5,6). Throughout most of the northern Mediterranean this compensated for reduced stomatal conductance, and led to a small increase in annual canopy transpiration. However, since transpiration efficiency also rose, reduced water availability did not limit the CO₂-induced rise in NPP (Fig. 6). In the southern Mediterranean, increases in LAI were smaller and less widespread than those in the north (Fig. 6), and tended to balance reductions in stomatal conductance, leaving annual transpiration unchanged. Although total annual transpiration tended to increase or remain unchanged with rising CO₂, these model results do not preclude the possibility of seasonal benefits for water economy arising from reduced stomatal conductance.

Model predictions of LAI during the 1980s were supported by satellite observations of land-surface radiance in the Mediterranean region. We estimated the normalized-difference vegetation index (NDVI) from model calculations of vegetation and soil reflectance in the photosynthetically active and near infra-red wavebands (Osborne & Woodward 2000). The NDVI indicates absorption of radiation by leaf canopies, and depends on

leaf spectral properties, foliage orientation and density, and vegetation cover (Cary & Rosenzweig 1987; Sellers *et al.* 1992; Myneni *et al.* 1995). Model predictions of NDVI for the Mediterranean region showed good agreement with spatial variation in satellite estimates, and reproduced the upward 'greening' trend observed in NDVI during the 1980s (Myneni *et al.* 1997; Osborne & Woodward 2000). Changes in the model NDVI were attributable to variation in LAI, and a sensitivity analysis indicated that this was driven largely by variation in precipitation and rising CO₂ (Osborne & Woodward 2000), in keeping with mechanisms driving the decadal-scale changes reported here.

Experiments testing the effects of CO₂ concentration on woody species have shown no general responses in LAI (Saxe *et al.* 1998). In the only reported observations for Mediterranean sclerophyllous vegetation, LAI was inferred from optical measurements under closed canopies of *Q. ilex* trees growing in natural CO₂ springs, and found to be insensitive to CO₂ concentration (Hättenschwiler *et al.* 1997). However, this method would have been unable to resolve the differences of 0.1–0.3 m² m⁻² suggested by our model (Welles & Cohen 1996), and a small increase of this magnitude cannot be discounted (Hättenschwiler *et al.* 1997).

Theoretical considerations suggest that compensation between CO₂-induced changes in stomatal conductance and LAI is likely to be greatest: (i) in open, aerodynamically rough canopies, where canopy size and conductance exert a high degree of control over transpiration; (ii) where NPP responds strongly to CO₂, supporting the additional leaf production; (iii) where water is the most strongly limiting resource for growth; and (iv) when nutrient-uptake permits an increase in leaf production (Field *et al.* 1995). Nutrient uptake is not explicitly considered in our model at present; however, modelled shrub canopies were open and aerodynamically rough, NPP responded significantly to CO₂ concentration (Fig. 5) and LAI was strongly limited by drought (Fig. 6). As a consequence, increased LAI compensated for the effects of reduced stomatal conductance on transpiration across most of the region.

Conclusions

Modelling suggested that rising atmospheric CO₂ concentration during the past century has led to significant increases in NPP and LAI of Mediterranean sclerophyllous vegetation, despite the tendency of both to decline in response to climate change. Impacts of CO₂ were mediated through an increase in the efficiency of water-use in NPP, and counteracted limitation by drought. However, higher LAI compensated for reductions in stomatal conductance with increasing CO₂,

leading to similar or slightly greater total water-use by vegetation. Our results suggested that changes in atmospheric CO₂ might already have played an important role in mediating the productivity, structure and water relations of this vegetation type.

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