

## Biological mechanisms underlying recent increases in the NDVI of Mediterranean shrublands

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**Abstract.** Long-term satellite observations of normalized difference vegetation index (NDVI) for Mediterranean shrublands suggest an increase in vegetation activity during the 1980s, caused by climatic warming. However, whether this was due to artificial trends in the satellite data remains in question. We used a mechanistic model of vegetation growth and a database of observed climate to test whether the observed increase in NDVI could have been caused by changes in canopy structure driven by changes in climate. The model reproduced the long-term upward trend in maximum seasonal NDVI between 1981 and 1991, indicating that a change in vegetation structure could feasibly explain the satellite observations. The model indicated that the NDVI trend was caused by a 12% increase in leaf area index (LAI), mainly owing to changes in precipitation and rising atmospheric CO<sub>2</sub>. By contrast, climatic warming during the 1980s exerted little control over this variation in LAI. Simulated trends in canopy structure exerted significant impacts on canopy function, being associated with a 15% rise in net primary productivity and a 30% increase in transpiration. From this analysis, we conclude that trends in historical satellite observations of NDVI have a plausible biological basis.

### 1. Introduction

The foliage density of vegetation, as indicated by the leaf area index (LAI), plays a key role in mediating fluxes of CO<sub>2</sub>, water vapour, radiation and momentum between vegetation and the atmosphere. Quantifying these fluxes and understanding the mechanisms of their control have become important aims of global change research, since they may moderate the current rise in atmospheric CO<sub>2</sub> and temperature through feedbacks to the global carbon cycle and regional energy balance (Sellers *et al.* 1996, Betts *et al.* 1997, Woodward *et al.* 1998). Changes in the LAI of open vegetation, such as Mediterranean shrublands, are particularly important in these respects, since fluxes are strongly limited by LAI in sparse canopies (Larcher 1995). Conversely, the physiological processes that regulate these fluxes are themselves implicated in the control of the LAI (Woodward 1987, Thomas *et al.* 1992, Hirose *et al.* 1997).

Satellite measurements of land surface radiance potentially provide a powerful tool for monitoring large-scale impacts of global change on the regional structure and function of vegetation (Sellers *et al.* 1992). However, they must be interpreted

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with caution since sensor degradation, decay in satellite orbits, aerosols from volcanic eruptions and drifts in the local observation time can introduce artificial trends in radiance data (Gutman 1999, Rasool 1999). In addition, any inferences about changes in canopy structure from these data are complicated by nonlinear relationships between spectral indices and LAI (Curran 1983, Sellers 1989).

Myneni *et al.* (1997, 1998) analysed NDVI data derived from National Oceanic and Atmospheric Administration (NOAA) weather satellite measurements, accounting for potential artificial trends using empirical correction techniques. They found a clear upward trend in NDVI between 1981 and 1991 at northern temperate latitudes, and showed that some of the larger increases of more than 50% occurred in the Mediterranean region. Increasing NDVI was associated with climatic warming, which suggested that the trend was caused by greater canopy growth at higher temperatures, and earlier growth during the spring.

A subsequent analysis of NOAA weather satellite measurements (Gutman 1999) highlighted a number of problems in interpreting these data and cast doubt on their use in studies of long-term trends. The observation of a trend in NDVI during the 1980s therefore remains uncertain. However, if real, this trend could indicate significant changes in LAI, with important implications for fluxes of gases and energy at the vegetated land surface. Changes in canopy water loss would have particular significance in the Mediterranean region, where precipitation has declined since 1980 as a consequence of an unusual, continuous, positive phase of the North Atlantic Oscillation (Hurrell 1995, Palutikof *et al.* 1996).

Here, we use a model of plant physiological processes and canopy structure in evergreen Mediterranean shrub vegetation to investigate whether observed climatic and CO<sub>2</sub> trends during the 1980s could have driven an increase in LAI. The model provided an independent method for testing the biological basis of trends in NDVI, and quantified associated changes in canopy function. We addressed three questions raised by the results of Myneni *et al.* (1997).

1. Did climatic change and rising CO<sub>2</sub> cause a rise in LAI during the 1980s, leading to the observed long-term increases in NDVI of Mediterranean shrublands?
2. Were increases in LAI driven by climatic warming in this vegetation type, as suggested as a general mechanism by Myneni and co-workers?
3. Was variation in LAI associated with significant changes in canopy function, as indicated by CO<sub>2</sub> and water fluxes between vegetation and the atmosphere?

## 2. Methods

### 2.1. Model description

The model was designed specifically for Mediterranean vegetation and is described in detail by Osborne *et al.* (2000). Here, it was used to simulate evergreen sclerophyllous shrub vegetation, comprised of species such as *Quercus coccifera* and *Pistacia lentiscus*, which remain physiologically active throughout the Mediterranean summer drought. These plants tend to be deep-rooted, increasing access to water during drought, and have tough leaves that conserve water through a relatively low stomatal conductance (Archibold 1995).

Briefly, canopy CO<sub>2</sub> and water vapour exchange were simulated using a fully coupled model, accounting for canopy photosynthesis and respiration (Farquhar *et al.* 1980, Amthor 1994, de Pury and Farquhar 1997), stomatal conductance

(Leuning 1995), evapotranspiration and energy balance (Shuttleworth and Wallace 1985, Shuttleworth and Gurney 1989). Net primary productivity (NPP) was derived from canopy photosynthesis, accounting for maintenance and growth respiration (Thornley 1970), and the LAI was obtained from the balance between NPP and litter production. Partitioning of NPP and litter production between different plant organs depended on phenology, storage reserves and soil water potential (Osborne *et al.* 2000). The model was run for each year using an hourly time-step, requiring only climatic data, CO<sub>2</sub> concentration and soil texture as inputs. Since it required no input information about radiation interception or vegetation structure, the model was completely independent of satellite measurements.

The NDVI was derived in our model as follows. Firstly, absorption of photosynthetically active radiation (PAR) and near-infrared radiation (NIR) were estimated on a 'per unit ground area' basis for vegetation and soil components. These were added to obtain total PAR and NIR absorption for the land surface. Secondly, total absorbed and incident fluxes were used to obtain reflection coefficients for PAR and NIR at the vegetated land surface, from which the NDVI was calculated (Monteith and Unsworth 1990). Incident radiation was estimated and partitioned between direct and diffuse PAR and NIR following the empirical relationships of Weiss and Norman (1985). We assumed clear-sky conditions in order to match those during satellite measurements.

Absorption of PAR and NIR by vegetation was estimated for the vegetated fraction of the land surface from incident direct and diffuse radiation fluxes, using a 'big-leaf' model (de Pury and Farquhar 1997). The assumptions about canopy leaf arrangement in this model are appropriate for Mediterranean sclerophyllous vegetation (Caldwell *et al.* 1986), and we used general values of leaf absorptance that are typical for species of this vegetation type (PAR absorptance = 0.85; NIR absorptance = 0.17; (Björkman and Demmig 1987, Tenhunen *et al.* 1990, Hollinger 1992)). Absorption by grasses was not considered. The vegetated fraction of the land surface was estimated from LAI using an empirical relationship developed by Betts *et al.* (1997), and used to convert radiation absorption by vegetation to a ground area basis.

Absorption of radiation at the soil surface was calculated separately for vegetated and un-vegetated land surface fractions and added to obtain a soil total for PAR and NIR. Incident radiation for the vegetated fraction was attenuated according to absorption by the plant canopy. Soil absorption of PAR and NIR were estimated using the National Center for Atmospheric Research (NCAR) Land Surface Model (LSM), as a function of soil moisture content and colour (Bonan 1996). In the absence of suitable observations, we assumed a uniform soil colour mid-way between 'light' and 'dark' (Bonan, 1996).

## 2.2. Model testing and simulations

The model reproduces observations of diurnal and seasonal variation in photosynthesis, stomatal conductance, evapotranspiration and soil water content in sclerophyllous vegetation, and adequately estimates NPP and LAI at shrubland sites throughout the Mediterranean region (Osborne *et al.* 2000). Here, we tested the procedures implemented for estimating NDVI by comparing predictions with estimates derived from satellite data for 1987 and 1988 (Los *et al.* 1994). These latter estimates were compiled for the global land surface at a spatial resolution of 1° × 1° by re-sampling of an earlier, higher resolution dataset from the Global Inventory Monitoring and Modelling Studies (GIMMS) group (Los *et al.* 1994). The GIMMS

dataset was originally derived from land surface radiance observations by NOAA weather satellites. It was processed and re-sampled by Los *et al.* (1994) in order to reduce variation in NDVI due to cloud contamination, atmospheric perturbations, solar zenith angle, sensor viewing angle and sensor degradation. However, the authors estimate that possible errors remain, of 0 to  $-0.3$  due to cloud contamination,  $-0.1$  to  $-0.2$  due to atmospheric perturbations, and 0 to  $-0.2$  due to solar zenith angle, with smaller errors attributable to various additional factors.

The model was run for the period 1901–1995 using historical records of climate interpolated to a  $0.5^\circ \times 0.5^\circ$  resolution (New *et al.* 1999, 2000). It was applied only for areas in Europe and North Africa dominated by Mediterranean scrub vegetation (Olson *et al.* 1983), and the temperature and precipitation data for these sites are summarized in figure 1. Soil texture and hydraulic properties were derived following Zobler (1986) and Cosby *et al.* (1984), and atmospheric  $\text{CO}_2$  data from Keeling and Whorf (1998) and Friedli *et al.* (1986).

A sensitivity analysis was conducted in order to test the influence of individual climatic variables on LAI. In each case, the last twenty years of the model run (1976–1995) were repeated, holding either temperature or precipitation at its mean monthly value, allowing seasonal but not interannual variation. In other words, each year of the 20-year run had the same weather, represented by monthly means for the twenty years. The impact of rising atmospheric  $\text{CO}_2$  was tested by holding it constant at its 1975 concentration of 330 ppm (Keeling and Whorf 1998).

### 3. Results and discussion

#### 3.1. Model simulation of spatial patterns in NDVI

Model predictions for Mediterranean shrub vegetation tend to overestimate NDVI in comparison with data from satellite observations, on average by 0.07 for

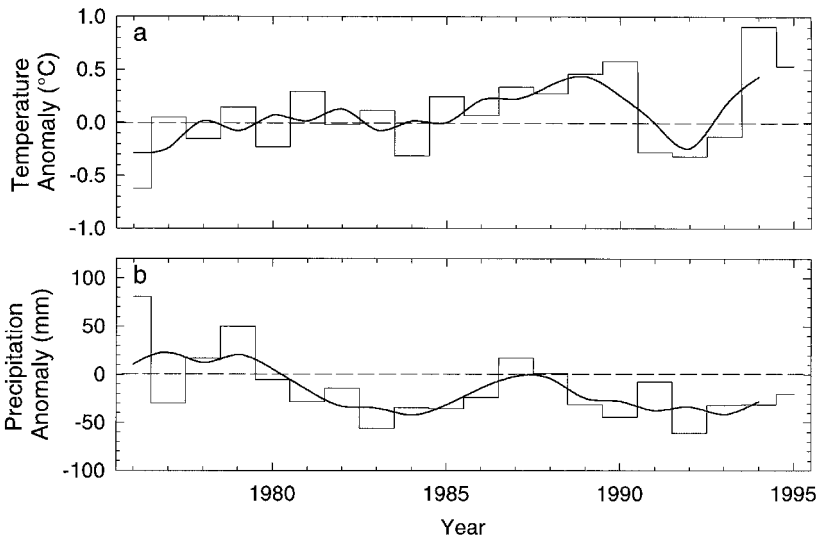


Figure 1. Annual temperature (a) and precipitation (b) area-weighted mean anomalies for pixels dominated by shrubland vegetation in the Mediterranean basin. Anomalies for 1975–1995 are expressed in relation to the 1961–1990 mean, which is now widely used as a reference period in climatology (e.g. New *et al.* 1999), and the sum of anomalies therefore does not equal zero. Values were calculated from the historical dataset used in model simulations (New *et al.* 1999, 2000), and trends are indicated using a 3-year running mean (full curve).

1987 and 0.08 for 1988 (figure 2). This overestimation is in keeping with the errors associated with estimating NDVI from satellite measurements, which are principally caused by atmospheric scattering and cloud contamination, and which introduce a negative bias in data of up to  $-0.1$  to  $-0.2$  (see §2 and Los *et al.* 1994). Correction of the model output for this bias (by subtracting the mean model overestimation of 0.075) results in 85% of model estimates falling within  $\pm 0.1$  of satellite data, and 93% within  $\pm 0.15$  (figure 2). The model therefore adequately captures the majority of spatial variation in NDVI in the Mediterranean basin, lending confidence to our model predictions.

Model underestimation of NDVI at sites in eastern Turkey and the Mahgreb region of North Africa (Algeria, Morocco and Tunisia), and consistent overestimation in the Mahgreb and parts of the eastern Mediterranean, are unlikely to be entirely due to satellite bias. Similar results were obtained when the model was run using independent climate data for 1987–1988, derived for the International Satellite Land Surface Climatology Project [ISLSCP], using the European Centre for Medium-Range Weather Forecasts [ECMWF] model (Brankovic and Van Maanen 1985, Mitchell and Lin 1994). This suggests that the differences between model predictions and satellite estimations are not caused by errors in climate input data. Instead, they may be the result of errors in designating land-use in the model.

We assume that Mediterranean scrub vegetation, as defined by Olson *et al.* (1983), is principally composed of sclerophyllous shrub vegetation for the purposes

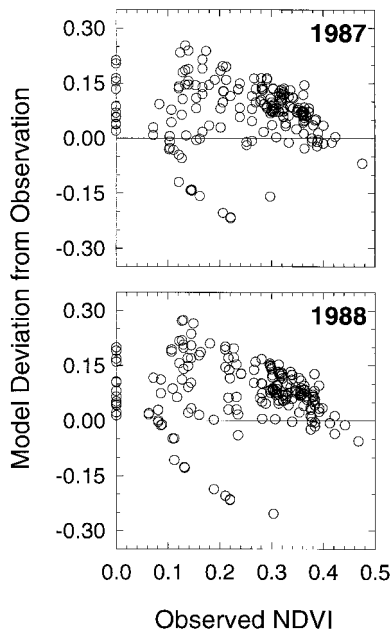


Figure 2. Deviation of model simulations from observations of NDVI. Deviations were calculated as (model NDVI—observed NDVI), and positive deviations therefore indicate an overestimation by the model, while negative deviations represent an underestimation. ‘Observed NDVI’ was estimated from satellite-based measurements of radiance by the GIMMS group (Los *et al.* 1994). Model predictions of NDVI at each site were made for midday under a clear sky, in order to match the conditions during satellite measurements (Los *et al.* 1994), and were only made for areas where the land cover was dominated by Mediterranean scrub vegetation (Olson *et al.* 1983).

of model runs. However, this may be unreasonable in the Mahgreb, where firewood harvesting during the past fifty years has progressively caused replacement of sclerophyllous vegetation by steppe grasses and desert-like shrubs (Puigdefàbregas and Mendizabal 1998). This potential error in specifying land-use highlights the difficulty in modelling actual vegetation in the Mediterranean without accounting for human activity (Pausas 1999). However, good agreement between model and satellite estimates of NDVI (figure 2) suggests that the assumption of sclerophyllous shrub vegetation may be reasonable for large areas of Mediterranean scrub ecosystems, as designated by Olson *et al.* (1983).

### 3.2. Model reproduction of long-term trends in NDVI and underlying changes in LAI

The predicted seasonal maximum NDVI shows a good match with the magnitude of data and the general upward trend extracted by Myneni *et al.* (1997) from the Pathfinder dataset (figure 3). The modelled NDVI also matches the similar trend extracted from GIMMS data, but the magnitude of values deviates slightly (figure 3). Our model therefore provides independent evidence that canopy dynamics in Mediterranean shrublands during the 1980s could feasibly have caused trends in NDVI over this period. The model results suggest that a response of vegetation to climatic change and rising CO<sub>2</sub> is sufficient to explain the observed NDVI, without the need to evoke instrumental bias. On the basis of this evidence, it therefore seems unlikely that changes in NDVI were solely an artificial consequence of drifting sensor calibration, aerosols from volcanic eruptions, a decay in satellite orbit or a shift in the timing of measurements (Gutman 1999, Rasool 1999).

Since our model has a mechanistic basis, it allows further conclusions to be drawn regarding the quantitative changes in canopy structure that underpin variation in NDVI. The value of the NDVI depends on the vegetated fraction of the land surface (Cary and Rosenzweig 1987), the canopy size of the vegetated fraction (Sellers *et al.*, 1992), and leaf absorption of PAR within the canopy (Myneni *et al.*, 1995). Vegetated fraction and canopy size are both dependent on LAI in our model following Betts *et al.* (1997). Since we know of no evidence that leaf absorptance responds to variation in macroclimate, we have adopted a constant value, and changes in LAI are therefore the principal cause of variation in NDVI.

The model results indicate an increase in LAI during the 1980s of approximately  $0.2 \text{ m}^2 \text{ m}^{-2}$  (1982–1992), around 12%, of the mean LAI for Mediterranean shrubland

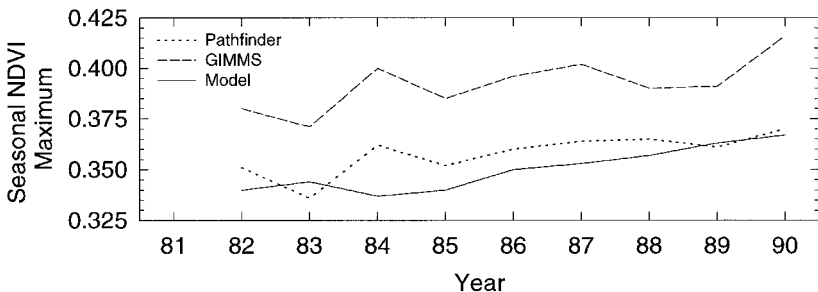


Figure 3. Comparison between modelled and satellite-based estimates of the annual (seasonal) maximum NDVI. Model values are area-weighted means for pixels dominated by shrubland vegetation in the Mediterranean basin (approx. 30–45° N, see text for details). Satellite estimates for 35–45° N were derived from the GIMMS dataset and a revised version of the Pathfinder dataset by Myneni *et al.* (1997).

during this period (figure 4, control). However, extending the time series to the period 1976–1995 reveals that the strong trend in LAI during the 1980s was both preceded and succeeded by rapid decreases (figure 4, control). As a consequence, modelled LAI shows little net change for this 20-year period.

### 3.3. Trends in climate and CO<sub>2</sub> driving the changes in LAI

The period 1976–1995 was characterized by a climatic warming trend in the Mediterranean (figure 1(a)), but this does not seem to have been the principal cause of variation in shrubland LAI. Sensitivity analysis using 20-year monthly mean temperatures (1975–1995) predicted similar variation in LAI to that in the control run (figure 4(a)), leading us to reject warming as a cause of variation. Rising LAI was also not attributable to an increase in the length of the growing season in this evergreen vegetation type, in contrast with observations for vegetation from cooler temperate areas (Myneni *et al.* 1997, Schwartz 1998, Menzel and Fabian 1999).

Our results suggest that precipitation and CO<sub>2</sub> were the principal factors mediating LAI changes in Mediterranean shrublands during the past twenty years. When precipitation was held constant for each month, variation in LAI became minimal, suggesting that changes in precipitation during this period could have exerted a major control on canopy structure (figure 4(b)). Overall, precipitation tended to decrease from 1976–1995, with a minimum in 1983, subsequent rise to a peak in 1987, and reduction to a second minimum in 1992 (figure 1(b)). Canopy LAI tended to lag these changes (figures 1 and 4), since sclerophyllous leaves have an average lifespan of around 18 months (Diamantoglou and Mitrakos 1981, Specht 1988). Storage of carbohydrates and lipids in this vegetation provides a buffer against

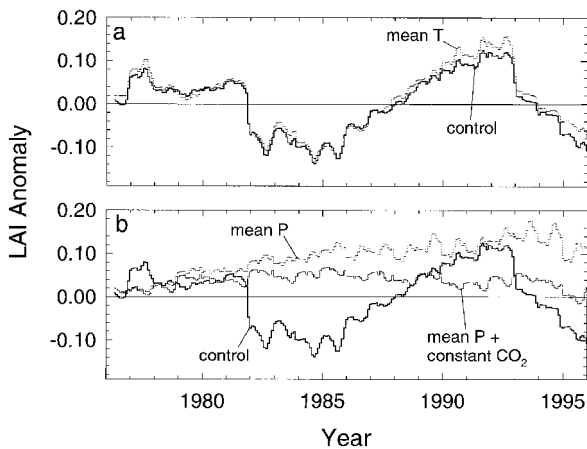


Figure 4. Modelled leaf area index (LAI) in Mediterranean sclerophyllous vegetation for the period 1976–1995, and its regulation in response to climate. In each case, the control run indicates model results obtained with unmodified historical records of climate and CO<sub>2</sub> as data inputs. The LAI anomalies were calculated for each  $0.5^\circ \times 0.5^\circ$  pixel in relation to the 20-year mean for each month, and are shown as an area-weighted mean for this vegetation type in the Mediterranean basin. (a) The effect of removing interannual variation in temperature on LAI. Twenty-year mean monthly temperatures were used in a model run (mean T). (b) The effect of removing interannual variation in precipitation and atmospheric CO<sub>2</sub> concentration on LAI. Twenty-year mean monthly precipitation was used in a model run alone (mean P), and in combination with a constant CO<sub>2</sub> concentration of 330 ppm (mean P + constant CO<sub>2</sub>).

metabolic starvation during drought (Larcher and Thomaser-Thin 1988), and their deep root systems exploit a large volume of soil, allowing access to water during dry periods (Specht 1988, Rambal 1995). These characteristics of sclerophyllous vegetation meant that modelled LAI, and hence modelled NDVI, showed an increasing trend throughout the period 1982–1990, despite a gradual reduction in precipitation in the last three years (figures 1, 3 and 4).

Our results also indicate a key role for rising  $\text{CO}_2$  during the 20-year study period. With constant precipitation and a constant level of atmospheric  $\text{CO}_2$  (the 1975 concentration of 330 ppm), variation in LAI diminished further than with a constant precipitation alone (figure 4(b)). These results therefore suggest that rising LAI during the period 1985–1992 was driven by increases in both precipitation and atmospheric  $\text{CO}_2$  concentration, with a minor additional contribution from temperature (figure 4). The significant role of  $\text{CO}_2$  was unexpected, since it only increased by around 30 ppm, less than 10%, between 1976 and 1995 (Keeling and Whorf 1998).

Water availability is a key control on LAI in semi-arid ecosystems such as Mediterranean shrublands. The LAI is an important determinant of transpiration in this open, aerodynamically rough vegetation (Osborne *et al.* 2000), and tends to be limited by soil water balance, since potential evapotranspiration commonly exceeds precipitation in the Mediterranean basin (Specht 1988). Atmospheric  $\text{CO}_2$  enrichment stimulates leaf  $\text{CO}_2$  uptake and may reduce stomatal conductance in Mediterranean sclerophyllous species, leading to improved leaf water-use efficiency (Scarascia-Mugnozza *et al.* 1996). Previous model simulations suggest that this mechanism may have led to significant increases in LAI during the past century (Osborne *et al.* 2000), and the same mechanism may have reduced the sensitivity of LAI to declining precipitation in the period 1988–1992 (figures 1 and 4).

Although our model suggests that vegetation responses to climate and rising  $\text{CO}_2$  caused NDVI trends during the 1980s, we cannot exclude the influence of changing patterns of land-use. Human pressures on land in the Mediterranean have decreased in the last century, with the abandonment of agricultural land, reduced grazing and a decline in the collection of naturally occurring products (Margaris *et al.* 1996, Rackham and Moody 1996). Reduced land exploitation has tended to allow secondary succession, and reversion of vegetation towards Mediterranean shrubland and forest types, but it may also be associated with land degradation (Margaris *et al.* 1996, Grove and Rackham 1998, Stamou *et al.* 1998). We suggest that secondary succession is unlikely to fully explain the trend in NDVI during the 1980s, which showed significant dips as well as increases (figure 3). Furthermore, our model simulates a significant decrease in LAI in response to drought between 1992 and 1995 (figure 4), and a decline in the observed NDVI for this period would support this result.

### 3.4. Changes in canopy function associated with the variation in LAI

Modelled variation in LAI for the last two decades was associated with significant changes in canopy function over the same period, as indicated by  $\text{CO}_2$  and water exchange. Canopy photosynthesis varied by up to  $1.0 \text{ mol C m}^{-2} \text{ month}^{-1}$  either side of the 20-year mean total for each month, giving a total interannual variation for this period of up to 20% (figure 5), which impacted on modelled values of annual net carbon uptake by vegetation (NPP). The mean annual NPP for above-ground parts of plants during these twenty years was  $14 \text{ mol C m}^{-2} \text{ y}^{-1}$ , but varied by  $\pm 1.0$  (figure 5), an interannual range of around 15%, and a significant fraction of annual

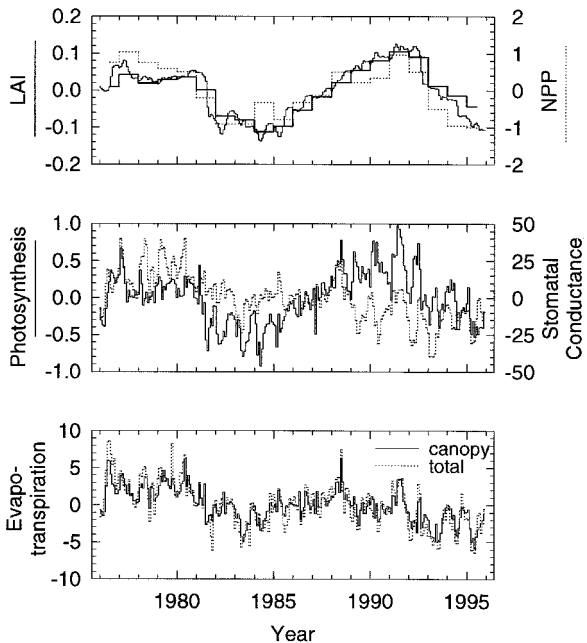


Figure 5. Modelled  $\text{CO}_2$  and water vapour fluxes between Mediterranean sclerophyllous vegetation and the atmosphere for the period 1976–1995. Canopy photosynthesis ( $\text{mol C m}^{-2} \text{ month}^{-1}$ ), net primary productivity (NPP;  $\text{mol C m}^{-2} \text{ y}^{-1}$ ), stomatal conductance ( $\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$ ) and evapotranspiration ( $\text{mm H}_2\text{O month}^{-1}$ ) are expressed as area-weighted mean anomalies, the latter being shown for the canopy alone, and as a total for canopy and soil. Each was calculated for pixels in relation to the 20-year mean for each month, with the exception of NPP, which was calculated on an annual basis. The LAI anomalies are shown on an annual and monthly basis for comparison with fluxes.

growth. Similar changes were modelled below ground, with fine root NPP rising by around 20% between 1983 and 1990 (Woodward and Osborne 2000). Therefore NPP tended to follow a similar trend to, and varied on a relative basis by roughly the same magnitude as, LAI (figure 5).

In contrast with NPP, modelled values of total canopy stomatal conductance in Mediterranean shrub vegetation showed significantly greater interannual variation than LAI throughout the 20-year study period, with monthly values varying by between  $-23\%$  and  $+16\%$  of the 20-year mean for each month (figure 5). Similarly, canopy transpiration and total evapotranspiration each varied significantly around their 20-year mean values for each month (figure 5), having interannual ranges of 43% and 41% respectively. Rising LAI during the 1980s was associated with an increase in canopy transpiration of almost 30%.

Variation in modelled monthly canopy  $\text{CO}_2$  and water vapour fluxes is therefore substantially larger than that in LAI (figure 5). In addition, patterns in the exchanges of both  $\text{CO}_2$  and water from the canopy deviate substantially from that of LAI on a monthly basis (figure 5), since climatic variation has a direct impact on these processes through canopy physiology as well as an indirect effect via canopy structure. Leaf photosynthetic  $\text{CO}_2$  uptake and stomatal conductance to water vapour are regulated in response to light, atmospheric  $\text{CO}_2$  and vapour pressure, temperature

and soil water availability (von Caemmerer and Farquhar 1981, Leuning 1995, McDonald and Davies 1996). Apart from the modification of leaf microclimate by the canopy, particularly with respect to light (Monteith and Unsworth 1990), this regulation of physiology is independent of canopy size. It is therefore not surprising that the exchange of CO<sub>2</sub> and water on short timescales were not strongly dependent on canopy structure in our results (figure 5).

#### 4. Conclusions

Model simulations of Mediterranean vegetation reproduce long-term trends in NDVI inferred from satellite observations during the 1980s. Results indicate that the mechanism for this change is a rise in LAI, suggesting that historical increases in NDVI could have been caused by changes in canopy structure, rather than artificial trends in satellite data. In contrast with the general mechanism proposed for northern temperate vegetation (Myneni *et al.* 1997), our model suggests that changes in the LAI of Mediterranean shrublands were driven by variation in precipitation and rising atmospheric CO<sub>2</sub>, and not increasing temperature. Variation in canopy structure was accompanied by relative changes of a similar or greater magnitude in canopy function, as indicated by CO<sub>2</sub> and water fluxes. Our results for Mediterranean vegetation provide a plausible biological explanation for the long-term increases in NDVI inferred from satellite measurements.

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