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Olive phenology as a sensitive indicator of future climatic warming in the Mediterranean

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ABSTRACT

Experimental and modelling work suggests a strong dependence of olive flowering date on spring temperatures. Since airborne pollen concentrations reflect the flowering phenology of olive populations within a radius of 50 km, they may be a sensitive regional indicator of climatic warming. We assessed this potential sensitivity with phenology models fitted to flowering dates inferred from maximum airborne pollen data. Of four models tested, a thermal time model gave the best fit for Montpellier, France, and was the most effective at the regional scale, providing reasonable predictions for 10 sites in the western Mediterranean. This model was forced with replicated future temperature simulations for the western Mediterranean from a coupled ocean-atmosphere general circulation model (GCM). The GCM temperatures rose by 4·5 °C between 1990 and 2099 with a 1% per year increase in greenhouse gases, and modelled flowering date advanced at a rate of 6·2 d per °C. The results indicated that this long-term regional trend in phenology might be statistically significant as early as 2030, but with marked spatial variation in magnitude, with the calculated flowering date between the 1990s and 2030s advancing by 3–23 d. Future monitoring of airborne olive pollen may therefore provide an early biological indicator of climatic warming in the Mediterranean.

Key-words: *Olea europaea*; airborne pollen; Mediterranean; phenology models; regional climate change.

INTRODUCTION

Phenology is the study of the timing of periodic biological events, and their relationship with the environment, especially climate (Lieth 1974). In recent years, there has been a surge of interest in phenology as an indicator of global climatic change, particularly during spring months (Myneni *et al.* 1997; Schwartz 1998; Crick & Sparks 1999; Parmesan *et al.* 1999; Thomas & Lennon 1999). For example, studies indicate that rising spring temperatures during the past

century have advanced the timing of leafing and flowering in many species at high northern latitudes in both Europe and the USA (Schwartz 1998; Bradley *et al.* 1999; Menzel & Fabian 1999).

Early leaf and flower phenology in temperate trees is, in part, mediated by chilling, which is involved in breaking bud dormancy during spring. The subsequent rate of bud development, and hence the phenology of budburst, depends on the duration and warmth of temperatures or 'thermal time', usually summarized as a cumulative 'heat sum' (Hänninen 1995). Photoperiod may have an additional influence on the timing of vegetative and reproductive bud initiation in some temperate tree species (Wareing 1956; Heide 1993). Since temperatures have a cumulative effect on bud development, the spring phenology of buds may reveal relatively small seasonal changes in temperature. For example, satellite evidence suggests an 8 d advance in the leafing date of high-latitude forests between 1982 and 1990, in association with an increase of about 0·4 °C per year in the spring temperature, mainly during March (Myneni *et al.* 1997).

In cultivated olive (*Olea europaea* L.), flowering occurs between April and June in the Mediterranean, which is late compared to most temperate tree species, but in keeping with a large heat sum to allow inflorescence development and maturity (Chuine, Cour & Rousseau 1998). For this reason, inter-annual variation in temperatures during inflorescence growth exerts the dominant control over the phenology of flowering in this species (Chuine *et al.* 1998). Several models based on thermal time and chilling have been developed for predicting the flowering date in olive, and their comparison shows that the best predictions, from a statistical standpoint, are from thermal time models based solely on spring temperatures (Chuine *et al.* 1998; Chuine, Cour & Rousseau 1999). Chilling temperatures are required to trigger inflorescence development in olive (Denney *et al.* 1985; Rallo & Martin 1991), but the long period of subsequent inflorescence growth means that they have little influence over the timing of flowering. The initiation of inflorescence growth is insensitive to photoperiod in olive (Hackett & Hartmann 1964), and the annual flowering date for an individual site may vary by 20–29 d within a decade (Domínguez Vilches *et al.* 1993; Bricchi *et al.* 1995; Chuine *et al.* 1998). This variation indicates insensitivity of

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floral maturation to photoperiod, but a strong response to temperature. The flowering date in olive may thus be a direct, simple and sensitive biological indicator of climatic warming. Since the geographical limits of olive cultivation approximately delimit the extent of the Mediterranean climate in Eurasia and North Africa (Dallman 1998), this species may be useful as an indicator of temperature changes for the whole Mediterranean region.

Olive pollen is one of the principal causes of allergies in the Mediterranean basin (Domínguez Vilches *et al.* 1993), therefore the timing of pollen release and airborne pollen concentrations have been studied throughout the region (e.g. Frenguelli *et al.* 1989; Belmonte & Roure 1991; Gioulekas *et al.* 1991; Keynan *et al.* 1991). Airborne pollen data are a valuable source of information on flowering phenology, because they record the response of tree populations surrounding the sampling station, rather than the responses of individual trees, as with direct phenological observations. Since airborne pollen may be sampled up to 50 km from its point of release (Cour & Villemur 1985), these data reflect regional variation in phenology due to climate, and smooth out the local effects of microclimate.

Models of phenology can be fitted and tested using dates of flowering inferred from airborne pollen data (Chuine *et al.* 1998, 1999). In conjunction with airborne pollen measurements, these models could provide an important means of interpreting changes in olive phenology in terms of temperature during the spring, and could be applied regionally at a network of sites throughout the Mediterranean. However, phenology may show adaptation to the local temperature regime, since the timing of flowering affects reproductive success (O'Neil 1999). Some studies have found differences in tree phenology between populations (Perry & Wang 1960; Kuser & Ching 1980; van Niejenhuis & Parker 1996; Li, Beaulieu & Bousquet 1997a; Li *et al.* 1997b), while others have not (Farmer 1993; Li, Beaulieu & Bousquet 1993; von Wuehlisch, Krusche & Muhs 1995), and local adaptation depends on the species and spatial scale considered. Any phenological model fitted to a single population of olive must therefore be tested across a wide range of sites and cultivars before use at the regional scale.

Models that simulate the physics of the global climate system and its interaction with deep-ocean circulation provide the current best estimates of future climatic change (Mitchell *et al.* 1995). Simulations of these coupled ocean-atmosphere general circulation models (GCMs) can be replicated by starting the forcing of climate by greenhouse gases at different points in time within an unforced model run (Tett, Johns & Mitchell 1997). This replication accounts for natural variation in climate, and allows the potential variation in future climatic change to be assessed. In combination with the current best models of vegetation processes, these GCM simulations provide a powerful tool for assessing potential future responses of the terrestrial biosphere to climatic change, and allow statistical confidence limits to be attached to estimated responses.

Here, we examine the potential for olive phenology, as indicated by the annual maximum airborne pollen concen-

tration, to be used as a proxy for spring warming in the Mediterranean region. First, we use the findings of recent studies to choose four of the best current models for olive phenology. We fit each to flowering dates inferred from 19 years' pollen data for Montpellier in France, and select the most precise on the basis of its performance at the regional scale. Finally, we drive this model with replicated, state-of-the-art GCM simulations, in order to explore potential changes in phenology that could accompany future spring temperature changes in the Mediterranean. In particular, we suggest the likely time scale on which future trends in flowering date may be distinguishable from fluctuations due to natural climatic variability, and identify geographical locations where phenology could be the most sensitive.

MATERIALS AND METHODS

Fitting and testing regional phenology models

Recent work has shown that thermal time models give more effective predictions of flowering phenology in olive than models that also incorporate the effects of chilling (Chuine *et al.* 1998, 1999). Four thermal time models were therefore compared in this study (Table 1): the Thermal Time model (TT; Cannell & Smith 1983); ForcTT and ForcSar models (Chuine *et al.* 1999); and the Unified Forcing model (UniForc; Chuine, unpublished data). Each was fitted to flowering dates inferred from 19 years' airborne pollen data for Montpellier, France, following the method described in Chuine *et al.* (1998). Flowering date, the date of anthesis or male flower maturation, was estimated as the midpoint of the week when airborne pollen concentrations reached their maximum. In each case, the proportion of total variation in pollen data explained by the model was quantified using R^2, and statistical significance of the model fit was tested using the F statistic (Sokal & Rohlf 1981). All of the phenology models gave highly significant fits to inferred flowering dates ($P < 0.0001$), with R^2 values of 0·86 (TT), 0·84 (ForcTT), 0·70 (ForcSar) and 0·77 (UniForc).

Phenology model fits for Montpellier were tested at the regional scale in comparison with data from Spain, Portugal, Algeria, Israel and Greece (13 sites and 60 records in total), which were independent of those used in model fitting ('cross-validation' *sensu* Chatfield 1988). Models were driven using mean daily temperature records, obtained from national meteorological organizations in each country, or grid-based 0·5° × 0·5° mean monthly temperature data, which were compiled using interpolation of historical observations between 1901 and 1995 (New, Hulme & Jones 1999, 2000). Models were not tested using maximum and minimum temperatures, since mean temperatures from meteorological stations are calculated as the average of these values, and essentially provide the same information. In each case, model performance was assessed using R^2. R^2 may be negative in these tests with external data (Chuine *et al.* 1998), and a positive value indicates that

Table 1. Model definitions and functions

Symbol	Definition
y	Date of flowering (day of year, DOY), as indicated by maximum pollen release
x_t	Daily/monthly mean temperature (°C)
$R_f(x_t)$	Forcing rate function
S_f	State of forcing
F^*	Critical value of S_f for the transition from quiescence to flowering
t_0	Date of the onset of quiescence (DOY)/starting date for heat sum calculation
T_b	Base temperature (°C)

TT model (T_b, F^*, t_0)

$$y \text{ such that } S_f = \sum_{t_0}^{y} R_f(x_t) = F^*$$

$$R_f(x_t) = \begin{cases} 0 & x_t \leq T_b \\ x_t - T_b & x_t > T_b \end{cases}$$

ForcTT model (F^*, T_b)

$$y \text{ such that } S_f = \sum_{t_0}^{y} R_f(x_t) = F^*$$

$$R_f(x_t) = \begin{cases} 0 & x_t \leq T_b \\ x_t - T_b & x_t > T_b \end{cases}$$

$$t_0 = 1$$

ForcSar model (F^*)

$$y \text{ such that } S_f = \sum_{t_0}^{y} R_f(x_t) = F^*$$

$$R_f(x_t) = \begin{cases} 0 & x_t \leq 0\,°C \\ \dfrac{28\cdot4}{1 + e^{-0\cdot185(x_t - 18\cdot4)}} & x_t > 0\,°C \end{cases}$$

(from Sarvas 1974 in Hänninen 1990)

$$t_0 = 1$$

UniForc model (F^*, w, c, t_0)

$$y \text{ such that } S_f = \sum_{t_0}^{y} R_f(x_t) = F^*$$

$$R_f(x_t) = \dfrac{1}{1 + e^{w(x_t + c)}} \quad \text{(where } w \text{ and } c < 0)$$

ForcTT, TT and ForcSar are discussed by Chuine *et al.* (1999), and UniForc by Chuine (unpublished data). All depend solely on the action of forcing temperatures during quiescence, the period when bud ontogeny progresses, and assume that flowering occurs when a critical state of forcing is reached. Forcing is a linear function of temperature in TT and ForcTT (with a base temperature, above which temperatures are active in forcing), but a sigmoidal function in ForcSar and UniForc, its shape being fixed in ForcSar, but fitted to data in UniForc. The date of the onset of quiescence is fitted for the TT model, but constant for ForcTT, and the base temperature is fitted for the TT and ForcTT models.

the model gives a better prediction of annual flowering dates than the inter-annual mean observed flowering date. The value of R^2 increases with the proportion of inter-annual and between-site variation in flowering date explained by the model.

First, models were tested for Valencia, Barcelona, Tortosa, Gerona (Spain) and Oran (Algeria), using both daily and monthly data. This test allowed us to quantify the decline in model performance resulting from the use of large-scale, grid-based monthly meteorological data,

such as those from the GCM, rather than site-based daily weather records. For logistic reasons, simulated temperatures from the GCM are summarized as monthly means for each grid cell, and phenology model runs for the future therefore had to be performed on this basis.

Testing showed that the TT model gave the best prediction of flowering date using these large-scale, grid-based monthly temperature data, with an R^2 value of 0·62 (Table 2). In this case, using monthly rather than daily temperature records made little difference to the effectiveness

Table 2. Effectiveness of four thermal time models in predicting flowering date for olive

Model	TT	ForcTT	ForcSar	UniForc
Temporal resolution of temperature records				
Daily	0·57	0·60	0·55	0·56
Monthly	0·62	0·59	0·40	0·51
Regional differences				
All sites	0·14	0·12	0·12	0·23
Western Mediterranean	0·46	0·45	0·40	0·45

Models were fitted to 19 years' airborne pollen data from Montpellier, France, and tested using independent data from sites throughout the Mediterranean (see Fig. 1 for data sources). Values are the R^2 statistic for model predictions of these independent data, the proportion of variation in pollen data explained by model predictions (Sokal & Rohlf 1981). Comparisons are shown between model predictions made using either daily or monthly temperature (five sites, 23 records) and for all sites (13 sites, 60 records) versus sites in the western Mediterranean only (10 sites, 53 records). Grid-based monthly temperatures were used for the latter comparisons.

of predictions (Table 2). However, predictions using the ForcTT, ForcSar and UniForc models were slightly less effective using monthly, rather than daily, data (Table 2).

Secondly, models were tested for all sites, including those previously listed, plus Córdoba, Málaga, Granada, Sevilla (Spain), Lisbon (Portugal), Jerusalem, Kefar-Sava (Israel) and Thessaloniki (Greece), and also only for those sites located in the west of the region (< 15°E, as defined by Blondel & Aronson 1999). This allowed us to quantify any regional variation in model performance using grid-based monthly temperature data. Regional comparisons showed that model predictions were significantly more effective in the western Mediterranean than in the region as a whole (Table 2). Values of R^2 for all sites were in the range 0·12–0·23, but these improved to 0·40–0·46 if data for sites in the eastern Mediterranean were excluded (Table 2). Since model performance for the whole region was poor, all phenology model runs with GCM data were confined to the western Mediterranean only.

The TT model gave the best predictions for the western Mediterranean using monthly, grid-based temperature data, accounting for 46% of the variation in observations (Table 2; Fig. 1), and this model was selected for runs with GCM data. Airborne pollen concentrations were measured on a weekly basis at all sites, and the flowering date could only be estimated with a weekly precision. Given this limitation, model performance was therefore reasonably good. Simulations by the TT model showed no obvious bias, and almost 70% of predictions for the western Mediterranean were within 1 week of observations (Fig. 1).

Deviations of model predictions from the observed date of maximum airborne pollen concentration were partly due to variation in the meteorological conditions after flower
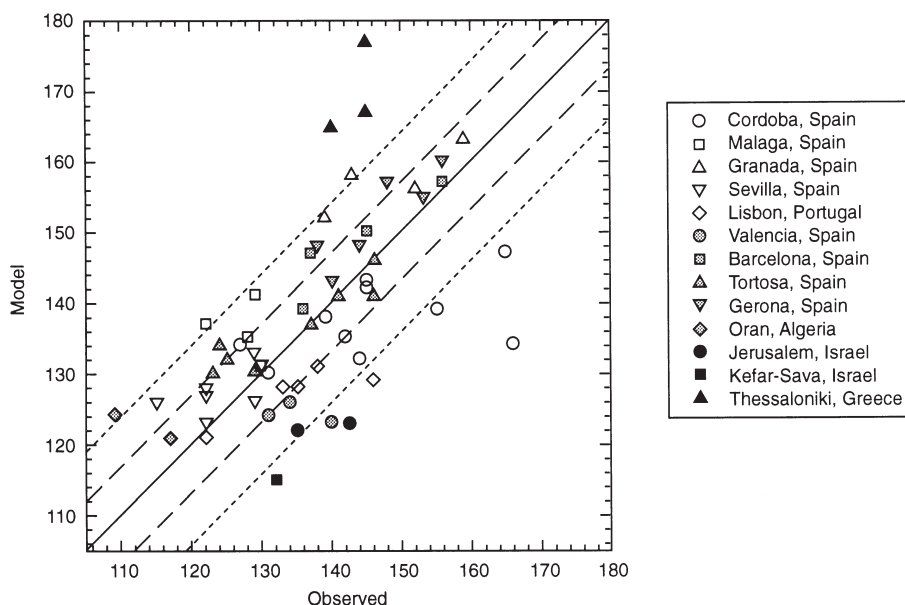

Figure 1. Precision of olive flowering date predictions using the Thermal Time (TT) model (Table 1), fitted to data for Montpellier, France ($F^* = 1370$, $T_b = 2\cdot3$, $t_0 = 5$), and driven by grid-based monthly mean temperature. Observations are the day of year estimated from weekly airborne pollen data, and therefore have a resolution of approximately 1 week. Sites used for the comparison of model runs using daily and monthly temperature records (Table 2) are shown in grey, and additional sites for model testing in the western Mediterranean (Table 2) are in white. Sites in Israel and Greece, where the model performed poorly, are shown in black. The solid '1:1' line indicates a perfect match between model and observations, the dashed lines enclose a precision of ± 1 week, and the dotted lines ± 2 weeks. Sources of published data: Pinto da Silva (1960); Tas & Feinbrun (1962); Gioulekas *et al.* (1991); Keynan *et al.* (1991); Díaz de la Guardia *et al.* (1993); Domínguez Vilches *et al.* (1993); Recio *et al.* (1996); González Minero & Candau (1997).

bud burst. Precipitation and high relative humidity during anthesis 'washes' pollen from the atmosphere, tending to reduce airborne concentrations (Recio *et al*. 1996), and this effect was partially accounted for in estimations of the peak flowering date following the method described by Chuine *et al*. (1998). In addition, the length of time between flower bud burst and pollen release depends strongly on the dry conditions, high incident solar radiation and temperatures required for anther dehiscence (Chuine *et al*. 1998). Wind strength and direction may also play a part in determining the airborne pollen concentrations sampled during anthesis, particularly if olive groves are distributed unevenly around the sampling station (Recio *et al*. 1996).

In driving the TT model using GCM simulations for the western Mediterranean, we have the greatest confidence in the results for southern France, where the model was fitted, followed by those for the Iberian Peninsula, where the model performed well (Fig. 1). Simulations were run for north-west Africa because model predictions were reasonable for 2 years in Oran, Algeria (Fig. 1); however, these should be regarded as preliminary findings, since more extensive model testing is needed for this region.

GCM climate scenarios and phenology

Regional olive phenology for the period 1990–2099 was estimated by driving the TT model of flowering date with monthly temperature simulations from the Hadley Centre GCM (HadCM2). Future rates of climate change will depend on the rate of increase in atmospheric concentrations of greenhouse gases, which cause warming via radiative forcing. Since changes in future greenhouse gas concentrations will depend largely on political controls of emission rates, we considered two alternative scenarios, each starting in the model year 1990.

The first was the Intergovernmental Panel on Climate Change (IPCC) 'IS92a' scenario, in which controls on anthropogenic greenhouse gas emissions are not initiated in the future. This would result in an approximately 1% increase in radiative forcing per annum – the GGa climate change scenario. The second was a scenario in which significant controls on anthropogenic emissions of greenhouse gases are imposed, the IPCC 'IS92d' scenario (Schimel *et al*. 1994, 1996). This would cause an approximately 0·5% increase in radiative forcing per annum – the GGd climate change scenario. The GCM was used for each climate change scenario to produce four replicate series of future temperatures for the Mediterranean region (Mitchell *et al*. 1999). The mean increase in regional temperature simulated by the GCM between 1990 and 2099 was 4·5 °C for the GGa scenario and 2·4 °C for the GGd scenario.

Monthly temperature series were constructed using temperature anomalies for each GCM integration calculated in relation to its 1961–1990 reference period. Data for driving phenology model runs were obtained by adding these anomalies to temperature observations for the reference period from the 0·5° × 0·5° grid-based observed climate dataset described above.

Results of phenology model runs with the GCM data were used to suggest when future trends in flowering date caused by climatic warming might be distinguishable from changes due to natural climatic variation. Systematic and routine monitoring of pollen at the genus level is not yet widespread in the Mediterranean, and data to test model results at the regional scale will therefore only be available in the future. For this reason, trends were analysed for the period 2000–2099. Data were divided into time series of increasing length from the year 2000, i.e. 2000–2003, 2000–2005, 2000–2007, and so on. In each series, linear variation over time was quantified by using orthogonal coefficients to partition the total sum of squares between linear and residual components (Table 16·5 in Sokal & Rohlf 1981). The statistical significance of the linear component was determined using the *F* statistic, which is a measure of the variation in data caused by a linear trend, relative to the residual variation in data (Sokal & Rohlf 1981).

RESULTS

Model simulations indicated that the flowering date for olive in the western Mediterranean could become significantly earlier by 2099, irrespective of future rates of greenhouse gas emissions. The 4·5 °C rise in temperature produced by the GCM for the GGa future climate change scenario led to an average advance in modelled flowering date of nearly 30 d, or 6·2 d per °C (Fig. 2a). The equivalent average advance for the GGd scenario was 10 d in response to a 2·4°C warming, or 4·2 d per °C (Fig. 2b). The four replicate climate simulations for each future scenario produced different rates of warming in the GCM, and hence changes in modelled phenology. However, every replicate GCM run led to a marked regional change in the simulated date of flowering for olive by 2099 (Fig. 2a,b), suggesting that phenology in this species is highly likely to show a climate signal in the future.

To provide an estimate of future years when this climate signal might become distinguishable from background variation in flowering date, statistical confidence was attached to the trends in modelled phenology using an *F* statistic (Fig. 3). For each year in the future, a significant value of *F* indicates a statistically significant trend in modelled phenology during the preceding years. The value of *F* is significant if it exceeds the critical values indicated by solid lines in Fig. 3, which correspond to increasing levels of significance.

Statistical analysis suggested that significant regional trends in olive phenology may be largely independent of future rates of greenhouse gas emissions. Modelled trends could not be detected from background variation earlier for the GGa than the GGd scenario, despite a nearly 2 °C faster rate of warming in the GCM. Statistically significant linear trends in phenology appeared as early as 2011 in the model run for GGd, and 2019 for GGa, but non-significant results in following years indicated that these were short-term progressions, which could be offset by subsequent dips in the simulated GCM temperature (Fig. 3). Long-term, regional
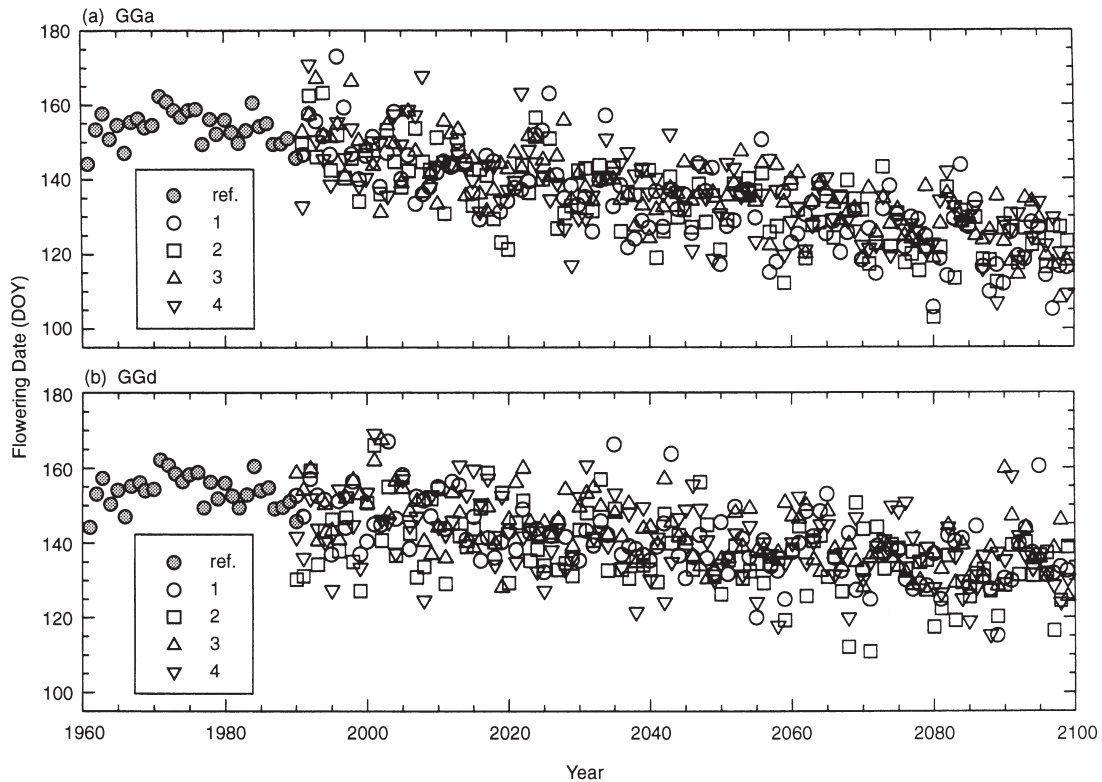
Figure 2. Model simulations of future olive flowering date in the western Mediterranean. Predictions were made using the Thermal Time (TT) model (Table 1), driven using future temperature simulations from the Hadley Centre General Circulation Model (HadCM2). Results are day of year (DOY) for four replicate runs of the GCM, under two future scenarios for radiative forcing by greenhouse gases: GGa, with a 1% annual increase in radiative forcing of climate from 1990 (top panel), and GGd, with a 0·5% annual increase (bottom panel). Further details of climate change scenarios are given in the text. Results for the 1961–1990 reference period are also shown, obtained from a model run using observed temperature data. Symbols distinguish results for this reference period (ref) and the four replicate runs of the GCM (1, 2, 3, 4).

changes in modelled phenology, which were not reversed by later decreases in temperature, were only statistically significant from 2021 in the GGd scenario and 2029 in GGa (Fig. 3). Our results therefore suggest that, if long-term and extensive regional monitoring of airborne pollen starts in the western Mediterranean within the next few years, a clear temperature signal in olive phenology will be apparent by the 2030s. This signal may be detected earlier for sites where routine long-term recording has already begun, such as those locations in Spain and France indicated in Fig. 1.

The rate of future climatic warming simulated by the GCM varied significantly within the Mediterranean region, and caused marked geographical variation in the advance in phenology predicted for olive (Fig. 4). The model predicted that phenology will advance most strongly in large parts of southern France and Algeria, Tunisia, isolated areas in Morocco, most of the southern Iberian Peninsula, and on Mediterranean islands (light grey areas in Fig. 4). The weakest model responses occurred at the northern limits of olive cultivation in Portugal, Spain and parts of southern France (black areas in Fig. 4). Simulated changes
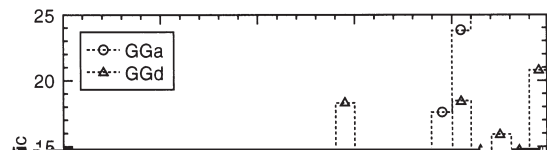

Figure 3. Values of the *F* statistic obtained by using orthogonal coefficients to partition the variation of data in Figure 2 between linear and residual components. Data for the year 2000 onwards were analysed as successively longer time series: 2000–2003, 2000–2005, 2000–2007, and so on, and the results are plotted against the last year in the series. Critical values of *F* for $P = 0·10$, $P = 0·05$ and $P = 0·01$ are shown for comparison. A value of *F* greater than the critical value indicates a significant linear trend in modelled flowering date for the preceding years.

Change in Flowering Date (DOY), 1990s to 2030s
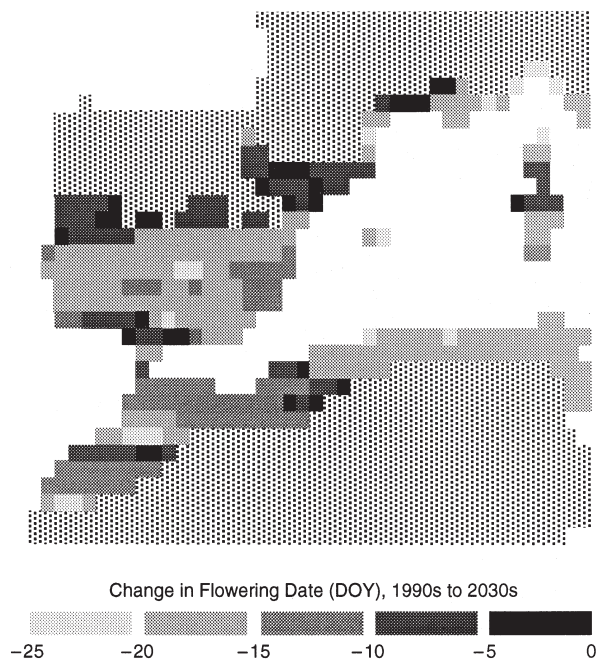
−25   −20   −15   −10   −5   0

Figure 4. The spatial response of modelled flowering date to future climatic warming in the western Mediterranean. The flowering date for olive (day of year, DOY) was predicted using the Thermal Time (TT) model (Table 1) driven using future temperature simulations from the Hadley Centre General Circulation Model (HadCM2). Predictions were made within the limits of olive cultivation, following the distribution map of Dallman (1998), for grid squares of 0·5° × 0·5° in size. Shaded grid squares on the map represent the difference between decadal mean predictions for the 2030s and 1990s. Negative values indicate that flowering phenology advanced to an earlier date during this period. Each decadal mean was calculated from the four model simulations for the GGa climate change scenario (see text for details).

in phenology for the 2030s were also small in the south of Spain, the western and eastern extremities of the Atlas Mountains in North Africa, and parts of Corsica and Sardinia (black areas in Fig. 4). Our model therefore indicates that the magnitude of future temperature-induced changes in phenology is likely to vary considerably within the region, advancing by 3–23 d between the 1990s and 2030s. This variation indicates high spatial variation in the response of GCM spring temperature to radiative forcing of climate in the Mediterranean.

Marked spatial variation in temperature changes is illustrated by results of the phenology model for grid cells containing Montpellier and Nice, located approximately 275 km apart in southern France (Fig. 5a). Mean spring temperatures are similar in the two cells, but the increase in temperature during spring is more pronounced at Montpellier, causing olives to flower earlier (Fig. 5a). In addition, altitude varies markedly in the grid cell containing Nice, from sea level to more than 1500 m, and small parts of this area are marginal for olive production at present. Modelled

olive phenology showed a marked forward trend at Nice, but little net change at Montpellier, changing the difference between predicted flowering dates at the two sites from 49 d in the 1990s to 23 d in the 2040s (Fig. 5a). However, a long-term forward trend in simulated phenology was only distinguishable from natural variation in 2038, the same date for both sites ($P < 0.05$; Fig. 5b).

DISCUSSION

Model results suggest that olive phenology may be a sensitive indicator of inter-annual trends in spring temperature, and demonstrate its potential as a measure of the biological impacts of future climatic warming (Figs 2–5). The flowering phenology of olive in the Mediterranean may be at least as sensitive to rising spring temperatures as the phenology of plants in cold temperate biomes, where climatic warming may already be having a detectable impact on the phenology of terrestrial vegetation. For example, at sites throughout north-west and central Europe, leaf bud burst during spring, the timing of flush growth and flowering advanced by an average of 6 d between 1959 and 1993 (Menzel & Fabian 1999). Similarly, modelled spring leaf emergence in the central and eastern USA moved forward by around 11 d between 1978 and 1990 (Schwartz 1998). Over a longer period, between 1936 and 1998, the date of first bloom of 10 spring flower species in Wisconsin, USA,
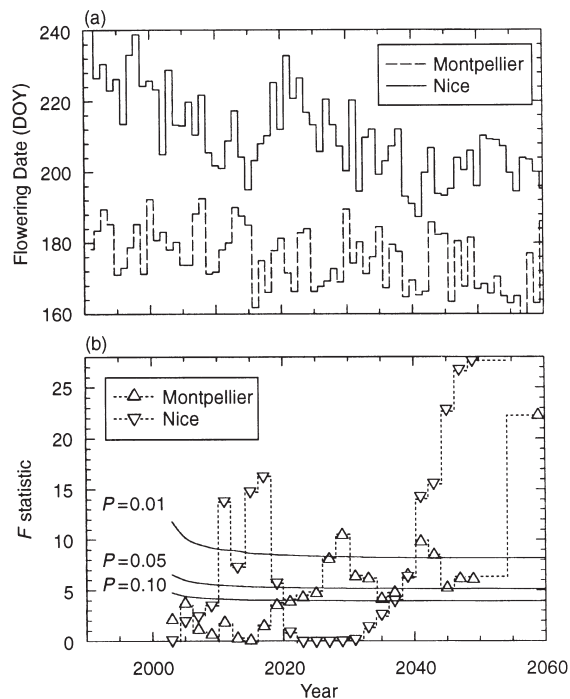

Figure 5. Predicted flowering date for olive at Nice and Montpellier in southern France, and linear partitioning of the variation in these data. The top panel (a) shows the mean modelled flowering date for each site, calculated for the GGa climate change scenario, as in Figure 2. The lower panel (b) shows values of the F statistic for each site, as in Figure 3.

became earlier by an average of 13 d, although flowering dates in 15 other species did not change (Bradley *et al.* 1999). These reported changes in phenology accompanied increases in temperature during March–May of approximately 1–2 °C across central, southern and western Europe, and a similar or larger rise in temperature during December–February in the central and eastern USA (Jones *et al.* 1999).

Spring temperature in the Mediterranean has risen by 1–2 °C during the past two decades (Jones *et al.* 1999), and, if our analysis for olive is correct, we expect that significant changes in flowering phenology will already be recorded in airborne pollen data. To test this expectation, we examined data from Montpellier for the years 1973–1992 (Chuine *et al.* 1998). Although our results suggest only relatively small future changes for the site, these historical data indicate that spring temperature rose significantly at Montpellier during the period 1984–1992 (Fig. 6b). Linear regression showed that the flowering date inferred from pollen data occurred at progressively earlier dates during this period, supporting expectations (Fig. 6a). Data showed that the timing of maximum pollen concentrations advanced by approximately 8·5 d per °C (Fig. 6a,b), suggesting a similar temperature sensitivity for olive flowering phenology to that of spring phenology in cool temperate species. Future
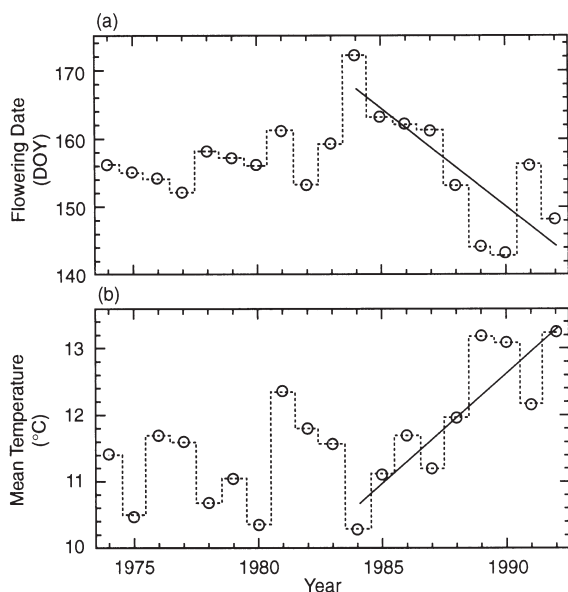
temperature-induced changes in olive phenology of 30 d or more are feasible, as suggested by the inter-annual variability for individual sites in Fig. 1.

Future changes in the radiative forcing of climate, and hence temperature, will be largely driven by an increase in atmospheric CO_2 concentrations (Schimel *et al.* 1996). This increase is likely to have a significant direct impact on the physiology and structure of vegetation in the Mediterranean (Osborne & Woodward, 2000; Osborne *et al.* 2000); however, the effects of CO_2 enrichment on the phenology of Mediterranean species remain unknown. Elevated CO_2 may retard or have no effect on the timing of leaf bud burst in trees, and responses vary between species and varieties (Murray & Ceulemans 1998). Experiments are needed in the future to address the possibility of direct CO_2 effects in olive, which could interact with those of increasing temperature, and potentially offset changes in phenology. However, if direct effects of CO_2 do occur, they are likely to be weak, probably less than 5 d over the next century (Murray & Ceulemans 1998), and less significant than the probable temperature effect of up to 30 d (Fig. 2).

A phenology model fitted to olive flowering dates for Montpellier gave accurate predictions of flowering dates for sites throughout the western Mediterranean (TT model, Table 2, Fig. 1). This suggests that local adaptation of phenology to temperature does not occur to a significant extent for olive populations in the western Mediterranean (Table 2), supporting the regional application of a phenology model in this case. Previous studies have drawn similar conclusions for this region, with phenology model estimates for olives in southern France and western Spain differing by only 0·6% (Chuine *et al.* 2000). However, *O. europaea* has a very complicated genetic structure for historical reasons (Ouazzani *et al.* 1993; Ouazzani, Lumaret & Villemur 1996). More than 1000 different cultivated varieties exist after thousands of years of artificial selection, and, although selection was primarily on fruit properties such as size, oil content and colour (Rosenblum 1997), it may have affected reproductive phenology. Varietal similarities between Portugal, Spain, France and Algeria and differences with Israel and Greece may therefore explain regional variation in model precision (Table 2), but more data for the eastern and southern Mediterranean are necessary to confirm this suggestion.

Airborne pollen concentrations at a sampling station reflect the phenology of olive populations over an area of up to around 8×10^3 km^2 (Cour & Villemur 1985), and in the future pollen monitoring may therefore provide a useful method to complement direct phenological observations, allowing observations at a larger, regional scale. Inferences about the timing of leaf bud burst in spring have already been made at a similar scale from satellite radiance measurements over deciduous vegetation at high latitudes (Myneni *et al.* 1997). However, this method is less useful for monitoring changes in the spring phenology of vegetation in the Mediterranean, which is largely evergreen (Osborne & Woodward, 2000). Systematic future measurements of airborne olive pollen could therefore complement existing

Figure 6. Observed trends in the flowering date of olive (top panel, a) and the spring temperature (bottom panel, b) in Montpellier, France. Flowering dates are the day of the year (DOY) when maximum airborne pollen concentrations were recorded for this species (Chuine *et al.* 1998). Mean temperatures are for March–May from a monthly grid-based data series (New *et al.* 1999, 2000). Least-squares regression of mean temperature and flowering date on year indicated that trends for 1984–1992 were statistically significant at the $P = 0.01$ level, and these are indicated by solid lines. Regressions for 1974–1983 were not significant.

approaches in this region, and provide valuable information about the biological impacts of climatic change.

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