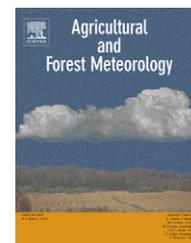


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## Modelling interannual and spatial variability of leaf senescence for three deciduous tree species in France

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### ABSTRACT

The annual timing of temperate forest leaf colouring is affected by climate change; to date, its modelling remains a challenge. We take advantage of a ca. 400 leaf colouring observations database acquired in France during the period of 1997–2006 in order to develop a new modelling framework aimed at predicting the spatial and year-to-year variability of leaf colouring in European beech and oak (*Fagus sylvatica* L., *Quercus petraea* (Matt.) Liebl. and *Quercus robur* L.). We postulate colouring to be the outcome of a one-way process triggered by photoperiod and progressing through a photoperiod-sensitive cold-degree day summation procedure. Observations were pooled according to genus for the fitting and ensuing validation procedures. Parameters of the model suggest that colouring processes start earlier, and are sensitive to higher temperatures for *Quercus* than for *Fagus*. Errors associated with the modelled predictions are up to 13.0 days in *Fagus* and 10.3 days in *Quercus*, which are significantly lower than errors associated with (1) the overall mean (null model) or (2) previously published modelling frameworks. When averaged on a site basis, model predictions reproduced spatial variability of leaf colouring over the French territory with good efficiency (modelling efficiencies: 0.44 for *Fagus*, 0.45 for *Quercus*). The interannual variability of leaf colouring over France was fairly reproduced ( $r^2 = 0.74$  for *Fagus*, 0.83 for *Quercus*). On that basis, we claim that the modelling framework developed herein can be efficiently integrated into more general schemes aimed at simulating matter and energy fluxes on a regional scale, and we provide a generic parameterisation of the model to be integrated into such schemes. When used in a prospective analysis, the model predicts a trend towards delay in leaf colouring of 1.4 and 1.7 days per decade in *Fagus* and *Quercus*, respectively, over the period of 1951–2009 in France.

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## 1. Introduction

Phenology is the science dealing with periodic biological events in animals and plants, as influenced by environmental

conditions. The compilation of phenological data dates back centuries (Sparks and Menzel, 2002), though the scientific community's interest in phenological studies renewed only a few decades ago, with the recognition of phenological data as a

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valuable tool for addressing the question of ecosystems responses to climate change (Menzel et al., 2006).

For deciduous trees, the timings of bud burst and leaf senescence define canopy duration and thereby determine the timing of carbon assimilation from stand to global scale (e.g. Baldocchi and Wilson, 2001; Barr et al., 2007; Keeling et al., 1996). Both phenological phases ultimately influence vegetative growth and species fitness (Lechowicz and Koike, 1995; Rathcke and Lacey, 1985). Springtime phases have been reported to dominate the influence of autumn phases in modulating the timing of carbon assimilation in deciduous forests. Early leaf out has been related to longer carbon uptake period and to increased net annual flux (Churkina et al., 2005; Goulden et al., 1996), while the timing of leaf senescence shows less year-to-year variability and is concomitant with less favourable conditions for photosynthesis (Morecroft et al., 2003). Leaf senescence is nonetheless of primary importance in determining heterotrophic (and therefore ecosystem) respiration dynamics (Hibbard et al., 2005; Knohl et al., 2003), as leaf litter represents half of annual litter input. Authors therefore recognise the importance of accurate modelling for the timing of leaf fall, especially for capturing the autumnal pattern of net ecosystem carbon exchange (Davi et al., 2006; Del Grosso et al., 2005).

While spring and summer phenological phases have shown a recent trend towards earlier occurrence, trends towards a delayed leaf colouring and fall were depicted for deciduous species, from a regional scale (+ 3 and +5 days over the period of 1951–1999 for German *Fagus* and *Quercus* plots, in Schaber and Badeck, 2005) to a continental scale (+4.8 days over the period of 1959–1993 in Menzel and Fabian, 1999). Trends in the timing of phenological stages observed over the last 50 years have been related to temperature increase for leaf out (Chmielewski and Rötzer, 2001; Menzel et al., 2006) and leaf senescence (Menzel et al., 2006). The resulting lengthening of the leafy season at temperate latitudes, through an earlier spring and delayed autumn, has been proposed as a cause of an increase in the terrestrial carbon sink during the 1980–1990s (Myneni et al., 1997; Nemani et al., 2003). However, this functional link was questioned in a recent study by Piao et al. (2008), who suggested that the increased ecosystem respiration associated with warmer autumnal temperatures may offset the carbon uptake related to an advanced spring.

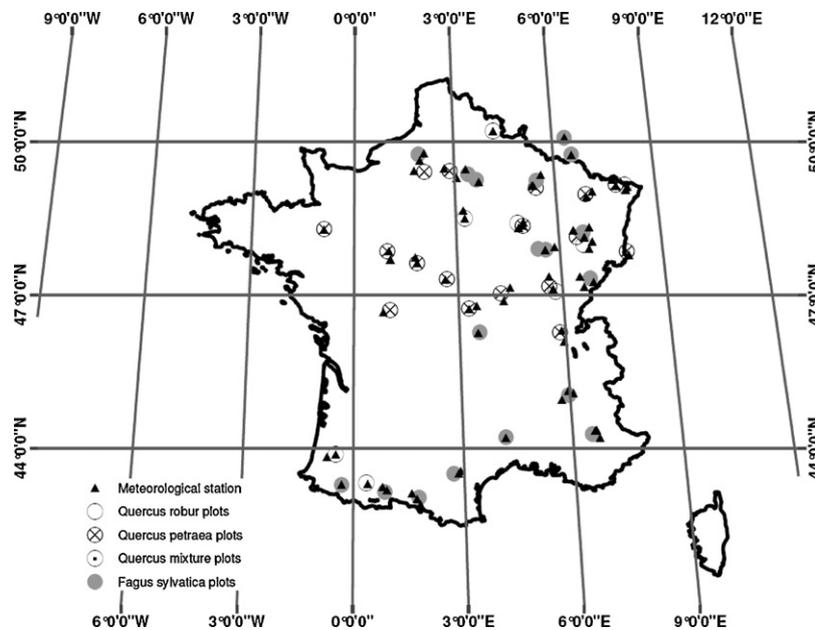
To date, understanding the processes behind leaf senescence is still a challenge. Though some of the implied molecular agents of senescence have been identified and related to stress-responses pathways (Lim et al., 2007), environmental triggers and their interactions are still far from clear. Several studies suggest low temperatures (e.g. daily mean temperature below a 8 °C threshold; Estrella and Menzel, 2006) and short days (e.g. Addicott, 1968; Koike, 1990; with a 13-h photoperiod threshold by 63°N latitude in Keskitalo et al., 2005) to be among the main factors involved in triggering leaf senescence in deciduous trees. Consistent with the low temperature trigger hypothesis, Menzel (2003) reported positive correlations between August and September mean temperature and leaf colouring dates in *Fagus sylvatica* and *Quercus robur*. Severe drought (e.g. Bréda et al., 2006), as well as water logging or mineral deficiencies (Smart, 1994) were similarly invoked as possible factors hastening leaf fall in

deciduous species. Estrella and Menzel (2006) reviewed published hypotheses proposed to predict the onset of leaf colouring (most of which were temperature-related). These authors further reported that most hypotheses were theoretical, and that none had been thoroughly validated. Application of these hypotheses on the German International Phenological Gardens (IPG) database proved that all failed to accurately predict leaf colouring occurrence of deciduous tree species in temperate regions.

As a result of the lack of experimental evidence regarding involved factors, and contrary to other phenological stages such as leafing and flowering, no consensus can be found in the literature concerning the formulation of leaf senescence models (Chuine et al., 2003; Schaber and Badeck, 2003). Most models are based on empirical relationships (e.g. minimum temperature threshold under which senescence is triggered as in Krinner et al., 2005; Sitch et al., 2003), or they invoke leaf carbon-balance hypotheses (Arora and Boer, 2005), but none has been thoroughly validated. For instance, White et al. (1997) reported a model based on a temperature-modulated photoperiod trigger, aiming at representing leaf fall date monitored through remote sensing (NOAA-AVHRR Normalised Difference Vegetation Index (NDVI) time series). This model was fitted and validated on the same 21-point dataset and simulated the observed senescence state with 1-week accuracy. Jolly et al. (2005) proposed the use of a Growing Season Index, modulated at temperate latitudes by photoperiod and daily minimum temperature, to model the occurrence of leaf colouring for 7 years at the Harvard forest. Though small (2 days), the predicted mean absolute error was not different from the null (overall mean) model error.

Apart from uncertainties regarding the factors controlling senescence processes, one reason for the scarcity of published literature regarding leaf senescence modelling is the lack of ground observations. Despite the increasing interest in using remotely sensed spectral vegetation indices to monitor canopy dynamics, these indices still remain to be validated against ground observations (Fisher and Mustard, 2007; Soudani et al., 2008). Field colouring observations are far less common than bud burst observation, being (1) more difficult to monitor than leaf out stages in trees from an observer's viewpoint and (2) more frequently disturbed by weather (e.g. winds) or biological (i.e. pathogens) events. However, leaf senescence has been continuously monitored for more than 50 years within the European IPG network, through observations of the 50% canopy yellowing (see Estrella and Menzel, 2006 for details).

Unfortunately, France is not involved in the IPG network, but it did recently develop its own phenological observation network. We took advantage of this new database to propose a modelling framework for leaf colouring. Objectives of this study are: (1) to present an original modelling framework aimed at predicting the interannual and spatial variability of leaf colouring for two temperate deciduous genera over France, (2) to compare the model with pre-existing modelling frameworks defined in the literature, (3) to provide a generic parameterisation of the model to be integrated in regional SVAT schemes and (4) to use the model as a prospective tool for predicting leaf colouring occurrence in *Fagus* and *Quercus* over France for the 21st century.



**Fig. 1** – Location of the RENECOFOR and associated METEOFRACTE stations. Distinction is made between *Quercus robur* (circles), *Quercus petraea* (cross circles), *Quercus* sp. (dot circles), *Fagus sylvatica* (disks) sites. Triangles locate meteorological stations.

## 2. Methodology

### 2.1. Phenological observations

A long-term observational network (RENECOFOR) was set by the French forestry service (Office National des Forêts) in 1992. The network includes 51 deciduous forest sites over the French and Luxembourgian territories (latitude 42°55'53"N to 50°10'16"N, longitude 3°32'34"W to 7°43'46"E) (Fig. 1). Sites are located between 20 and 1400 m ASL, encompassing a mean annual temperature (MAT) range from +5.7 to +13.9 °C. Three of the most representative deciduous species in Western Europe are represented: *F. sylvatica* L. (European Beech: 22 sites), *Quercus petraea* (Matt.) Liebl. (Sessile Oak: 19 sites) and *Q. robur* L. (Common Oak: 8 sites). Two extra sites are composed of a mixture of the two oak species. Except for the latter, all sites are monospecific homogeneous stands of an area of 2 ha. For the period of 1997–2006, phenological observations were carried out weekly from March to June for budburst and from September to November for leaf colouring. Over all RENECOFOR sites, observations were performed on the same day of year (DoY) for each weekly campaign. For every site, phenological observations were performed on a sample of 36 trees located in the central 0.5 ha area of the study plot. Two phenological stages were defined during the colouration phase: (1)  $Y_{10,obs}$  represents the date (DoY) on which 10% of the trees show yellow leaves over 20–50% of their crowns, (2)  $Y_{90,obs}$  represents the date (DoY) on which 90% of the trees show yellow leaves over 20–50% of their crowns. Occurrences of both phenological stages are correlated ( $r = 0.81$ ,  $p < 10^{-4}$  for both genera), and modelling was performed on both data sets. Model performances were always better for the later stage of senescence (not shown). We therefore focus in the present study on the  $Y_{90,obs}$  observations dataset. As no assessment of

the observer bias was performed, and due to the weekly timing of observation campaigns, we assume that the error associated with each observation had a uniform distribution of a 7-day range. Among the 407 observations spread over 43 sites present in the original database, a total of 36 (9%) were excluded for being recognised as unreliable (from fieldworkers comments) or lacking meteorological data. A brief description of the phenological dataset is reported in Table 1.

### 2.2. Meteorological data

Eleven RENECOFOR stands were equipped with meteorological stations recording the temperatures daily minimum ( $T_{min}$ ) and maximum ( $T_{max}$ ). For all other stands, we constructed temperature time series from daily data collected by meteorological stations of the French meteorological service (METEOFRACTE). Meteorological stations had to meet a distance criterion (<25 km) in order to be included in the reconstructed time series (Fig. 1). A lapse rate of 0.6 °C per hectometre (Thornton et al., 1997) was applied to correct for altitudinal differences between the meteorological and RENECOFOR stands. Reconstructed  $T_{min}$  and  $T_{max}$  time series were computed as the mean of the daily observations over all retained meteorological stations, weighted by the inverse of the distance to the RENECOFOR stand. We used daily mean temperature as a meteorological driver to our bioclimatic model. Daily mean temperature was computed as the arithmetic mean of  $T_{min}$  and  $T_{max}$ .

### 2.3. Modelling framework

The model developed herein postulates leaf colouring to be driven by both photoperiod and low temperatures. A basis for this modelling framework was exposed in a former modelling

**Table 1 – Statistical description of the colouring observations datasets. The mean, minimum and maximum dates (DoY), number of observations within the dataset (n), mean annual temperature (MAT, °C) and altitude (median [min; max], m) are reported.**

	Mean (SD)	Min	Max	n	MAT (SD)	Altitude
<i>Quercus robur</i> (6 sites)	302 (15)	272	345	50	11.7 (1.1)	170 [20; 370]
<i>Quercus petraea</i> (17 sites)	299 (11)	264	334	148	11.4 (0.7)	220 [55; 330]
<i>Quercus robur + petraea</i> (2 sites)	305 (6)	297	318	14	11.0 (1.0)	215 [80; 350]
<i>Quercus</i> sp. (25 sites)	301 (13)	264	345	212	11.4 (0.8)	190 [20; 370]
<i>Fagus sylvatica</i> (18 sites)	293 (16)	244	332	159	9.8 (1.8)	400 [50; 1400]

work exposed by Dufrière et al. (2005; their Eq. (16)), who proposed a dependence of leaf colouring date on a cold-degree day sum.

The aim of the present model is to predict the occurrence of leaf colouring at the stand scale. Leaf colouring is postulated to be the outcome of continuous senescence processes starting on date  $D_{start}$  (DoY). We let  $D_{start}$  vary with latitude according to the photoperiod parameter  $P_{start}$ . We define a colouring state ( $S_{sen}$ , arbitrary units) for each day ( $d$ ) following  $D_{start}$ , representing the progress of the senescence processes. Leaf colouring is achieved on  $Y90_{mod}$  date (DoY), when  $S_{sen}$  reaches a threshold value ( $Y_{crit}$ , arbitrary units). We model the time derivative of the state of colouring ( $R_{sen}$ , arbitrary units) on a daily basis as:

$$\text{If } P(d) < P_{start} \begin{cases} \text{if } T(d) < T_b & R_{sen}(d) = [T_b - T(d)]^x \times f[P(d)]^y \\ \text{if } T(d) \geq T_b & R_{sen}(d) = 0 \end{cases} \quad (1.1)$$

so that,

$$\text{If } \begin{cases} P(d) \geq P_{start} & S_{sen}(d) = 0 \\ P(d) < P_{start} & S_{sen}(d) = S_{sen}(d - 1) + R_{sen}(d) \end{cases} \quad (1.2)$$

$$\text{If } S_{sen}(d) \geq Y_{crit} \quad Y90_{mod} = d \quad (1.3)$$

where  $P(d)$  is the photoperiod on the day of year  $d$ ;  $T(d)$ , the daily mean temperature (°C);  $T_b$ , the maximum temperature at which senescence processes are effective (°C);  $f[P(d)]$ , a photoperiod function that can be expressed as follows:

$$f[P(d)] = \frac{P(d)}{P_{start}} \quad (2.1)$$

or

$$f[P(d)] = 1 - \frac{P(d)}{P_{start}} \quad (2.2)$$

The complete model therefore includes five parameters ( $P_{start}$ ,  $T_b$ ,  $x$ ,  $y$ ,  $Y_{crit}$ ). The dummy parameters  $x$  and  $y$  (Eq. (1.1)) may take any of the {0, 1, 2} discrete values, to allow for any absent/proportional/more than proportional effects of temperature and photoperiod to be included. Higher (up to three) and continuous (non-discrete) values of the  $x$  and  $y$  parameters were tested in preliminary runs, but did not provide better fitting quality. This approach allows for the testing of four model structures, the progress of colouring processes being dependent ( $x > 0$ ) or not ( $x = 0$ ) on temperature and modulated ( $y > 0$ ) or not ( $y = 0$ ) by photoperiod. If the

Eq. (2.1) photoperiod modifier is included ( $y > 0$ ), photoperiods shorter than the  $P_{start}$  threshold weaken the cold-degree sum effect (i.e. Eq. (2.1) modifier starts from unity on  $P_{start}$  and shows subsequently a monotonic decreasing trend). On the other hand, the use of the Eq. (2.2) modifier amplifies the cold-degree sum effect under short photoperiod conditions relative to  $P_{start}$ . We term our bioclimatic model “DM” in the following.

Besides developing our own framework for modelling colouring processes, we considered the modelling frameworks proposed by White et al. (1997; hereafter termed WM) and Jolly et al. (2005; hereafter termed JM). WM is based on the assumption of photoperiod and temperatures thresholds required for senescence to occur. JM consists of a greenness index depending, at temperate latitudes, on photoperiod and minimum daily temperature. In the following, we compare the modelling performances of the null model (overall mean; NM), WM, JM and our bioclimatic models. We term our bioclimatic model DM in the following.

#### 2.4. Model fitting and validation

All bioclimatic models (JM, WM and DM) were fitted independently for each genus (*Fagus* and *Quercus*) based on a subset of phenological observations. We mixed both *Quercus* species datasets after having checked for the absence of significant “species” effect on the  $Y90_{obs}$  observations within the *Quercus* genus for three pairs of neighbour sites, to ensure the exposure of the plots to analogous temperature conditions (two-ways ANOVA, not shown). Statistical validation of the models was performed by dividing the original dataset into two subsets used (1) to fit the model parameters and (2) to assess the genericity of the model in analogous geographic and climatic ranges. Observations incorporated within each subset were selected so that the differences of overall variances and means between fitting and validation subsets were not significantly different from zero (F-test and t-test, respectively, 5% threshold).

In order to provide a generic parameterisation for modelling leaf colouring in deciduous broadleaf forests (DBF), we additionally fitted and validated the DM model over the complete colouring observation database (without distinction between genera).

The optimisation procedure consisted of exploring the whole space of parameters for  $P_{start}$  (from 10 to 16 h with a 0.5 h step),  $T_b$  (from +7 to +30 °C with a 0.5 °C step),  $x$  and  $y$  for

both formulations of the photoperiod function (Eq. (2)). The  $Y_{\text{crit}}$  parameter was elected through the Powell (gradient-descent) optimisation method (Press et al., 1992), completed by a sensitivity test to local minima (i.e. the stability of the  $Y_{\text{crit}}$  parameter was assessed after perturbation of the elected value). The optimised set of parameters was elected on the basis of lowest mean squared difference between  $Y90_{\text{obs}}$  and  $Y90_{\text{mod}}$ . The quality of the model predictions was assessed through classical statistics:

modelling efficiency (ME), defined as ME

$$= 1 - \frac{\sum_{i=1}^n (O_i - P_i)^2}{\sum_{i=1}^n (O_i - \bar{O})^2}, \quad (3)$$

and root mean square error (RMSE), defined as RMSE

$$= \sqrt{\frac{\sum_{i=1}^n (O_i - P_i)^2}{n}}, \quad (4)$$

where  $O_i$  represents an elementary observation in the observed dataset ( $n$  observations) and  $P_i$  represents an elementary prediction in the modelled dataset ( $n$  predictions).

## 2.5. Models performance comparison

We compared the DM, WM and JM models abilities to simulate colouring observations on the basis of their root mean square errors (RMSEs). When comparing two models' RMSEs, we assessed the reliability of the null hypothesis: "H0: the difference of models' RMSEs is not significantly different from zero" through a non-parametric procedure, as we had no presupposed idea of the distribution of the differences of RMSEs under H0. The probability density function (PDF) of the differences of RMSEs was computed through a Monte Carlo procedure: for comparing models A and B, we pooled the squared errors from A and B and randomly divided  $n$  ( $10^4$ ) times the resulting dataset into two groups (A' and B'), whose root means were subtracted ( $d_n = \text{RMSE}(A') - \text{RMSE}(B')$ ). The distribution of the  $d_n$  statistic is therefore the PDF of the differences of RMSEs from models A and B under the null hypothesis (i.e. assuming that A and B originate from the same statistical population). The null hypothesis was rejected in case  $|d| = |\text{RMSE}(A) - \text{RMSE}(B)| > d^*$ , where  $d^*$  is the threshold value above which 10% of the  $d_n$  statistic is distributed under H0.

## 2.6. Prospective modelling of leaf colouring occurrence

We use the model as a predictor of a likely trend in leaf colouring over France for the period of 1951–2099. Prospective simulations were performed by using temperature data simulated by the ARPEGE model (Déqué et al., 1998) under the A1b IPCC-defined scenario. The original ARPEGE grid has a 60-km spatial and a 1-day time resolutions. A statistical downscaling method, described in Boé et al. (2006), provided temperature data on an 8-km grid. The same distance criterion and altitude correction procedure defined for METEOPRANCE stations were used to generate temperature time series with ARPEGE.

## 3. Results

### 3.1. Phenological observations – general remarks

For the time period of 1997–2006, the mean  $Y90_{\text{obs}}$  for *Fagus* (DoY  $293 \pm 16$ , mean  $\pm 1$  SD) occurred 8 days earlier than for *Quercus* (DoY  $301 \pm 13$ ;  $p < 10^{-6}$ , Table 1). When averaged on a site basis, the mean  $Y90_{\text{obs}}$  date was positively correlated to the mean site temperature ( $r^2 = 0.42$ ,  $p < 0.01$  in both genera). When averaged on a yearly basis, the mean  $Y90_{\text{obs}}$  date was positively correlated to mean autumnal (September and October) temperature, with a 2.2-day ( $r^2 = 0.53$ ,  $p < 0.05$ ) and a 3.3-day ( $r^2 = 0.55$ ,  $p < 0.05$ ) delay in observed leaf colouring for each degree increase in *Fagus* and *Quercus*, respectively.

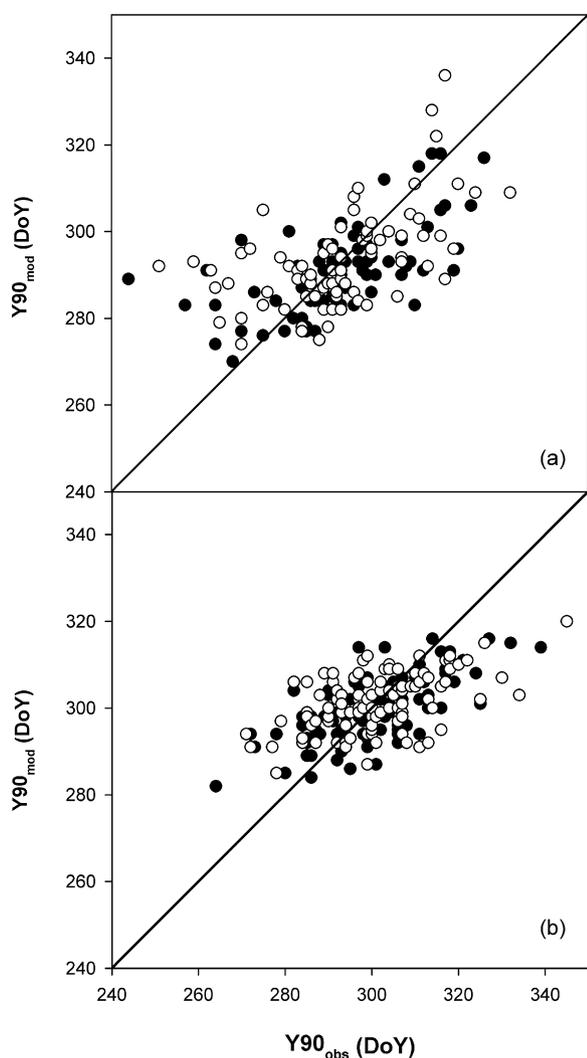
### 3.2. Modelling performances

Bioclimatic approaches (JM, WM, DM) lead to a lower RMSE than the null model (NM) in most cases (Table 2). DM systematically showed the lowest absolute RMSE and significantly outperformed the other bioclimatic approaches and NM on the complete datasets, with RMSE reaching 13.0 days for *Fagus*, 10.3 days for *Quercus* and 11.6 days for DBF.

**Table 2 – Quality assessment of colouring models. NM: null (overall mean) model, JM: Jolly et al. (2005) model, WM: White et al. (1997) model, and DM: new bioclimatic model.**

Fagus						
Model	Fitting subset (n = 79)		Validation subset (n = 80)		Overall (n = 159)	
	RMSE	ME	RMSE	ME	RMSE	ME
NM	15.6 <sup>a</sup>	0	15.9 <sup>ab</sup>	0	15.8 <sup>a</sup>	0
JM	14.3 <sup>ab</sup>	0.16	15.6 <sup>ab</sup>	0.03	15.0 <sup>a</sup>	0.10
WM	13.3 <sup>ab</sup>	0.28	16.8 <sup>a</sup>	−0.12	15.1 <sup>a</sup>	0.07
DM	12.3 <sup>b</sup>	0.38	13.5 <sup>b</sup>	0.28	13.0 <sup>b</sup>	0.33
Quercus						
Model	Fitting subset (n = 106)		Validation subset (n = 106)		Overall (n = 212)	
	RMSE	ME	RMSE	ME	RMSE	ME
NM	12.0 <sup>a</sup>	0	12.9 <sup>a</sup>	0	12.8 <sup>a</sup>	0
JM	11.0 <sup>a</sup>	0.15	12.2 <sup>a</sup>	0.11	11.8 <sup>a</sup>	0.15
WM	10.7 <sup>ab</sup>	0.21	12.2 <sup>a</sup>	0.10	11.7 <sup>a</sup>	0.17
DM	9.2 <sup>b</sup>	0.41	11.0 <sup>a</sup>	0.27	10.3 <sup>b</sup>	0.35
Deciduous broadleaf forests						
Model	Fitting subset (n = 185)		Validation subset (n = 186)		Overall (n = 371)	
	RMSE	ME	RMSE	ME	RMSE	ME
NM	14.6 <sup>a</sup>	0	14.8 <sup>a</sup>	0	14.7 <sup>a</sup>	0
JM	12.9 <sup>a</sup>	0.22	14.1 <sup>a</sup>	0.10	13.5 <sup>a</sup>	0.16
WM	12.2 <sup>ab</sup>	0.30	14.4 <sup>a</sup>	0.05	13.4 <sup>a</sup>	0.17
DM	11.1 <sup>b</sup>	0.42	12.2 <sup>b</sup>	0.32	11.6 <sup>b</sup>	0.37

Superscript letters indicate grouping according to RMSE values (see Section 2.5).



**Fig. 2 – Comparison of predicted (DM) versus observed dates of leaf colouring for (a) *Fagus* and (b) *Quercus* sites. Disks = fitting dataset, circles = validation dataset. The identity line is reported.**

The ability of the DM model to accurately predict the  $Y90_{obs}$  date is severely impaired by a few observations (Fig. 2). The predicted range is narrower than the observed one (observed range: 89 days, 82 days; predicted range: 67 days, 39 days for *Fagus* and *Quercus*, respectively). The DM model is not able to simulate extreme  $Y90_{obs}$  observations. The bias is particularly important for early observations in *Fagus* (Fig. 2a), but is more systematic in *Quercus* (Fig. 2b). These observations are not related to any particular site or year, as the RMSE did not decrease sharply after excluding the site or year showing the highest RMSE (not shown). The exclusion of the 10% worst simulated points improved the DM model’s overall ME to 0.65 for *Fagus* ( $n = 143$ ) and 0.60 for *Quercus* ( $n = 191$ ).

**3.3. Genus-specific model structures**

The threshold photoperiod for senescence processes to be triggered ( $P_{start}$ ) is higher for *Quercus*, leading to an earlier starting of the leafy season for a given latitude (Table 3). In

**Table 3 – Leaf colouring models parameters. NM: null (overall mean) model, DM: new bioclimatic model, and DBF: deciduous broadleaf forests. See text for parameters description and units.**

	NM		DM				
	Mean date	$P_{start}$	$T_b$	$x$	$f[P(d)]$	$y$	$Y_{crit}$
<i>Fagus</i>	293	12.5	25	2	Eq. (2.1)	2	5160
<i>Quercus</i>	301	14.5	26.5	2	–	0	10178
DBF	297	12.5	28.5	2	Eq. (2.1)	2	8268

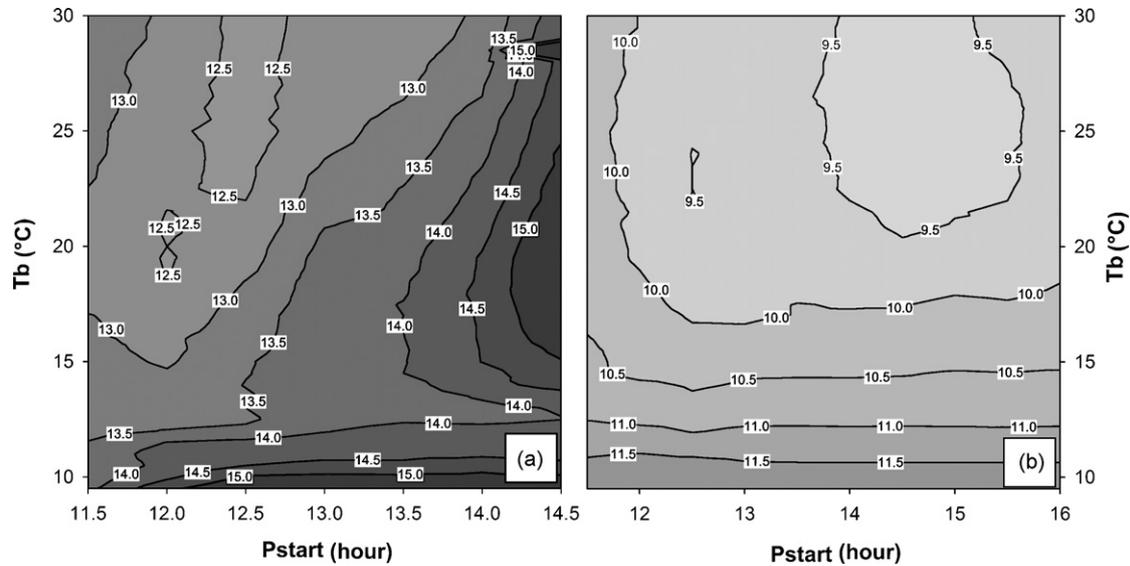
both genera, the modelled senescence was promoted by low temperatures ( $x > 0$ ), with progress rates being more than proportional to the temperature differences from the threshold values ( $x = 2$ ). The baseline temperature below which senescence progresses were found to be lower for *Fagus* (+25.0 °C) than for *Quercus* (+26.5 °C). Contrary to *Quercus*, whose senescence rates were not modulated by photoperiod ( $y = 0$ ), the daily rate of senescence ( $R_{sen}$ ) of *Fagus* was promoted by longer days (relative to the onset of senescence processes on  $P_{start}$ ): for a given temperature departure from the baseline of senescence processes ( $T_b$ ), the highest  $R_{sen}$  occurred earlier in the season (Eq. (2.1)). The optimised model structure for DBF was analogous to the one fitted for *Fagus* (Table 3). Fig. 3 illustrates the evolution of RMSE for the calibration dataset within the  $\{P_{start}, T_b\}$  parameters space. The RMSE function shows a clear minimum around the fitted parameters for *Fagus*. The root mean square error gradient is steeper along the  $T_b$  axis for *Quercus*.

**3.4. Intersite variability**

We compared the ability of the DM model to represent the intersite variability of the leaf colouring date with a multiple regression model, based on the geographic location of the observation sites (latitude and altitude). The trends depicted by the parameters of the geographic model were consistent with predictions from the DM model: in both genera, sites exposed to lower temperatures (i.e. located at higher altitudes or latitudes) showed earlier leaf colouring (Table 4). The geographic formulation of the model (i.e. latitudes and altitude as independent variables) performed better than a simple regression of mean site  $Y90_{obs}$  against mean site temperature (not shown). We noticed similar performances for the geographic and DM models in representing the intersite variability of leaf colouring. For both genera, RMSEs from the geographic or DM model were lower than the RMSE from the null model. For *Fagus*, the RMSE from the DM model was slightly lower than the RMSE from the geographic model.

**3.5. Interannual variability**

We assessed the DM model’s ability to represent the interannual variability of leaf colouring date by comparing the annual means of the  $Y90_{mod}$  and  $Y90_{obs}$  dates over all sites (Fig. 4). Though the  $Y90_{obs}$  observations were collected on a weekly basis, this investigation used overall sites means, which permitted us to consider any differences in mean  $Y90_{obs}$



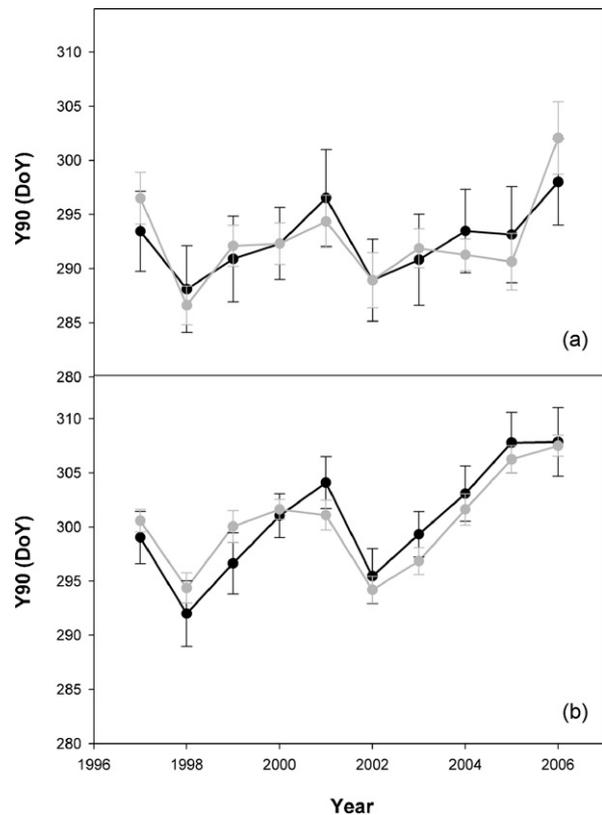
**Fig. 3** – Root mean square error (days) of the predicted  $Y90_{mod}$  for the calibration subsets in *Fagus* (a) and *Quercus* (b). The model structures used are reported on Table 3. Interval bounds and increment for  $P_{start}$  and  $T_b$  as noticed in text.

from 1 year to another to be meaningful even if less than 7 days. The interannual dynamics of mean  $Y90_{obs}$  were similar for both genera, though earlier shifted for *Fagus*. This earlier shift was consistently reproduced by the model (Fig. 4). The earliest and latest observed mean annual colouring dates occurred in 1998 and 2006 for both *Fagus* and *Quercus*. We note that the DM model correctly reproduced the main features of the interannual  $Y90_{obs}$  time series (delayed colouring from 1998 to 2000 and from 2002 to 2006 after the 2002 decline) with high determination coefficients ( $r^2 > 0.70$ ) and good modelling efficiencies (ME = 0.46 and 0.83 for *Fagus* and *Quercus*, respectively). The higher ME for *Quercus* was due to (1) a wider range in mean annual  $Y90_{obs}$  observations (17 days as compared to 11 days for *Fagus*) and (2) a better overall prediction of mean annual colouring date (Table 2). Bias in the simulated mean annual colouring dates was not significantly different from zero in both cases ( $-0.1$  days in *Fagus* and  $+0.2$  days in *Quercus*,  $p > 0.70$ ). The highest discrepancy between the observed and predicted mean annual dates for *Fagus* was a 4-day overestimation in 2006.

**Table 4** – Intersite model validation. Comparison of the DM model with a multiple regression model based on geographic characteristics of the sites (altitude and latitude).

	<i>Fagus</i> (n = 18)		<i>Quercus</i> (n = 25)	
	RMSE	ME	RMSE	ME
Null model	12.8	0	8.6	0
Geographic model	9.7	0.42	6.0	0.50
DM model	9.5	0.44	6.3	0.45

Geographic models parameters – *Fagus*:  $Y90_{mod} = 455 - 3.07 \times Lat - 0.03 \times Alt$  ( $p < 0.01$ ); *Quercus*:  $Y90_{mod} = 423 - 2.33 \times Lat - 0.05 \times Alt$  ( $p < 0.01$ ).



**Fig. 4** – Interannual variability of measured (black) and modelled (grey) leaf colouring dates for (a) *Fagus* and (b) *Quercus* sites. Mean date  $\pm 1$  SE are presented. Linear regression statistics are *Fagus*:  $Pred = 1.18 \times Obs - 52$  ( $r^2 = 0.73$ ,  $p < 0.001$ ) and *Quercus*:  $Pred = 0.78 \times Obs + 67$  ( $r^2 = 0.83$ ,  $p < 0.001$ ).

**Table 5 – Summary of leaf colouring trends (days per decade). We report observed trends as published by Schaber and Badeck (2005) over Germany and trends (SE) predicted by the DM model under ARPEGE climate over France (this study). Asterisks mark non-significant difference from zero ( $p > 0.05$ ).**

	1951–1999		1951–2099	
	<i>Fagus</i>	<i>Quercus</i>	<i>Fagus</i>	<i>Quercus</i>
Germany	+0.6	+1.0	–	–
France	+0.3 (0.3)*	+0.7 (0.3)	+1.4 (0.07)	+1.7 (0.07)

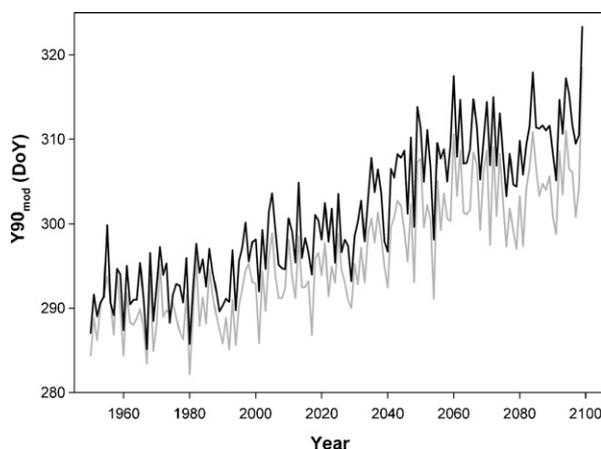
### 3.6. Simulation of leaf colouring occurrence for 1951–2099

For the period of 1951–1999, simulated trends appeared to be similar to observed trends reported in Schaber and Badeck (2005; their Table 3) for German stands in both the *Fagus* and *Quercus* genera (Table 5). This result strengthened our confidence in our use of the model as a prospective tool, though the mean absolute difference in predicted colouring date caused by the use of ARPEGE instead of METEOFRENCE data reached 6 (4) days in *Fagus* (*Quercus*) for the period of 1997–2006. According to the DM model, leaf colouring was predicted to be delayed for 1.4 days per decade in *Fagus* and 1.7 days per decade in *Quercus*, over the period of 1951–2099 (Fig. 5). These predicted trends were significantly different between genera ( $p < 0.05$ ). The colouring date trends predicted by the DM model for 1951–2099 were significantly higher than those predicted for 1951–1999 ( $p < 0.05$ ; Table 5).

## 4. Discussion

### 4.1. Stand scale leaf colouring model

We focused our modelling effort on the prediction of one particular stage of colouring (Y90, see Section 2.1 for



**Fig. 5 – Interannual variations of predicted leaf colouring dates by the DM model over the 1951–2099 period in France for *Fagus* (grey) and *Quercus* (black). Linear regression statistics are *Fagus*:  $Y90_{mod} = 0.14 \times \text{year} + 18$  ( $r^2 = 0.70$ ,  $p < 10^{-6}$ ) and *Quercus*:  $Y90_{mod} = 0.17 \times \text{year} - 38$  ( $r^2 = 0.77$ ,  $p < 10^{-6}$ ).**

definition). The phenological database included another set of observations, relative to an earlier (Y10) stage of colouring. We intended to model both stages with the same modelling framework, but the results for the earlier stage were deceiving (with a RMSE of up to 16.5 and 14.2 days for *Fagus* and *Quercus*, respectively, which is worse than the null model in both cases). We suggest that the failure of the DM model to represent the occurrence of the first stage of colouring (Y10) is related to the increased observation uncertainty inherent to this stage. Indeed, the Y90 state marks the stand’s response (90% of 36 trees) to environmental conditions, while Y10 is observed when a few trees (10% of 36 trees) have reached the critical stage. The latter stage is therefore more dependent on the intra-stand (inter-individual) variability of leaf colouring, which can span up to 3 weeks (e.g. Brügger et al., 2003 for *F. sylvatica*).

### 4.2. Environmental dependence of leaf colouring

The commonly postulated dependence of colouring processes on photoperiod and temperature proved to be efficient at predicting leaf colouring at stand scale when integrated into the proposed modelling framework. For both genera, yellowing processes are triggered by a photoperiod threshold and progress through a cold-degree day summation procedure, until reaching the threshold required to complete the process. Photoperiodism has been invoked as the main driver for leaf senescence to occur (Keskitalo et al., 2005; Lee et al., 2003). Our analysis of the RENECOFOR phenological database, showing annual means ranges of 16 days for *Quercus* and 11 days for *Fagus* (Fig. 4), together with our bioclimatic approach contest these viewpoints. We claim that photoperiod is of secondary importance in determining leaf colouring in *Quercus*, as suggested by the flatness of the predicted error along the  $P_{start}$  parameter axis (Fig. 3b) and the non-sensitivity of modelled senescence rates to photoperiod ( $y = 0$ ; Table 3). In *Fagus*, photoperiod influences yellowing processes in both their triggering ( $P_{start}$ ) and progression ( $fP(d)$ ), Table 3).

### 4.3. Model performance – alternative models formulations

The predicted model error for leaf colouring date remains large (13.0 days and 10.3 days, for *Fagus* and *Quercus*, respectively; Table 2) when compared to the usual accuracy of bioclimatic models for other phenological phases (5–7 days for budburst; Schaber and Badeck, 2003). Such an error may impact the seasonality of simulated matter and energy fluxes, when integrating our scheme in a SVAT model. However, this error would moderately impact the simulated annual balances, given the low fluxes values in autumn.

One reason for such large errors may be the misrepresentation of colouring processes. The DM model does not take into account any potential effect of high-temperature ( $>35^\circ\text{C}$ ) induced damages to the photosynthetic apparatus (Berry and Björkman, 1980), which could hasten leaf senescence, whether combined with drought or not. Another model structure, in which high (above a  $T_c$  threshold) as well as low temperatures (below the  $T_b$  threshold, with  $T_b < T_c$ ) promoted senescence, was tested but it did not perform better than the DM model (not shown). No assessment of a model structure including a

drought index was intended, given the intersite heterogeneity of soil conditions (Brethes et al., 1997) and low influence of water balance on senescence phases, as revealed by a statistical analysis of the database (Lebourgeois et al., 2008). Aside from the simplicity of the DM model in terms of included environmental drivers, the structure of the model itself might be too trivial to properly represent senescence processes. We simulated colouring as the outcome of one-way processes (no reversibility of  $S_{\text{sen}}$ ), which is supported by observations at multiple scales (from monitored PSII activity to leaf yellowing observation on a single *Populus tremula* L. individual) in a study by Keskitalo et al. (2005). It is possible that more systematic approaches, such as these developed by Schaber and Badeck (2003) for bud burst (i.e. introducing potential reversibility in the modelling of  $S_{\text{sen}}$ ), yield more accurate predictions of leaf colouring.

#### 4.4. Spatial variability of leaf colouring

When averaged over time, the ability of the DM model to predict mean leaf yellowing dates for individual sites is similar to predictions from a multiple regression model based on site geographic characteristics and outperforms the null model (Table 4). Some studies (e.g. Chuine and Beaubien, 2001) used latitude as a single predictor of mean site leaf colouring date. Other studies reported that the date of senescence was constant between years for a given site, based on observations over a few years (e.g. Keskitalo et al., 2005; Lee et al., 2003). This is equivalent to presuming the existence of a threshold photoperiod for leaf colouring to occur, and it imposes a monotonic trend for leaf colouring date along the considered latitudinal gradient. We assessed such a correlation and found either no significant ( $r = +0.10$ ,  $p < 0.80$  for *Fagus*) or weakly significant ( $r = -0.30$ ,  $p < 0.10$  for *Quercus*) relationships between latitude and site mean date. This is mainly due to the presence in our dataset of mountainous sites, whose MAT is low although located at low latitudes (Pyrénées and Alps mountains). We therefore support the use of the DM bioclimatic model to predict the spatial variability of mean leaf yellowing occurrence.

Validation of the DM model was assessed on a limited latitudinal and climatic range, analogous to the range used in the fitting procedure. This range encompasses the southern two-thirds and southern half of the latitudinal ranges of *Quercus* and *Fagus*, respectively, though the temperature ranges for both genera are well covered (Bary-Lenger and Nebout, 1993; Teissier du Cros, 1981). This limitation must be noted when one applies the model to a different latitudinal range. The model's accuracy may be challenged when applied to range limits, as the model was fitted neither for northern sites, that are characterised by an earlier occurrence of short photoperiod, nor for sites that are experiencing pronounced summer droughts.

#### 4.5. Influence of genetic differentiation/acclimation

Aside from the simplicity of the modelling framework, and uncertainty of the temperature and colouring observation time series, part of the residual variance of the predicted leaf colouring dates may be due to genetic differences or

acclimation between populations. Chuine et al. (2000) introduced a modelling methodology to test for genetic differences between populations when considering phenological traits. According to this protocol, sites are grouped into populations according to a latitudinal gradient, hypothesising a higher genetic similarity between geographically close populations, and models are then fitted to each population. A genetic dissimilarity between populations is revealed by a significant reduction of the model residual variance (SSR) when fitted locally, when compared with the global fit over the whole database. We applied the methodology of Chuine et al. (2000) and observed a reduction of SSR for locally fitted models in both genera. However, we could not conclude to genetic differences between populations defined according to the latitudinal gradient as these local SSRs were not significantly different from SSRs obtained under random grouping of the sites (not shown). We further intended to reveal such genetic/acclimation effects through site-specific fitting of the DM model, as phenological model parameters have already been related to tree provenance (e.g. see von Wuehlisch et al., 1995 for *Fagus* budburst phase parameters). Site-specific fitting was done after fixing the model structure ( $x$ ,  $y$ ,  $f[P(d)]$ ) and base temperature ( $T_b$ ) and starting photoperiod ( $P_{\text{start}}$ ) parameters in order to deal with parameters correlations. Therefore, the sole critical temperature sum  $Y_{\text{crit}}$  was free to vary between sites. We observed no correlation of the sitewise critical temperature sum  $Y_{\text{crit}}$  with either latitude ( $p < 0.74$  in *Fagus*;  $p < 0.86$  in *Quercus*) or mean temperature ( $p < 0.75$ ;  $p < 0.73$ ). This lack of correlation does not support the hypothesis of local thermal and/or photoperiod-dependent acclimation determining the critical sum of temperature needed to achieve leaf senescence.

#### 4.6. Prospective modelling of leaf colouring date

We predict a delayed leaf colouring date of about 1.4 days per decade in *Fagus* and 1.7 days per decade in *Quercus* over the period of 1951–2099. A significant trend toward later leaf colouring in *Quercus* as compared to *Fagus* is therefore predicted (0.3 days per decade; Table 5). Given the similarity of mean autumnal temperature trends predicted by ARPEGE at both the *Fagus* and *Quercus* sites (+0.3 °C per decade, not shown), the difference in colouring trends is thought to be related to a higher sensitivity to autumnal temperature for *Fagus* leaf colouring. This trend might modify the relative fitness of *Quercus* and *Fagus*, and participate in the modification of the geographic range (Chuine and Beaubien, 2001) that is predicted to occur over the next decades for both genera (Badeau et al., 2004).

## 5. Conclusions

This study presented a modelling framework aimed at simulating leaf colouring at the stand scale for two common European deciduous genera (*Fagus* and *Quercus*). When spatially averaged, predictions of our bioclimatic model show a very good agreement with mean annual dates of leaf colouring. We therefore consider our model to be a primary tool for predicting leaf yellowing (i.e. the end of leafy season) in

process-based SVAT models run at a national/regional scale. As most SVAT schemes used on such geographic scales are parameterised according to Plant Functional Type (i.e. temperate deciduous forest for the genera of concern here), we provide a parameterisation of our bioclimatic model for temperate deciduous broadleaf forests. When used as a prospective tool, the model predicts a trend toward significantly delayed leaf colouring occurrence for the period of 1951–2099. The predicted trend is more marked for *Quercus* than for *Fagus*.

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