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Responses of canopy duration to temperature changes in four temperate tree species: relative contributions of spring and autumn leaf phenology

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Abstract While changes in spring phenological events due to global warming have been widely documented, changes in autumn phenology, and therefore in growing season length, are less studied and poorly understood. However, it may be helpful to assess the potential lengthening of the growing season under climate warming in order to determine its further impact on forest productivity and C balance. The present study aimed to: (1) characterise the sensitivity of leaf phenological events to temperature, and (2) quantify the relative contributions of leaf unfolding and senescence to the extension of canopy duration with increasing temperature, in four deciduous tree species (*Acer pseudoplatanus, Fagus sylvatica, Fraxinus excelsior* and *Quercus petraea*). For 3 consecutive years, we monitored the spring and autumn phenology of 41 populations at elevations ranging from 100 to 1,600 m. Overall, we found significant altitudinal trends in leaf phenology and species-specific differences in temperature sensitivity. With increasing temperature, we recorded an advance in flushing from 1.9 ± 0.3 to 6.6 ± 0.4 days °C^{-1} (mean ± SD) and a 0 to 5.6 ± 0.6 days °C^{-1} delay in leaf senescence. Together both changes resulted in a 6.9 ± 1.0 to 13.0 ± 0.7 days °C^{-1} lengthening of canopy duration depending on species. For three of the four studied species, advances in flushing were the main factor responsible for lengthening canopy duration with increasing temperature, leading to a potentially larger gain in solar radiation than delays in leaf senescence. In contrast, for beech, we found a higher sensitivity to temperature in leaf senescence than in flushing, resulting in an equivalent contribution in solar radiation gain. These results suggest that climate warming will alter the C uptake period and forest productivity by lengthening canopy duration. Moreover, the between-species differences in phenological responses to temperature evidenced here could affect biotic interactions under climate warming.

Keywords Growing season length · Leaf unfolding · Leaf senescence · Altitudinal gradient · Climate change

Introduction

The impact of climate warming on plant phenology has been considered to be particularly important in the high latitudes of the northern hemisphere as well as at high altitudes because of their short growing periods (Walther et al. 2002), and it is expected to change the distributions of terrestrial vegetation (Bertin 2008). The C balance of terrestrial ecosystems is highly sensitive to changes in climate, and some studies reported or suggested that the photosynthetic activity of terrestrial vegetation increased in response to climate warming in the last decades (Keeling et al. 1996; Myneni et al. 1997). In parallel, recent studies showed that climate warming has been responsible for lengthening the growing period of trees (Linderholm 2006; Menzel and Fabian 1999) by advancing the timing of flushing (Ahas et al. 2002; Chmielewski and Rotzer 2002; Menzel et al. 2006), especially at high latitudes (Delbart et al. 2008; Linderholm 2006). Moreover, climate warming has usually been reported to cause a delay in leaf senescence

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(Menzel et al. 2006) but this phenomenon is still poorly documented. In addition to these investigations based on direct phenological monitoring, indirect measurements based on seasonal variations of atmospheric CO_2 concentrations (Keeling et al. 1996; Myneni et al. 1997), or on red and near-infrared reflectances of the canopy (Chen et al. 2005; Tucker et al. 2001; Zhang et al. 2004), also indicated an extension of the growing season over the last decades.

Growing season length (GSL) has a strong effect on ecosystem functioning and tree productivity (Kramer et al. 2000; Picard et al. 2005; White et al. 1999). For deciduous trees, the timings of flushing in spring and senescence in autumn determine canopy duration and therefore vegetative growth and reproductive success (Rathcke and Lacey 1985). Although photosynthetic rate generally increases with temperature and CO_2 concentration (Foley et al. 1998; Saxe et al. 2001), the increase in terrestrial C sinks over the last decades has been, to a large extent, attributed to an increase in growing season under temperate climates (Churkina et al. 2005; Keeling et al. 1996; Myneni et al. 1997; Piao et al. 2007). However, a recent study showed that warmer autumn temperatures could result in a decrease in the net C ecosystem exchange, due to a higher increase in ecosystem respiration relative to the corresponding increase in gross primary production (Piao et al. 2008).

In mid-latitude areas, plant phenology is essentially affected by air temperature and photoperiod (Menzel 2002). For temperate trees, the timing of flushing and senescence is controlled by a trade-off between survival and productivity. Indeed, late flushing in spring allows avoidance of frost damage but reduces canopy duration and may consequently reduce productivity (Lechowicz 1984; Leinonen and Hanninen 2002; Lockhart 1983). In autumn, trees shed their leaves in order to protect themselves from frost damage, which is considered to constitute an adaptative response to unfavourable conditions for photosynthesis (Estrella and Menzel 2006). On the other hand, the timing of senescence also has an impact on growth of the following year because it is associated with nutrient remobilisation, especially N, and photosynthate storage (Lim et al. 2007). Indeed, late senescence can result in a larger photosynthate storage but can also increase the risks of incomplete nutrient remobilisations due to autumn frost on functional leaves (Keskitalo et al. 2005). The timing of spring events, such as flushing or flowering, is mainly regulated by temperature once dormancy is released, i.e. by temperatures in late winter and early spring (Chmielewski and Rotzer 2001; Menzel and Fabian 1999; Wielgolaski 1999). In perennial species, it is generally observed that in addition to temperature, day length plays a crucial role in the regulation of senescence for deciduous trees (Keskitalo et al. 2005; Larcher 2003; Lee et al. 2003). Nevertheless, contrary to spring phenological events, the climate signal that controls autumn phenology is less clearly identified (Estrella and Menzel 2006) and further studies are needed to characterise leaf senescence processes.

Only a few of the small number of studies which measured the timing of senescence along climatic or temporal gradients were able to quantify canopy duration, defined as the difference between the timing of flushing and leaf yellowing or leaf fall (Chmielewski and Rotzer 2001; Kramer 1995b; Matsumoto et al. 2003; Menzel and Fabian 1999; Richardson et al. 2006). At a large scale, some studies reported a global increase in canopy duration of trees with increasing temperature (Linderholm 2006; Menzel and Fabian 1999; Penuelas et al. 2002). However, these studies did not separate species' responses, even though it was demonstrated that different species display different phenological sensitivity to temperature changes (Chuine et al. 2000; Kramer 1995a; Murray et al. 1989). Thus, at the species level, little is known about how variations in timing of flushing and senescence contribute to variations of canopy duration and C balance. To contribute to an assessment of the impact of climate warming on forest ecosystems, we need to quantify the differences in phenological response to temperature across tree species in order to highlight potential shifts in species' competitive balance. Indeed, some species could enhance their competitive performances if they are able to rapidly improve their fitness under a warmer climate.

In order to assess variations in phenology and canopy duration in response to temperature, and to characterise between-species differences, we studied leaf unfolding and senescence in four widely distributed temperate deciduous tree species, all commonly used in the European timber industry (*Acer pseudoplatanus, Fagus sylvatica, Fraxinus excelsior* and *Quercus petraea*). We monitored phenology in 41 populations along altitudinal gradients in the Pyrenees, covering a large temperature range. The aims of the present study were: (1) to quantify temperature sensitivity of phenological events and canopy duration for these species, and (2) to assess the relative contributions of flushing and senescence to variation in canopy duration according to temperature.

Materials and methods

Study areas and species description

The study was conducted in two valleys of the Pyrenees in south-west France (42°47′N–43°45′N; 00°44′W–00°06′E). A first transect was set up in the Ossau valley (Pyrénées Atlantiques) and a second one in the Gave valley (Hautes Pyrénées). These valleys run parallel to each other, 30 km apart; their elevation increases from north to south. This region is characterised by a temperate oceanic climate, with a mean annual temperature of 12°C and mean annual precipitation of 1,079 mm (for 1946–2001) at low elevation (Tarbes, 43°11′N, 00°00′W, 360 m a.s.l.; Météo France). Analysis of monthly precipitation data in 2005–2007 showed no water stress along the whole altitudinal gradient: irrespective of year and elevation, precipitation values were higher than 235 and 200 mm before the leaf flushing period (March–May) and before the leaf senescence period (August–October), respectively.

We selected four deciduous tree species widely used in the timber industry with a wide range of natural distribution over Europe but contrasting ecological requirements. Sycamore maple (*Acer pseudoplatanus* L.) and common ash (*Fraxinus excelsior* L.) are rapid-growth species which occur more frequently in riparian ecosystems or in fertile soils. In contrast, European beech (*Fagus sylvatica* L.) and sessile oak [*Quercus petraea* (Matt.) Liebl.] are slow-growth species. Moreover, these four species are located here at the southern limits of their distribution which makes it particularly interesting to study their response to climate change. For each species and in each transect, naturally established populations were sampled at five altitudes: 100, 400, 800, 1,200 and 1,600 m (±50 m) (Table 1). We sampled four additional populations of oak at intermediate elevations in the Gave valley. The altitudinal gradient exceeded 1,400 m for all species except for sycamore ($\Delta = 1{,}164$ m), whose populations could only be found above 400 m. In each population, ten mature individuals of comparable height were sampled and monitored. The average diameter at breast height was, respectively, 0.23 m (±0.01), 0.45 m (±0.02), 0.30 m (±0.01) and 0.39 m (±0.01) for sycamore, beech, ash and oak (Table 1). The populations were sampled on north-facing slopes, except for sessile oak which only grew on south-facing slopes.

Phenology monitoring

Leaf unfolding and senescence were monitored every 10 days from March to June and September to December, respectively, for all the sampled trees for 2 or 3 consecutive years (2005–2006 for ash and sycamore; 2005–2007 for oak and beech). Observations were made using binoculars (magnifying power: 10×) at a distance of approximately 15 m from each tree, by the same observer. In spring, we noted the development stages from bud dormancy to leaf unfolding, using a scale with three to five intermediate stages according to the species (Vitasse et al. 2009). The date of flushing was reached in one tree when 50% of the buds had fulfilled the criterion “at least one leaf unfolding”. In autumn, we combined assessment of colouration and leaf fall to more accurately estimate the end of the growing season. Percentages of missing leaves, as well as percentages of coloured leaves of the total remaining leaves in the canopy were assessed visually. We considered that senescence date was reached in one tree when 50% of its leaves were either coloured or had fallen according to the following equation:

$$x_t = \frac{\alpha_t \times (100 - \beta_t)}{100} + \beta_t \quad (1)$$

where x_t is the percentage of coloured or fallen leaves in the selected tree at date t, α_t is the percentage of coloured leaves at date t and β_t is the percentage of missing leaves at date t.

Then, for each sample tree, the dates of flushing and senescence were estimated by linear interpolation between two consecutive field observations.

In phenological studies, several definitions of GSL have been used with the same terminology, introducing considerable confusion (White and Nemani 2003). Indeed, for deciduous species, the timing of leaf unfolding and leaf fall determines canopy duration, i.e. the number of days with a vegetative or green canopy, corresponding to the physical definition of GSL. Thus, in this study, the term “canopy duration” characterises the period between flushing and senescence dates for each sampled tree. At the population scale, flushing, senescence and canopy duration values correspond to the mean of the ten sampled individuals.

Meteorological measurements

Air temperature was measured using data loggers (HOBO Pro RH/Temp; Onset Computer, Bourne, Mass.) located in each population (27 sites). In each site, sensors were positioned 1.5 m above the ground on a pole located in an open area near to the studied population (10–100 m from the population, at the same elevation). Sensors were protected by a white plastic shelter to prevent any exposure to rain or direct sunlight. Data were recorded every hour from 1 January 2005 to 31 December 2007. Missing data were gap-filled by linear interpolation using data from the most correlated functional weather stations ($r^2 > 0.91$). All sensors were inter-calibrated in the laboratory before installation. The altitudinal gradient used here provided maximal amplitudes of mean annual temperature of 4.9, 6.1, 6.3 and 7.3°C for sycamore, oak, ash and beech, respectively (Table 1; 2005). Average annual temperatures decreased linearly with elevation, by about 0.43°C for every 100-m increase in elevation (average 2005—2007).

Data analysis

The objectives were to quantify: (1) the relative gain in canopy duration per one degree Centigrade increase, and

Table 1 Site descriptions

	Site	Valley	Altitude a.s.l. (m)	Aspect	DBH (m)	*T*a (°C)		
						2005	2006	2007
Acer pseudo-platanus	Béon	Ossau	450	Flat	0.30	10.8	12.1	
	Pierrefitte	Gave	481	North	0.21	10.1	11.4	
	Eaux-Bonnes	Ossau	824	North	0.37	9.5	11.2	
	Viella	Gave	885	North	0.19	9.0	10.7	
	Gourette	Ossau	1,186	North	0.12	6.7	8.1	
	Barèges	Gave	1,250	North	0.31	7.2	9.0	
	Lienz	Gave	1,533	North	0.17	5.9	7.5	
	Artouste	Ossau	1,614	South	0.10	6.6	8.1	
Fagus sylvatica	Laveyron	Gave	131	North	0.35	12.6	13.5	12.6
	Josbaig	Ossau	148	Flat	0.37	11.0	12.2	11.4
	Bager	Ossau	422	North	0.63	11.9	13.0	11.9
	Lourdes	Gave	488	North	0.60	11.1	12.1	11.0
	Chèze	Gave	773	North	0.38	9.7	11.1	10.0
	Eaux-Bonnes	Ossau	824	North	0.35	9.5	11.2	10.0
	Haugarou	Gave	1,190	North	0.54	5.9	7.5	6.4
	Fabrèges	Ossau	1,260	North	0.48	6.3	7.8	5.9
	Bious	Ossau	1,551	North	0.41	5.3	7.0	5.8
	Barèges	Gave	1,604	North	0.34	5.7	7.4	6.3
Fraxinus excelsior	Madiran	Gave	130	Flat	0.32	12.2	13.4	
	Josbaig	Ossau	148	Flat	0.24	11.0	12.2	
	Béon	Ossau	450	Flat	0.36	10.8	12.1	
	Pierrefitte	Gave	481	North	0.26	10.1	11.4	
	Eaux bonnes	Ossau	824	North	0.38	9.5	11.2	
	Viella	Gave	885	North	0.24	9.0	10.7	
	Gourette	Ossau	1,186	North	0.34	6.7	8.1	
	Barèges	Gave	1,250	North	0.37	7.2	9.0	
	Lienz	Gave	1,533	North	0.18	5.9	7.5	
Quercus petraea	Laveyron	Gave	131	Flat	0.52	12.6	13.5	12.6
	Josbaig	Ossau	259	South	0.64	12.7	14.0	12.8
	Ibos	Gave	387	South	0.32	12.0	13.1	12.2
	Bager	Ossau	422	South	0.41	11.9	13.0	11.9
	Adé	Gave	427	South	0.45	11.9	13.1	12.0
	Pierrefitte	Gave	627	South	0.30	11.2	12.7	11.6
	Chèze	Gave	803	South	0.20	10.3	11.9	10.7
	Le Hourcq	Ossau	841	North	0.36	8.2	10.0	8.9
	Bourdalats	Gave	1,082	South	0.57	9.1	10.7	9.6
	Gabas	Ossau	1,194	South	0.41	8.6	9.9	8.7
	Gèdre	Gave	1,235	South	0.44	9.0	10.7	9.5
	Gèdre haut	Gave	1,349	South	0.50	8.0	9.4	8.3
	Artouste	Ossau	1,614	South	0.11	6.6	8.1	6.9
	Péguère	Gave	1,630	South	0.21	7.0	8.6	7.4

DBH Diameter at breast height, *T*a mean annual temperature

(2) the relative contribution of spring and autumn phenology to this relative gain in canopy duration (in days). Furthermore, since day length and solar elevation vary according to the season (Fig. 3), we also assessed these variables in term of intercepted solar radiation, using the same incoming extraterrestrial solar radiation (R_0) for each population (from a geographical location established in the middle of the studied area; Argelès-Gazost, 43°14′N,

00°05′W, 453 m). R_0 was calculated on a daily basis according to the following equation (Brock 1981):

$$R_0 \approx \frac{3600 \times 24}{10^6} \times \frac{1}{\pi} \times Gsc \times k \times \sin \gamma_s \quad (2)$$

where Gsc is the solar constant ($\approx$1,367 W m^{-2}), k is the eccentricity correction factor (in radians), and γ_s is the solar elevation. Values of k and γ_s have been calculated using equations provided in Yorukoglu and Celik (2006). R_0 was cumulated over the canopy duration period for each population (MJ m^{-2}).

For each species, the relative gain in canopy duration for 1 year (G_y) was calculated according to the following equation:

$$G_y = \frac{\frac{X_L - X_S}{X_S}}{\Delta T} \quad (3)$$

where X_L and X_S are, respectively, the longest and the shortest canopy duration observed along the altitudinal gradient, and ΔT the corresponding temperature lapse rate. The relative gain in canopy duration (G) was calculated as the average over the 3 years of the study. This relative gain is either expressed in days (G_d) or in solar radiation (G_{SR}).

Then, when significant shifts in flushing and senescence dates with temperature were found, we estimated the relative contributions of each phenological event (C) to the extension of canopy duration [in days (C_d) or in solar radiation (C_{SR})], using the following equation:

$$C = \sqrt{\left(\frac{|Y_L - Y_S|}{X_L - X_S}\right)} \quad (4)$$

where Y_L and Y_S are, respectively, the dates of the phenological events (flushing or senescence) of the population exhibiting the longest and shortest canopy duration, for each year. For radiation, Y refers to the cumulative solar radiation from 1 January to the date of the phenological event.

Mean temperature values of spring (1 March–31 May), autumn (1 September–30 November) and the whole year were used to establish linear regressions between temperature and flushing, and between senescence and canopy duration, respectively. These periods were selected according to their suitability to correlate with phenological events. We also fitted linear relationships between flushing, senescence, canopy duration and altitude for each species. The shifts in leaf phenology per 100-m increase in elevation (day 100 m^{-1}) and per degree increase in temperature (day °C^{-1}) were calculated using the slopes of the corresponding linear regressions to compare phenological sensitivities between species. Before performing the regression analyses, phenological data were examined and found to conform to the homogeneity of variance and normal distribution assumptions (Shapiro–Wilk test). All the analyses were performed using SAS 9.1 software (SAS, version 9.1; SAS Institute, Cary, N.C.).

Results

Altitudinal trends

In general, similar altitudinal trends were observed in leaf phenology from year to year: populations at high altitudes exhibited a delayed flushing whatever the species, whereas an advance in senescence was observed for oak and beech only (Fig. 1). Consequently, a shortening of canopy duration was found with increasing elevation for each species and year. However, some between-year differences were found due to year to year variations in temperature. For oak and beech, slopes between phenology and elevation were stronger in 2005 than in 2007 (data not shown), as 2007 presented the lowest temperature range according to elevation (Table 1). In spring, altitudinal trends (slopes of flushing dates vs. elevation) were highly different among species. Indeed, flushing was gradually delayed with increasing elevation (Fig. 1) from 1.1 ± 0.2 days 100 m^{-1} (slope value ± 1 SD) to 3.3 ± 0.2 days 100 m^{-1} on average (2005–2007) for beech and oak, respectively. Thus, oak showed the largest amplitude in flushing between the lowest and the highest populations, about 59 days in 2005. Ash and sycamore presented intermediate variations of 2.9 ± 0.4 and 2.4 ± 0.4 days 100 m^{-1}, respectively (Fig. 1). It is worthwhile noting that below 400 m, flushing commenced 20 days earlier for populations of oak than for those of beech, whereas flushing approximately commenced 9 days later for oak than for beech above 1,500 m (average 2005–2007). In autumn, senescence was advanced with increasing elevation for oak and beech by 1.9 ± 0.3 and 3.0 ± 0.3 days 100 m^{-1}, respectively (Fig. 1). Beech had the largest amplitude in senescence between the earliest and latest populations, around 61 days in 2005. Sycamore showed a 40-day delay at most between the earliest and latest populations, but this large difference could not be related to altitude as only the two populations growing at 400 m showed a significant delay in senescence compared to the others (Fig. 1). Finally, no significant altitudinal trend in senescence was found for ash. Senescence in ash commenced earlier than for all other species, especially at low altitudes. It commenced, on average, on day 282 (9 October) and never exceeded day 300 (27 October) whatever the elevation. Slopes of relationships between elevation and canopy duration varied among species. Canopy duration linearly decreased with increasing elevation by 3.1 ± 0.4 and 5.3 ± 0.4 days 100 m^{-1} for ash and oak, respectively. Beech and sycamore followed intermediate trends with

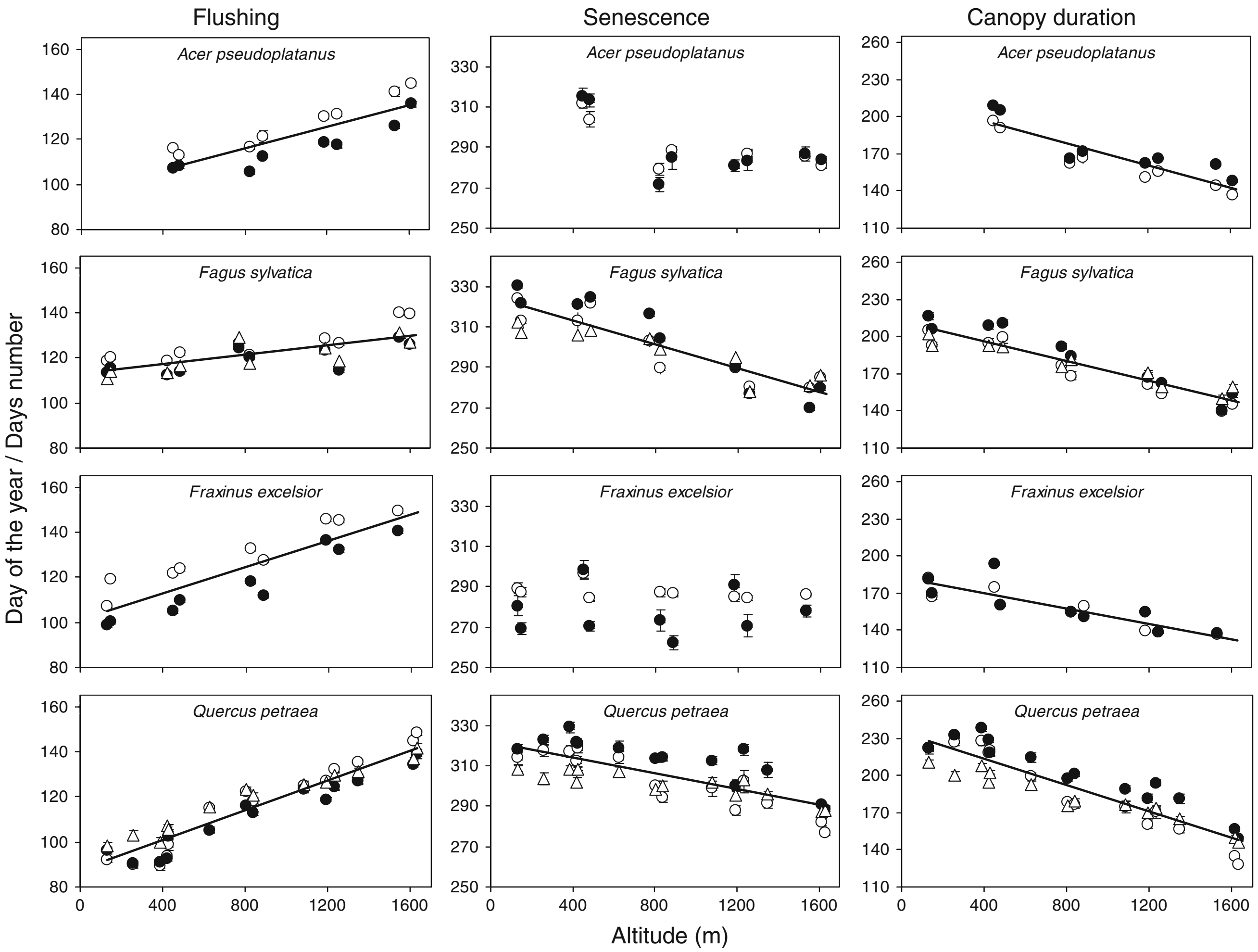

Fig. 1 Dates of flushing, leaf senescence and canopy duration versus elevation for four species in 2005 (*white circles*), 2006 (*black circles*), and 2007 (*white triangles*). Each *point* represents the mean value of ten trees per population and *bars* are SEs. Linear regressions were fitted for the whole dataset

-4.0 ± 0.3 and -4.5 ± 0.6 days 100 m^{-1}, respectively. Ash had the shortest canopy duration both at low and high altitudes (around 174 days below 500 m, and 141 days above 1,200 m). In contrast, oak populations presented the largest canopy duration at low altitudes (more than 218 days below 500 m) and the greatest variations in canopy duration according to elevation, with a 100-day reduction from the lowest to the highest populations in 2005.

Sensitivity to temperature

Overall, temperature better explained phenological variations than altitude whatever the variable (flushing, senescence and canopy duration) and the species. Indeed, highly significant linear relationships were found between flushing dates and spring temperatures for all species ($r^2 > 0.57$, $P < 0.0001$, Table 2). However, the slopes of the curves were strongly species dependent (Table 2; Fig. 2). Oak and ash presented the highest sensitivity to temperature, as flushing was advanced by 6.5 ± 0.4 and 6.6 ± 0.4 days $°\mathrm{C}^{-1}$ increase, respectively. In contrast, beech had the lowest sensitivity to temperature (-1.9 ± 0.3 days $°\mathrm{C}^{-1}$) and sycamore showed an intermediate one (-5.4 ± 0.6 days $°\mathrm{C}^{-1}$). In autumn, we found a significant and strong relationship between senescence and temperature for oak and beech only, with a delay of 5.1 ± 0.4 and 5.6 ± 0.6 days $°\mathrm{C}^{-1}$, respectively ($r^2 > 0.75$, $P < 0.0001$; Table 2, Fig. 2). Thus, for beech, the sensitivity of senescence to temperature was more than twice as high as that of flushing. For sycamore, there was no linear relationship between senescence and temperature, as all populations had the same dates of senescence over the gradient, except those growing at 400 m. For ash, no significant trend in senescence was found with temperature, whatever the year of monitoring. We observed a significant increase in canopy duration with increasing temperature for all species ($r^2 > 0.73$, $P < 0.0001$), ranging from 6.9 ± 1.0 to

Table 2 Slope of the regression (days °C^{-1}) between the timing of flushing, senescence and canopy duration and air temperature in 2005 and 2006 for ash and sycamore and in 2005–2007 for oak and beech

	Flushing/T_{3-5} (day °C^{-1})			Senescence/T_{8-11} (day °C^{-1})			Canopy duration/T_{1-12} (day °C^{-1})			*n*
	Slope	SE[a]	r^2	Slope	SE[a]	r^2	Slope	SE[a]	r^2	
A. pseudoplatanus	−5.0***	0.56	0.85	NS	–	–	+9.7***	1.50	0.75	16
Fagus sylvatica	−1.9***	0.31	0.57	+5.6***	0.60	0.75	+8.0***	0.53	0.89	30
Fraxinus excelsior	−6.6***	0.39	0.95	NS	–	–	+6.9***	1.04	0.73	18
Q. petraea	−6.5***	0.39	0.88	+5.1***	0.39	0.81	+13.0***	0.73	0.88	42

T_{3-5} Mean temperature 1 March–31 May, T_{8-11} mean temperature 1 August–30 November, T_{1-12} annual *T*, *n* sample size

*** $P < 0.001$, *NS* not significant ($P > 0.05$)

[a] SE of linear regression slopes

13.0 ± 0.7 days °C^{-1}, for ash and oak, respectively (Table 2). Beech and sycamore presented intermediate values of 8.0 ± 0.5 and 9.7 ± 1.5 days °C^{-1}, respectively.

Relative contributions of senescence and flushing

Day length and R_0 considerably varied from the beginning of spring to autumn (Fig. 3). Over the range of observed flushing dates, day length varied from 731 to 879 min and solar radiation varied from 29.8 to 41.1 MJ m^{-2} day^{-1}. In autumn, day length was shorter and varied from 539 to 711 min and solar radiation varied from 13.0 to 27.7 MJ m^{-2} day^{-1} (Fig. 3).

For one degree Centigrade increase in temperature, the relative gain in canopy duration ranged between 6 and 13% on a per day basis, or 4 and 10% on a solar radiation basis, according to the species (Fig. 4). The extension of canopy duration in days was only, or mainly, due to the advance in flushing for oak, ash and sycamore (Fig. 4). For the latter two species, there was no contribution of senescence to the extension of canopy duration with increasing temperature. On the contrary, for beech, the advance in flushing only contributed 31% to the extension of canopy duration. Regarding solar radiation, for oak, the gain due to a delay in senescence was lower than the gain due to the advance in flushing (less than 25%; Fig. 4). In contrast, for beech, flushing and senescence variations led to similar gains in solar radiation over the canopy's duration (47 and 53%, respectively).

Discussion

We found strong clines in leaf phenology with increasing temperature and therefore an increase in canopy duration for all the studied species (6.9–13 days °C^{-1}). Both flushing and senescence responses to temperature were highly species dependent. Although most of the previous studies only found weak relationships between senescence and temperature, a high sensitivity to temperature for autumn phenology for two of the studied species was evidenced here. However, for most of the species, the advance in flushing contributed more to the extension of canopy duration. Consequently, an advance in flushing could lead to a more significant gain in solar radiation than a delay in senescence, for all species except beech.

Altitudinal trends

Leaf phenology dramatically changed according to elevation, whatever the species and phenological events (with the exception of senescence for ash and sycamore). Similar results were found for flushing along altitudinal gradients, with a delay of 2–4 days 100 m^{-1}, also highlighting between-species differences (Dittmar and Elling 2006; Menzel 1997; Richardson et al. 2006; Rotzer and Chmielewski 2001). On the other hand, leaf senescence was poorly documented in these studies, especially along elevational gradients, even though these gradients are particularly relevant to the dissociation of day length and temperature effects. For sugar maple, Richardson et al. (2006) found a significant correlation between timing of senescence and altitude, with an advance of 2.5 days 100 m^{-1} (increase in elevation). Our study revealed contrasting results, as for some species, such as ash and sycamore, senescence showed no trend with altitude, suggesting that day length could play a role in the onset of senescence for these species. Finally, we found different altitudinal trends in canopy duration according to species, ranging from −3 to −5.3 days 100 m^{-1}. These results are consistent with the few existing studies (−2.6 to −5.2 days 100 m^{-1}; Dittmar and Elling 2006, Richardson et al. 2006, Rotzer and Chmielewski 2001). More investigations along altitudinal gradients including more species are necessary to strengthen our knowledge about these patterns, especially for autumn phenology.

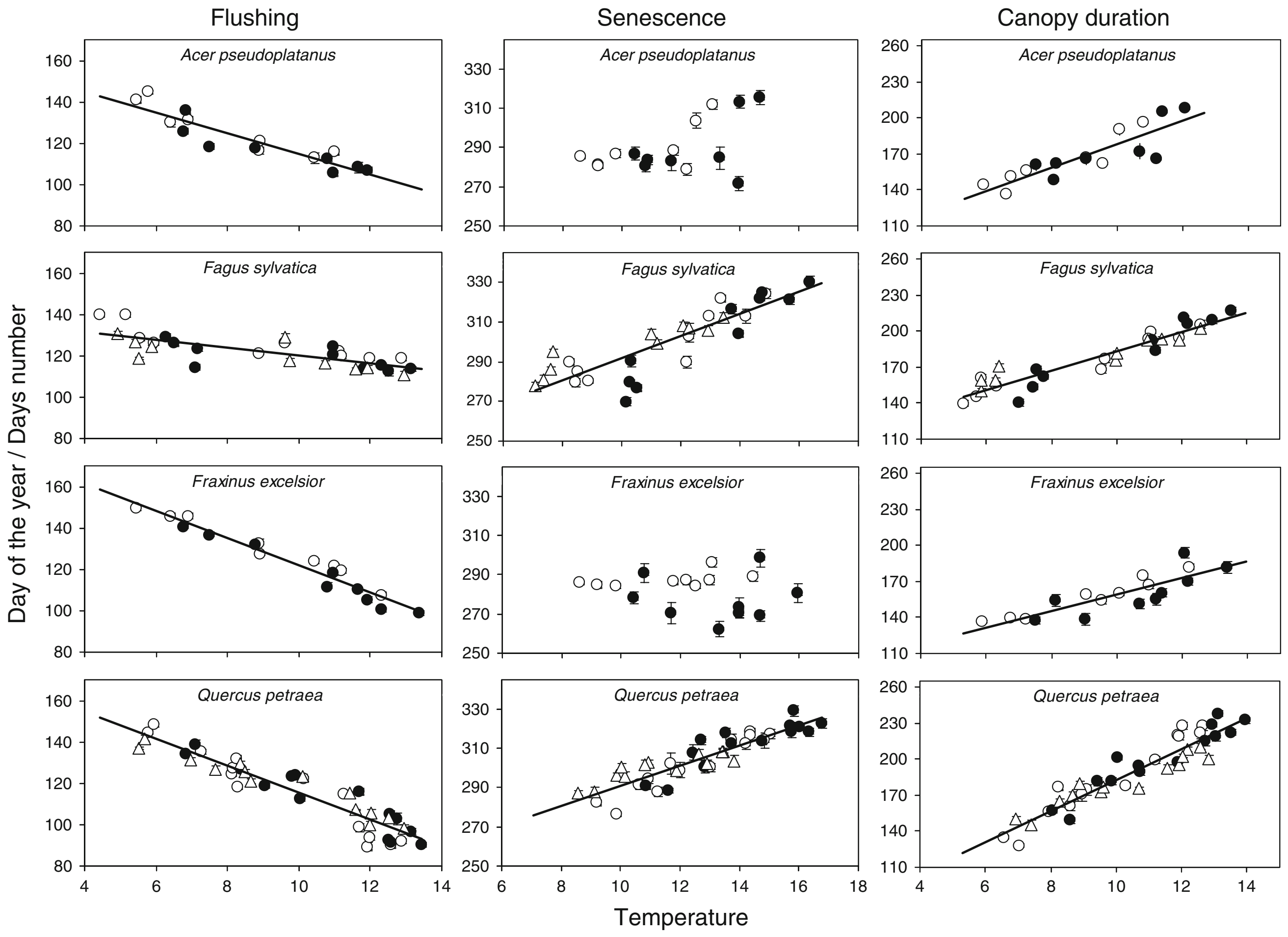

Fig. 2 Relationship between mean air temperature (*T*) and dates of flushing (1 March–31 May), leaf senescence (1 September–30 November) and canopy duration for four species in 2005 (*white circles*), 2006 (*black circles*) and 2007 (*white triangles*). Each *point* represents the mean value of ten trees per population and *bars* are SEs. We used *T* from 1 March to 31 May for the correlation with flushing, from 1 September to 30 November for the correlation with senescence, and annual temperature for the correlation with canopy duration

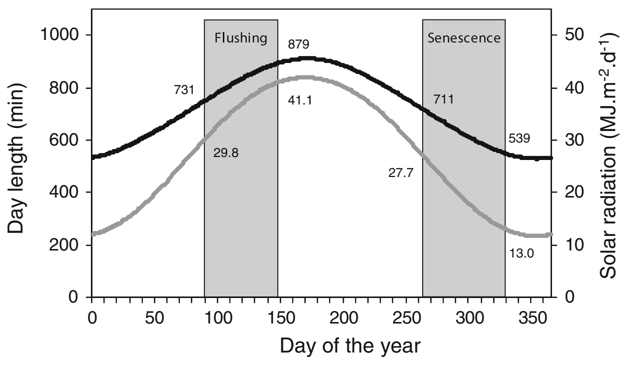

Fig. 3 Variations in day length (*black line*; min) and extraterrestrial solar radiation (*grey line*; MJ m^{-2} day^{-1}) throughout a year in Argelez Gazost (43°14′N, 00°05′W, 453 m a.s.l.). Periods of flushing and leaf senescence observed along the altitudinal gradients are represented by *grey bars* in order to visualise the potential radiation intercepted at each period. The *numbers above* and *below* the curves are values of day length and solar radiation, respectively, at the beginning and the end of flushing and senescence

Environmental determinism of leaf phenology

Flushing was more sensitive to temperature than senescence, except in beech, for which a temperature increase affected senescence far more than flushing. An increase of 1°C in air temperature in spring advanced flushing by 1.9–6.6 days, depending on the species. These results are close to those of previous studies that reported a 3–10 day shift per 1°C increase (Chmielewski and Rotzer 2001; Penuelas et al. 2002; Karlsson et al. 2003). In mid-latitude Europe, winter-spring temperatures (February–April) accounted for most of the variance observed in the timing of flushing (e.g. Chuine and Cour 1999; Chuine et al. 1998; Hunter and Lechowicz 1992). Our results also strongly indicated that air temperature in early spring is the main factor controlling flushing for temperate trees.

Although most other studies have shown that autumn phenological events are little affected by air temperature

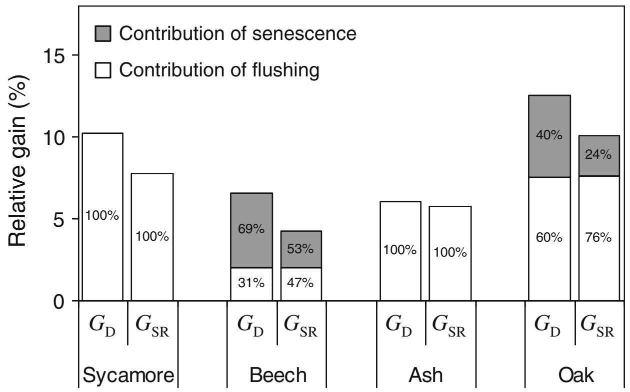

Fig. 4 Relative gain in canopy duration (%), on a per day basis (G_d) and a solar radiation basis (G_{SR}) for 1°C increase in temperature. Each value is the mean of the 3 monitored years and was calculated using the timing of the phenological events of the populations which exhibited the shortest and the longest canopy duration, standardised per 1°C increase, using the lapse rate between these two populations. *White bars* represent the contribution of flushing and *grey bars* the contribution of leaf senescence to the relative gain of canopy duration

(Chmielewski and Rotzer 2001; Menzel 2002; Sparks and Menzel 2002), we demonstrated that senescence was mainly driven by temperature, at least for two of the four studied species ($r^2 > 0.75$). In contrast, we found no significant relationship between these variables for ash and sycamore, which suggests that other environmental factors might play a role in the onset of senescence. In short, there is no agreement in the literature about the determinants of autumn leaf senescence (Estrella and Menzel 2006). Though some of the endogenous factors which promote leaf fall are well identified (for example, sugar concentrations or phytohormone concentrations; Koike 1990; Lim et al. 2007), environmental signals involved in triggering senescence are poorly understood. To our knowledge, four different explanations have been formulated. First, warmer autumnal temperatures would trigger a delay in senescence (Estrella and Menzel 2006; Matsumoto et al. 2003; Shutova et al. 2006). Secondly, in complete opposition to the latter, warmer summer/autumnal temperatures would accelerate senescence for several European deciduous species (Kramer 1995b), probably linked to summer drought. Thirdly, observing that dates of leaf fall remained constant from year to year although temperatures varied, some authors suggested that senescence could be solely induced by a day length decrease in autumn (Keskitalo et al. 2005; Lee et al. 2003). Finally, the last hypothesis states that low autumnal temperatures coupled to a reduction in day length and solar radiation could modulate the onset of senescence (Koike 1990). In our study, the sampled populations were very close to each other and consequently the day length they experienced hardly varied. Therefore, the large observed variability in dates of leaf senescence for beech and oak could not have been determined by the decreasing day length in autumn, but was rather due to temperature lapse rate. Our results supported the first hypothesis for beech and oak, but the third one for ash and sycamore, thus demonstrating that it is not possible to explain variations in the timing of senescence by temperature only. In accordance with our study, recent results showed that the environmental signals which induce the onset of senescence in temperate trees in North America were species dependent (Richardson et al. 2006): senescence in yellow birch was better described by a model that took both autumn chilling and the day of the year (i.e. potential effect of photoperiod) into account, whereas for sugar maple and American beech, including the day of the year did not improve the model.

Focusing on a linear response function (averaging temperatures over spring for leaf unfolding and over autumn for leaf senescence) is very useful in order to compare between-species differences and to quantify the relative contribution of each phenological event shift to the duration of the growing season. However, these functions do not allow the dual role of temperature (chilling vs. forcing temperatures) to be taken into account for leaf unfolding. Indeed, according to the prevailing theory, prolonged exposure to chilling during bud dormancy accelerates its completion whereas afterwards, prolonged exposure to warm conditions causes ontogenetic development leading to budburst (Saxe et al. 2001). In further studies, our data set could and will be used to fit spring and autumn phenological models to investigate the species' sensitivity to chilling and forcing temperatures, as well as day length (e.g. Chuine et al. 2000; Schaber and Badeck 2003; Hanninen and Kramer 2007).

Relative contributions of flushing and senescence

Previous studies generally concluded that leaf spring phenology mainly determines the lengthening of canopy duration under climate warming (Aerts et al. 2006; Chmielewski and Rotzer 2001; Saxe et al. 2001). In contrast, for two species, our results demonstrated that the increase in canopy duration with temperature can also be attributed to a delay in autumn phenological events. Overall, we found that advances in flushing could result in a larger gain in solar radiation than delays in senescence (except for beech). These results suggest that climate change will increase the trees' C uptake period (number of days with net CO_2 uptake from the atmosphere; White and Nemani 2003) and, therefore, could enhance tree growth and productivity, as proposed by previous studies (Keeling et al. 1996; Myneni et al. 1997; Piao et al. 2007). However, spring development from bud burst to mature leaves (full photosynthetic capacity) of deciduous species can be long, about 2 months for *Quercus robur* for example (Morecroft et al. 2003). This implies that little C could be assimilated in the first weeks after leaf unfolding. Hence, the impact of advanced flushing on annual C uptake might have been overestimated. On the other hand, for species such as beech, delays in senescence with increasing temperature can contribute to an increase in the gain from intercepted solar radiation to the same extent as advances in flushing. Consequently, a delayed senescence could increase autumn assimilation and C stocks in lower stems and roots, thereby conferring a growth advantage for the next season (Dunlap and Stettler 1998; Norby et al. 2003; Skomarkova et al. 2006). This advantage has been observed in spite of low solar radiation and lesser leaf photosynthetic efficiency in autumn. However, the extension of canopy duration in response to an increase in temperature does not necessarily result in a higher fitness. Both earlier leaf flush and later senescence can increase the risks related to frost damage: in spring, late frosts can induce a reduction in tree growth (Hanninen 1991), and in autumn, frosts on still functional leaves can entail partial nutrient remobilisation (Norby et al. 2003).

Spring warming in recent decades has been credited with inducing an increase in CO_2 uptake in high northern latitudes (Welp et al. 2007) and it has been shown that canopy duration is a crucial factor in the modulation of terrestrial C balance in temperate latitudes (Barr et al. 2007; Churkina et al. 2005; Richardson et al. 2009). Nevertheless, the links between phenological changes and the terrestrial C cycle are far from being clear (Piao et al. 2007) and the species' relative contributions to the latter remain unclear. Indeed, warmer spring temperatures generally enhance the net ecosystem C uptake, whereas warmer autumn temperatures seem to decrease it, due to a larger increase in respiration rates (Piao et al. 2008). Our study added to this knowledge by demonstrating that climate warming could hardly result in a reduction in canopy duration, but rather entails a lengthening of the potential C uptake period that might lead to an increase in primary production. Net ecosystem C losses in response to autumn warming may not—or hardly—be due to a decrease in tree C uptake, but should mainly result from changes in the C budgets of other ecosystem compartments (increased soil respiration for example). Consequently, our results suggested that climate warming could: (1) enhance C uptake at the tree level by lengthening canopy duration, provided that precipitation will not consistently be reduced, inducing a water limitation to CO_2 assimilation; and (2) lead to changes in the competitive balance between species by modifying their respective fitness due to differences in phenological sensitivity to temperature. This latter impact should play a role in the shift in the distribution of tree species and forest composition predicted for the next decades (Chuine and Beaubien 2001).

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