

# Long-term temporal changes in central European tree phenology (1946–2010) confirm the recent extension of growing seasons

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**Abstract** One of the ways to assess the impacts of climate change on plants is analysing their long-term phenological data. We studied phenological records of 18 common tree species and their 8 phenological phases, spanning 65 years (1946–2010) and covering the area of the Czech Republic. For each species and phenophase, we assessed the changes in its annual means (for detecting shifts in the timing of the event) and standard deviations (for detecting changes in duration of the phenophases). The prevailing pattern across tree species was that since around the year 1976, there has been a consistent advancement of the onset of spring phenophases (leaf unfolding and flowering) and subsequent acceleration of fruit ripening, and a delay of autumn phenophases (leaf colouring and leaf falling). The most considerable shifts in the timing of spring phenophases were displayed by early-successional short-lived tree species. The most pronounced temporal shifts were found for the beginning of seed ripening in conifers with an advancement in this phenophase of up to 2.2 days year<sup>-1</sup> in Scots Pine (*Pinus sylvestris*). With regards to the change in duration of the phenophases, no consistent patterns were revealed. The growing season has extended on average by 23.8 days during the last 35 years. The most considerable prolongation was found in Pedunculate Oak (*Quercus robur*): 31.6 days (1976–2010). Extended growing season lengths do have the potential to increase growth and

seed productivity, but unequal shifts among species might alter competitive relationships within ecosystems.

**Keywords** Climate change · Flowering · Growing season · Long-term trends · Phenology · Trees

## Introduction

Many countries have a long-standing tradition of observing phenological events. These long-term records have emerged as an essential tool for studying the present phenomenon of global climate change (Schwartz 2003). A variety of temporal shifts in phenological events have been documented across a range of species, communities and trophic levels (Root et al. 2003; Visser and Both 2005; Walther et al. 2002). In general, results suggest an advancement in spring and a delay in autumn phenology for tree species during the last few decades in Europe (Chmielewski and Rötzer 2001, 2002; Menzel et al. 2001; Schwartz et al. 2006; Sparks and Menzel 2002). However, the shifts in phenophases can substantially vary among countries—studies have found an advancement of spring phenophases of up to 4 weeks in Western and Central Europe and a delay of up to 2 weeks in Eastern Europe during the time period 1951–1998 (Ahas et al. 2002). These phenological changes have shown close correlations with increasing mean temperature in several countries (Menzel et al. 2006; Sparks et al. 2009). Accordingly, the growing season assessment coupled with data from International Phenological Gardens for tree species across Europe showed that 1 °C warming in early spring (February–April) caused a 7-day advancement in the beginning of the growing season (Chmielewski and Rötzer 2001). According to Menzel and Fabian (1999), the growing period lengthened by an average of 11 days in Europe during the period of 1959–1993.

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During the last 60 years, the growing season has widened up to 18 days in Spain for 29 perennial species (Gordo and Sanz 2009). Garzía-Mozo et al. (2010) found that the flowering of olive (*Olea europea*) has likewise significantly advanced by 40 days in Spain during 1986–2008. In Germany, the shifts in spring phenophases were in the range of 5–20 days between 1951 and 1999 (Schaber and Badeck 2005), and the growing season extended by 5 days on average between 1974 and 1996 in comparison to the period 1951–1973 (Menzel et al. 2001). In Switzerland, one of the oldest plant phenological time series in Europe shows an advancement in the onset of bud burst by 0.23 day year<sup>-1</sup> in Horse Chestnut (*Aesculus hippocastanum*) and by 0.06 day year<sup>-1</sup> for the flowering of Cherry trees (*Prunus avium*) (Defila and Clot 2001). Likewise, advancement in the onset of flowering and the peak of flowering of woodland herbaceous plants was documented by Sparks et al. (2009) in north-eastern Poland. Finally, the bud burst and the flowering of deciduous trees in Finland have advanced at a rate of 3–11 days per century during the last 160 years (Linkosalo et al. 2009).

The origins of phenological observations, including trees, in the Czech Republic can be traced back to the second half of the eighteenth century (Brázdil et al. 2011; Nekovář et al. 2008; Nekovář and Hájková 2010). Most recent studies on plant phenology in the Czech Republic deal with agricultural crops (Hlavinka et al. 2009; Mozny et al. 2009; Trnka et al. 2011a, b, c), but a comprehensive assessment of tree species is still lacking.

This study aims to identify and quantify temporal trends in phenological events of 18 common tree species across the Czech Republic. For this purpose, we evaluated three phenomena for each tree species. First, we evaluated changes in the annual mean values of a given phenophase in order to identify temporal shifts in the timing of their onsets. Secondly, we evaluated changes in the annual standard deviations of a given phenophase in order to explore the changes in duration of each phenophase. Finally, we evaluated the changes in the duration of the growing season.

## Materials and methods

### Phenological data

Data on the timing of particular phenological events were obtained from the archives of the Czech Hydrometeorological Institute. These data were collected from 149 phenological stations under the national phenological network across the entire Czech Republic (Fig. 1, ESM 1). Volunteer observers contribute annually observation data from the same locality. Data from the same individual trees are recorded over the years. For details on the network that runs since 1923, see Nekovář and Hájková (2010). The archive keeps records for

many more stations, but we have restricted our analyses only to those stations where there was at least a time series of 20 years of uninterrupted records. Similarly, we included only those tree species with at least 50 years of data. Thus, 18 common European tree species (Table 1) and their 8 phenophases (more than 317,000 records) were chosen for analyses. Because of the lack of data, the phenophases leaf colouring, the beginning of leaf falling and leaf falling could not be included for *Picea abies* and *Pinus sylvestris*. The phenophases were defined as:

Beginning of flowering	<10 % of flowers are in blossom
Flowering	>50 % of flowers are in blossom
Beginning of leaf unfolding	<10 % of leaves have already appeared
Leaf unfolding	>50 % of leaves have already appeared
Leaf colouring	>50 % of leaves have already coloured
Beginning of leaf falling	<10 % of leaves have already fallen
Leaf falling	>50 % of leaves have already fallen
Beginning of fruit ripening	<10 % of seeds /fruits have ripened.

### Data processing and analysis

First, it was necessary to check the database for mistaken values or outliers. All outliers were identified by the visual inspection of box-plots of records for each species and phenophase in a given year. Some of the mistakes could arise during the digitalisation of the original paper records or during data processing. In all cases when the records seemed to be clearly incorrect or suspicious, they were removed from the final dataset. The phenological observations by volunteers are standardised according to the published methodology and supervised by regional professional meteorologists.

We set a limit of a minimum of 10 observations for each phenophase in each year for a given tree species for inclusion into the analyses. All year-specific phenophases that did not meet this criterion were excluded from further analyses. All dates were expressed as days of the year (DOY), where January 1 was set as 1. However, some phenophases started in the second half of the calendar year (after September) and continuously overran to the following year. In those cases, the DOY had a value 365 (366 in leap years)+the number of days that overran to the next year. This was the case for leaf falling in *Fagus sylvatica* and *Larix decidua*, and beginning of fruit ripening in *Alnus glutinosa*, *L. decidua*, *Picea abies* and *Pinus sylvestris*.

In order to evaluate the temporal trends, mean and standard deviation were calculated for each phenophase of a given tree

**Fig. 1** Map of locations of 149 phenological stations in the Czech Republic involved in this study. Only stations with long-term continuous data were included



species in a given year from all available phenological stations. The mean gives us the information about the position of the phenophase in the calendar, whereas standard deviation illustrates the variability in the duration of the phenophase. In other words, as a consequence of the change in mean values, the plants delay or advance the onset of the phenophase. However, the shift in standard deviation values implies that the duration of the phenophase is either compressed or extended. For detailed explanation, see Gordo and Sanz (2009).

To evaluate long-term trends in phenology, multiple regression models were used with year and the quadratic effect of year as explanatory variables. First, quadratic regressions for the mean and the standard deviation for each phenophase and

species were examined for the period 1946–2010. In the case of non-significance of the quadratic term ( $P < 0.05$ ), only linear regression was calculated (ESM 2). Given that the quadratic regression fit was appropriate, we determined the turn-point of the curve—the year when the recent linear trend starts. This was a local maximum or minimum of each quadratic function, i.e. the point when derivatives of the quadratic functions were equal to 0. By simply averaging all of the turn-points for mean and standard deviation, we arrived at the global turn-point (in this case, the year 1976). Our aim here was to set a common year from which phenophases of all tree species showed a rather consistent linear temporal pattern. The curves that approached the shape of straight lines or the turn-points whose data series were short (minimum set at 50 years) were not included in calculation of the global turn-point (ESM 2).

Next, the linear regressions for all phenophases of each species were evaluated again for the period 1976–2010 to get the slope of the straight line. This represents the change of phenophase in the time span (ESM 3). Mean values and values of standard deviation of all species whose time series were minimally 30 years long (ESM 3) were used to compare the variability of data for each phenophase.

The length of growing season was defined as the time span between leaf unfolding and leaf colouring. For each species for which we had data for both phenophases, we calculated the change in the length of growing season. This was calculated from the differences of slopes for leaf unfolding and leaf colouring, multiplied by 35 (i.e. the number of years in the period 1976–2010).

Phenological data collected by volunteers might be biased by uneven effort during the week as a result of the observers preferentially making their phenological observations over the weekend (Menzel et al. 2001). To check for this bias, the day of the week for all observations was calculated (see ESM 4). We found a slight bias towards Sunday (14.80 %), while the day with the lowest number of records was Wednesday (13.97 %). This range fits within the values found in similar

**Table 1** Plant species included in this study ( $n$  number of observations per particular species)

	Scientific name	Common name	$n$
1.	<i>Sambucus nigra</i> L.	Black Elder	17.054
2.	<i>Pinus sylvestris</i> L.	Scots Pine	7.924
3.	<i>Betula pendula</i> Roth	Silver Birch	24.854
4.	<i>Fagus sylvatica</i> L.	European Beech	17.750
5.	<i>Quercus robur</i> L.	Pedunculate Oak	24.673
6.	<i>Crataegus laevigata</i> (Poir.) DC.	Midland Hawthorn	15.345
7.	<i>Acer pseudoplatanus</i> L.	Sycamore	19.249
8.	<i>Acer platanoides</i> L.	Norway Maple	21.539
9.	<i>Sorbus aucuparia</i> L.	Rowan	24.725
10.	<i>Tilia cordata</i> Miller	Small-leaved Lime	21.995
11.	<i>Corylus avellana</i> L.	Common Hazel	15.690
12.	<i>Larix decidua</i> Miller	European Larch	16.048
13.	<i>Alnus glutinosa</i> (L.) Gaertn	Common Alder	16.578
14.	<i>Prunus spinosa</i> L.	Blackthorn	20.480
15.	<i>Picea abies</i> (L.) Karsten	Norway Spruce	7.269
16.	<i>Cornus sanguinea</i> L.	Common Dogwood	5.975
17.	<i>Robinia pseudoacacia</i> L.	Black Locust	20.006
18.	<i>Salix caprea</i> L.	Goat Willow	20.593

studies (Gordo and Sanz 2009; Menzel et al. 2001). We consider the observers' effort very stable during the week, and thus, the influence of biased data is negligible and should not have a significant impact on the findings. All data were analysed using JMP (SAS Institute) and R (R Development Core Team 2012).

## Results

Temporal trends of plant phenology for the period 1946–2010

### Shifts in timing of phenophases

Out of 115 phenophases, 92 showed significant trends spanning the period of 65 years (ESM 2). With a closer look at the phenophases, 15 out of 18 species have significantly changed the beginning of flowering. Among them, three species showed a linear advancement, while in 12 others, there was a delay, followed by an advancement, beginning around the 1970s.

For flowering, changes in 11 out of 18 phenophases were significant. Three species showed linear advancement, and one species showed a linear delay. Non-linear response was found in six species with a delay followed by an advancement. Only one species, *Alnus glutinosa*, showed an advancement initially and then, beginning in 1985, a delay in onset of this phenophase. The beginning of leaf unfolding phenophase showed a high proportion of significant trends (16 out of 18). Five species showed significant linear advancement, while non-linear trends were found in 11 species. In 10 species, there was first a delay and a subsequent advancement. In *Cornus sanguinea*, there was initially no change and an advancement after 1968. For the leaf unfolding phenophase, eight out of 16 species showed significant change. Among them, *Crataegus laevigata* and *Sambucus nigra* showed a linear advancement. Non-linear changes, with a delay and subsequent advancement were found in four species. In two species (*Cornus sanguinea* and *Prunus spinosa*), the curves were flat first and later showed advancement. All 11 species' phenophase, leaf colouring showed significant non-linear change of an advancement in the initial period and later a delay. Similarly, all 11 considered species showed significant trends in beginning of leaf falling. Six species showed a linear trend of earlier leaf falling and five species showed a non-linear trend. These non-linear trends had the shape of a shallow convex function. For leaf falling, 10 out of 12 species showed a significant change. Three species linearly delayed the onset of this phenophase. Seven species showed a non-linear delaying change. In the case of beginning fruit ripening, nine out of 11 species displayed significant shifts. *Quercus robur* and *Sorbus aucuparia* showed a linear advancement in timing. In *Betula pendula*, *Crataegus laevigata*, *Prunus*

*spinosa* and *Sambucus nigra*, there was a non-linear concave advancement, while in *Robinia pseudoacacia*, *Corylus avellana* and *F. sylvatica*, there was initially a delay followed by an advancement.

### Changes in the duration of phenophases

Out of 115 studied phenophases, 73 were significant (ESM 2). The shifts in mean values were usually accompanied by shifts in standard deviations (49 cases). For beginning of flowering, 13 species out of 18 have significantly increased variability in the length of the phenophase. Four linear and nine non-linear trends were detected, with the latter showing a consistent pattern of expansion at the beginning of the period and compression since 1980s. For flowering, three species showed significant linear trends (two prolongations and one compression) and 10 non-linear significant trends. In all of the non-linear trends, there was first a compression followed by an expansion. The only exception was *Prunus spinosa*, which showed an opposite trend. Only two species (*Cornus sanguinea* and *Picea abies*) displayed significant non-linear shifts in the duration of beginning of leaf unfolding. Among 10 species with linear changes in duration, 9 showed a compressed phenophase and only *Robinia pseudoacacia* showed an extended phenophase. For leaf unfolding, nine significant trends were found; three linear (two compressions represented by *Salix caprea* and *Q. robur*, and one expansion found for *Sorbus aucuparia*) and six non-linear trends. For *Acer pseudoplatanus*, *F. sylvatica* and *Robinia pseudoacacia*, compression was found until the 1980s, and subsequently, the phenophase extended its duration. In contrast, for *Cornus sanguinea*, *Crataegus laevigata* and *Prunus spinosa*, the function had a convex shape. For leaf colouring, only four species (out of 11) showed significant change in duration. Linear extension was found for *Sorbus aucuparia*. Non-linear trends with compression followed by an expansion were found for *Acer platanoides* and *F. sylvatica*. For *Prunus spinosa*, the function had a shallow concave shape. The highest proportion of changes was found for the beginning of leaf falling (10 out of 11). All of them showed linear expansion. For the leaf falling, four linear expansions and two non-linear changes were found. The curves for *F. sylvatica* and *Q. robur* had a very similar shape with no change until 1967, respectively 1974, and then followed by considerable extension of the phenophase. For fruit ripening, seven species showed significant shifts in duration of the event. *Acer platanoides* linearly shortened the period, whereas *Robinia pseudoacacia* prolonged it. Non-linear trends for *Acer pseudoplatanus* revealed a very fast expansion and after 1981 a compression, while the function for *Corylus avellana*, *Prunus spinosa*, *Sambucus nigra* and *Sorbus aucuparia* had a rather shallow convex shape.



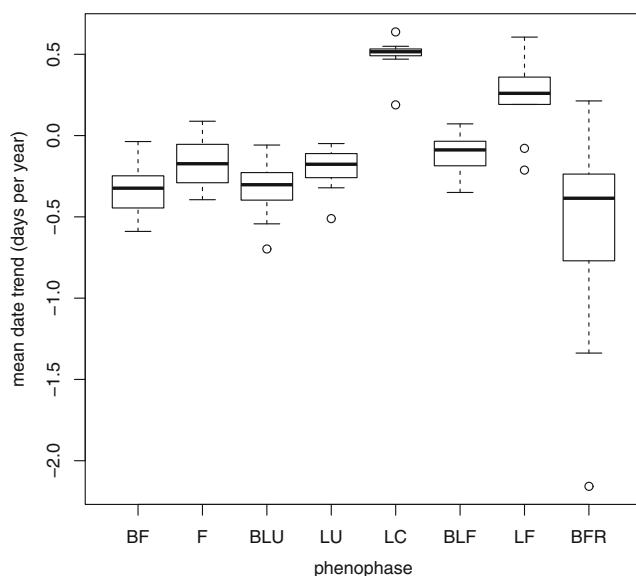
## Temporal trends in plant phenology 1976–2010

## Shifts in timing of phenophases

Out of 118 time series, 81 showed significant trends over the 35-year period (ESM 3). Overall, all spring phenophases (beginning of flowering, flowering, beginning of leaf unfolding and leaf unfolding) uniformly advanced the onset, whereas the autumn phenophases' shifts (leaf colouring, beginning of leaf falling, leaf falling and beginning of fruit ripening) were less uniform (Fig. 2). The phenophase leaf colouring had the smallest variability and was the most delayed phenophase. The phenophase beginning of leaf falling slightly advanced the onset contrary to leaf falling, which was delayed. The event beginning of fruit ripening advanced its onset but displayed the highest variance.

Looking closely at the beginning of flowering, all species showed an advancing pattern. For 13 species, this trend was significant. The largest shifts were documented in *Cornus sanguinea* ( $b=-0.590$  day year<sup>-1</sup>) and in *Tilia cordata* ( $b=-0.495$  day year<sup>-1</sup>).

Similarly, a coherent pattern of advancement was found across species (16 out of 18) for flowering. Out of 18 species, the trend was significant in 7. The most considerable shifts were found in *Cornus sanguinea* ( $b=-0.394$  day year<sup>-1</sup>) and in *Prunus spinosa* ( $b=-0.334$  day year<sup>-1</sup>). The highest proportion of significant changes for spring phenophases was found for beginning of leaf unfolding (16 out of 18), and all of them showed advancement. As in the previous cases, *Cornus sanguinea* showed the most markedly advanced position in



**Fig. 2** Box plot of mean temporal trends for each phenophase during the period 1976–2010. Beginning of flowering (BF), flowering (F), beginning of leaf unfolding (BLU), leaf unfolding (LU), leaf colouring (LC), beginning of leaf falling (BLF), leaf falling (LF) and beginning of fruit ripening (BFR) are shown

the calendar ( $b=-0.697$  day year<sup>-1</sup>), but *Robinia pseudoacacia* also displayed a noticeable shift ( $b=-0.543$  day year<sup>-1</sup>). In the case of leaf unfolding, the result was analogous to the above-mentioned phenophases—all species advanced the onset of the phenophase, and for eight species, this trend was significant. Again *Cornus sanguinea* ( $b=-0.511$  day year<sup>-1</sup>) and *Prunus spinosa* ( $b=-0.321$  day year<sup>-1</sup>) showed the most pronounced shifts. Leaf colouring was the first evaluated autumn phenophase, and all tree species showed a significant delay. The most considerable shift was found in *Q. robur* with a delay of 0.638 day year<sup>-1</sup>, but nearly all other species delayed leaf colouring by approximately half a day per year.

Beginning of leaf falling advanced in 9 out of 11 considered species, and for 4 of them, the trend was significant. The most pronounced shift was found in *Sorbus aucuparia* ( $b=-0.350$  day year<sup>-1</sup>). For leaf falling 10 out of 12 species delayed the onset of the phenophase. For all 10 species, this shift was significant. The most pronounced delays were found in *Q. robur* ( $b=0.606$  day year<sup>-1</sup>) and *L. decidua* ( $b=0.568$  day year<sup>-1</sup>).

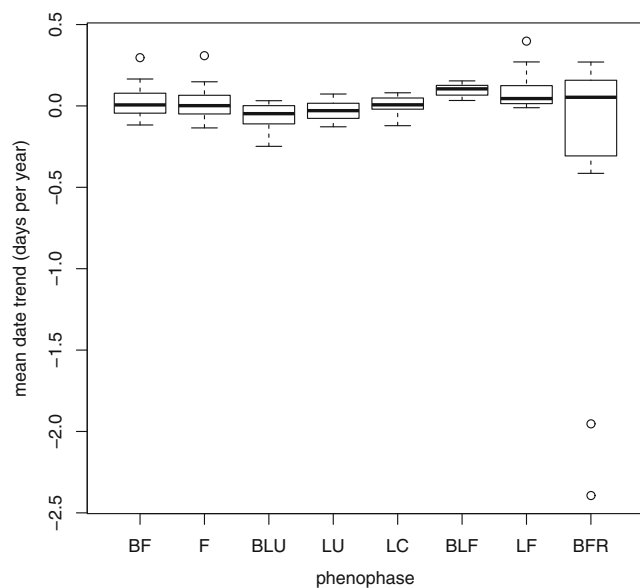
For the beginning of fruit ripening, 12 species showed significant shifts. Except for *Acer pseudoplatanus*, which delayed the seed ripening by 0.213 day year<sup>-1</sup>, all of the remaining species advanced this phenophase. Interestingly, the most advanced beginning of ripening was found in coniferous trees: *Pinus sylvestris* ( $b=-2.157$  day year<sup>-1</sup>) and *Picea abies* ( $b=-1.338$  day year<sup>-1</sup>). Among deciduous species, the most marked shift was found in *Prunus spinosa* ( $b=-0.823$  day year<sup>-1</sup>).

## Changes in the duration of phenophases

Overall, the trends in the durations of the phenophases were less coherent in comparison with the mean values. Out of 118 phenophases, there were significant trends in 46 species. The detected shifts were rather small, and no particular trend for spring or autumn phenophases was obvious (Fig. 3).

The first evaluated phenophase—beginning of flowering—showed five significant expansions and two compressions in data distribution. Whereas the onset of flowering in *Picea abies* has shortened by 0.117 day year<sup>-1</sup>, in contrast, *Alnus glutinosa* extended the time period of beginning of flowering by 0.296 day year<sup>-1</sup>.

Only six species showed significant change in flowering data distribution: Four species showed extension of the phenophase duration while two species showed contraction. The largest positive slope was found for *Alnus glutinosa* ( $b=0.308$  day year<sup>-1</sup>), while the largest negative trend was found in *Prunus spinosa* ( $b=-0.135$  day year<sup>-1</sup>). In the case of beginning of leaf unfolding, seven species displayed significant change, and in all cases, they shortened the duration of



**Fig. 3** Box plot of temporal trends in standard deviation for each phenophase during the period 1976–2010. Abbreviations as in Fig. 2

this phenophase. The most marked shift was found in *Cornus sanguinea* ( $b=-0.248$  day year<sup>-1</sup>). Five species showed significant shifts in leaf unfolding; four of them compressed and one, *Robinia pseudoacacia*, prolonged the duration of this phenophase by 0.073 day year<sup>-1</sup>. For leaf colouring, only 2 out of 11 time series showed a significant trend. *L. decidua* extended the duration of the phenophase by 0.081 day year<sup>-1</sup>, while *Prunus spinosa* contracted the duration by 0.121 day year<sup>-1</sup>. In the case of beginning of leaf falling, all 6 out of 11 species significantly prolonged the duration of the onset of leaf falling. The largest expansion was found in *Salix caprea* ( $b=0.154$  day year<sup>-1</sup>). Similarly, the phenophase leaf falling showed overall prolongation of duration. In four species, this trend was significant. The largest effect was found in *F. sylvatica* ( $b=0.398$  day year<sup>-1</sup>). A high proportion of significant shifts (9 species out of 14) was found for beginning of fruit ripening. This phenophase also displayed the highest variance in data distribution. The most extreme cases for contraction of timing of ripening were found in *Picea abies* by 2.393 day year<sup>-1</sup> and prolongation in *Prunus spinosa* ( $b=0.270$  day year<sup>-1</sup>).

#### Temporal changes in the growing season

Across 11 tree species, the growing season has extended by an average of 23.81 days during the period 1976–2010 (Table 2). The prolongation substantially varied among species from 10.55 days for *Sorbus aucuparia* to 31.57 days for *Q. robur*. Only rarely were the shifts in the timing of spring and autumn phenophases of similar magnitude. More often, the magnitude in shifts in the onset of leaf colouring exceeded the shifts in leaf unfolding.

**Table 2** Temporal trends of the growing season for the period 1976–2010

Species	LU (days year <sup>-1</sup> )	LU 35 (days)	LC (days year <sup>-1</sup> )	LC 35 (days)	GS 35 (days)
<i>Acer platanoides</i>	-0.080	-2.82	0.491	17.18	20.00
<i>Acer pseudoplatanus</i>	-0.160	-5.61	0.549	19.22	24.83
<i>Betula pendula</i>	-0.109	-3.81	0.503	17.62	21.43
<i>Fagus sylvatica</i>	-0.234	-8.17	0.516	18.50	26.67
<i>Larix decidua</i>	-0.206	-7.22	0.470	16.45	23.67
<i>Prunus spinosa</i>	-0.321	-11.24	0.520	18.19	29.43
<i>Quercus robur</i>	-0.264	-9.25	0.638	22.32	31.57
<i>Robinia pseudoacacia</i>	-0.290	-10.16	0.491	17.18	27.34
<i>Salix caprea</i>	-0.068	-2.40	0.542	18.97	21.37
<i>Sorbus aucuparia</i>	-0.113	-3.95	0.189	6.60	10.55
<i>Tilia cordata</i>	-0.193	-6.74	0.523	18.32	25.06

The change in timing of leaf unfolding (LU) and leaf colouring (LC) per 1 and per 35 years, and the extension of the growing season (GS) per 35 years are shown

#### Discussion

##### Shifts in timing of phenophases

Our results indicate a general trend in an advancement of spring phenophases, which has been widely described by other authors (Chmielewski and Rötzer 2001; Gordo and Sanz 2009; Menzel et al. 2006; Schwartz et al. 2006). For fruit ripening, we also found strong evidence for advancement, a pattern which has been rarely described to date (Menzel et al. 2006). For autumn phenophases, we found an overall delaying trend, but the effect was not as strong and uniform as in spring phenophases.

We found 1976 to be the mean break-point year. This is close to the global turn-point for Spain (1973) found by Gordo and Sanz (2009). Additionally, this is in accordance with the claim that two main time warm periods have been taking place in the twentieth century—between 1910 and 1945 and from 1976 onwards (Easterling 2002; Kunkel et al. 2004; Walther et al. 2002).

The primary force driving the onset of the spring phenophases is air temperature (Fitter and Fitter 2002; García-Mozo et al. 2010; Chmielewski and Rötzer 2002). However, it is sometimes overlooked that, in temperate zones, plants employ another two factors controlling the end of dormancy—chilling and photoperiod (Estrella et al. 2009; Harrington et al. 1999; Körner and Basler 2010; Tooke and Battey 2010). It is generally assumed that long-lived, late successional species (e.g. *Fagus* spp.) that become dominant in mature forests are sensitive to photoperiod, whereas shorter-lived, early successional and pioneer species, such as *Corylus* spp., *Populus* spp., and *Betula* spp., are photoperiod

insensitive (Körner and Basler 2010). Theoretically, those plants whose spring phenophases are triggered only by temperature might have a competitive advantage in comparison with those plants, which also require completion of chilling and photoperiod for the breaking of dormancy (Körner and Basler 2010). A rigorous evaluation of this hypothesis is hampered by a lack of studies dealing with the physiological demands of particular tree species, but some partial findings are in concordance with this assumption. While *Picea abies* is a photoperiod sensitive species (Partanen et al. 1998; Partanen et al. 2001), apple, pear and some other species of the Rosaceae family are not (Heide and Prestrud 2005). *B. pendula* and *B. pubescens* seem to be stimulated by photoperiod only to a limited extent (Myking and Heide 1995). Stříž and Nekovář (2010) also pointed out that the onset of generative phenophases (e.g. flowering, fruit ripening) might depend on the inner energy balance and accumulated energy of the plant, whereas vegetative phenophases (e.g. leaf unfolding, leaf colouring, leaf falling) are more influenced by climatic conditions.

Likewise, in this study, the most considerable shifts in timing of spring phases (beginning of flowering, flowering, beginning of leaf unfolding and leaf unfolding) were found for more or less shorter-lived early-successional species *Cornus sanguinea*, *Crataegus laevigata*, *Prunus spinosa*, *Robinia pseudoacacia* and *Tilia cordata*, and hence, the findings were in concordance with the above-mentioned hypothesis. However, another early-successional species expected to display this trend showed no or only slight changes. Specifically, *Alnus glutinosa* showed negative but non-significant change in the timing of beginning of flowering ( $b = -0.173 \text{ day year}^{-1}$ ), but data from the Alpine region (Ziello et al. 2009) proved a significant advancement by  $0.41 \text{ day year}^{-1}$  during the period 1971–2000. This discrepancy could be attributable to local environmental factors. Conversely, the trend of beginning of flowering for *Sorbus aucuparia* ( $b = -0.267 \text{ day year}^{-1}$ ) fitted the map of phenological trends found across Europe (Schleip et al. 2009). For the late-successional species *Q. robur*, the shift of leaf unfolding was only slight ( $b = -0.264 \text{ day year}^{-1}$ ), but in a close concordance with the findings from Germany ( $b = -0.23 \text{ day year}^{-1}$ ) for the periods 1951–1980 and 1967–1996 (Menzel et al. 2001). Similarly, the shifts of leaf unfolding for *F. sylvatica* by  $0.234 \text{ day year}^{-1}$  strongly agreed with the finding from Germany where an advancement by  $0.23 \text{ day year}^{-1}$  for the periods 1951–1973 and 1951–1980 was found (Menzel et al. 2001).

Another interesting pattern related to spring phenophases is that early flowering species (such as *Corylus* and *Betula*) show a much stronger response to warming than late flowering species (Ahas et al. 2002; Fitter and Fitter 2002; Menzel et al. 2006; Schleip et al. 2009). In contrast, our study did not find the largest responses in early flowering species. Therefore, this hypothesis cannot adequately clarify our findings.

While the spring phenophases are easily to recognise, the autumn phenophases are harder to define and detect. Furthermore, while there is a consensus on air temperature being the primary driving force of onsets of spring phenophases (Chmielewski and Rötzer 2002; Larcher 2006; Linkosalo et al. 2009; Menzel et al. 2006), the explanation of autumn forces is less straightforward (Menzel et al. 2006; Sparks and Menzel 2002). The activation of autumn phenophases seems to be more complex than just a simple temperature weighted function, and they are triggered by several factors in tandem (Chmielewski and Rötzer 2001; Menzel et al. 2001; Menzel et al. 2006; Rötzer and Chmielewski 2001; Sparks and Menzel 2002). Estrella and Menzel (2006) tested the influence of meteorological parameters on onset of leaf colouring. They included such parameters as monthly mean temperatures, threshold temperatures, sum of precipitation and number of dry days. They found that warm Septembers and Augusts delayed leaf colouring, whereas warm Junes and Mays advanced it.

The largest shifts in autumn phenophases (leaf colouring, beginning of leaf falling, leaf falling and beginning of fruit ripening) were displayed by a wider range of species compared with spring phenophases. Shifts in leaf colouring oscillated in many species around the value of  $0.5 \text{ day year}^{-1}$ . *Q. robur* showed largest delay in leaf colouring ( $b = 0.638 \text{ day year}^{-1}$ ), which exceeded the value from Germany ( $b = 0.23 \text{ day year}^{-1}$ ). Similarly, the delay of *F. sylvatica* ( $b = 0.516 \text{ day year}^{-1}$ ) was well over the finding from Germany ( $b = 0.07 \text{ day year}^{-1}$ ) during the periods 1951–1980 and 1967–1996 (Menzel et al. 2001). *Acer platanoides* significantly delayed leaf colouring by  $0.491 \text{ day year}^{-1}$ , while it has significantly advanced by  $0.63 \text{ day year}^{-1}$  in Latvia and between  $0.39$  and  $0.57 \text{ day year}^{-1}$  in Lithuania (Kalvāne et al. 2009). The shift of leaf colouring of *B. pendula* ( $b = 0.503 \text{ day year}^{-1}$ ) was in accordance with a delay of up to  $0.44 \text{ day year}^{-1}$  of this species in Germany (Menzel et al. 2001). However, it was partly inconsistent with the trend from Latvia where it has delayed in the eastern region ( $b = 0.33 \text{ day year}^{-1}$ ) and advanced in the western region ( $b = -0.27 \text{ day year}^{-1}$ ). In addition, in Lithuania, a uniform advancement was detected of up to  $0.80 \text{ day year}^{-1}$  (Kalvāne et al. 2009). In contrast to fruit trees or those with readily observable seeds such as *Quercus* spp. or *Acer* spp., the observation of conifers' fruit ripening is rather difficult even for experienced observers. This may explain the lower number of records in comparison to other species. Except for *Acer pseudoplatanus*, all significant shifts represented an advancement of beginning of fruit ripening. This might be attributed to the fact that fruit ripening is closely related to the flowering, and therefore, the accelerated flowering consecutively influenced the onset of fruit ripening.

An intriguing finding is the pronounced advancement of seed ripening in two coniferous species when compared to

deciduous species. The shifts of *Pinus sylvestris* ( $b = -2.157 \text{ day year}^{-1}$ ) and *Picea abies* ( $b = -1.338 \text{ day year}^{-1}$ ) are remarkable, while the most pronounced advancement among deciduous trees was displayed by *Prunus spinosa* ( $b = -0.823 \text{ day year}^{-1}$ ). The hygroscopic movements of conifers cones depend on air humidity. The cones open when it is dry and close when it is wet (Reyssat and Mahadevan 2009). There is a significant increase in air humidity in the autumn months of October–December during the period 1961–2005 in the Czech Republic (Brázdil et al. 2008). Thereby, the conifers might be forced to shed seed sooner during dry periods. Among other species where comparable published data exists, *Sambucus nigra* significantly advanced fruit ripening by  $0.458 \text{ day year}^{-1}$ , which is similar to the finding from Germany where the advancement was  $0.30 \text{ day year}^{-1}$  during 1951–1996 (Menzel et al. 2001).

#### Temporal trends in duration of phenophases

No apparent trend in shifts of standard deviation was found. Among the species that have changed the duration of the phenophases, the majority were shorter-lived trees such as *Alnus glutinosa*, *Cornus mas*, *Cornus sanguinea*, *Prunus spinosa* and *Salix caprea*. Because all of them are short-lived, early-successional species, the change in the duration of the phenophase could be only a different form of the same phenomenon, which was described above—pioneer species are more adapted to a risky life and thus probably more adaptable to changing climate (Körner and Basler 2010). The marked shifts of *Alnus glutinosa* and *Salix caprea* support the widely assumed prediction that early flowering plants react more sensitively and rapidly to warming than later flowering plants (Ahas et al. 2002; Fitter and Fitter 2002; Menzel et al. 2006; Schleip et al. 2009). Further research is needed to test this hypothesis with a larger sample of species at different sites.

#### Temporal trends in the length of the growing season

Growing season is considered to be the time between spring and autumn phenophases (Rötzer and Chmielewski 2001; Schwartz et al. 2006; Menzel et al. 2006). The length mainly depends on the beginning of spring phenophases, which vary more than those in autumn (Chmielewski and Rötzer 2001). As a result of the acceleration of spring events and postponement of autumn events, the winter is squeezed, and thus, the growing season gets longer (Schaber and Badeck 2005). An average length of the growing season is related to the annual air temperature, and an increase in temperature by  $1 \text{ }^\circ\text{C}$  prolongs the growing season by approximately 5 days (Chmielewski and Rötzer 2001). According to Menzel and Fabian (1999), the growing season has lengthened by nearly 11 days in Europe since the early 1960s. Almost the same figure was

found for Germany—about 10 days for the time period 1951–1999 (Schaber and Badeck 2005). In Latvia and Lithuania, the growing season extended by an average of 7 days during 1971–2000 (Kalvāne et al. 2009).

Our results show a lengthening of the growing season for a sample of 11 species by nearly 24 days on average during the period 1976–2010. The smallest change was found in *Sorbus aucuparia* (10.55 days), while the largest change was found in *Q. robur* (31.57 days). The range of variability in the length of the growing season was documented by Rötzer and Chmielewski (2001). They showed that, in comparison with the long-term mean, the growing season lengthened by 12 days in the warm year of 1990, while in the cold year of 1970, it shortened by 10 days. Our results for particular species were in line with other studies. The prolongation of the growing season of *B. pendula* by  $0.61 \text{ day year}^{-1}$  in our dataset (1976–2010) slightly exceeded the values of  $0.44 \text{ day year}^{-1}$  found in Germany for the period 1951–1996 (Menzel et al. 2001). The differences among other species were of similar magnitudes—the growing season of *F. sylvatica* in our dataset was prolonged by  $0.76 \text{ day year}^{-1}$ , whereas in Germany, it was prolonged by  $0.33 \text{ day year}^{-1}$  (Menzel et al. 2001). For *Q. robur*, the season was prolonged by  $0.90 \text{ day year}^{-1}$  in the Czech Republic vs. by  $0.49 \text{ day year}^{-1}$  in Germany (Menzel et al. 2001). The growing season of *Robinia pseudoacacia* has considerably extended as well—all the more significant because it is an important invasive species in the Czech Republic. The timing of phenophases is a very complex phenomenon, which is driven and influenced by many exogenous and endogenous factors. The dataset presented here covers the entire Czech Republic. Therefore, the influence of local climatic conditions might be substantial. Factors such as slope and altitude of the locality are known to considerably influence the findings (Rötzer and Chmielewski 2001). For example, Ziello et al. (2009) showed that beginning of flowering of *Corylus avellana* can be delayed up to 5 days per 100 m of altitude. On the other hand, *Picea abies* from the Alpine region, included in the same study showed the delay of beginning of flowering only by 1 day per 100 m of altitude. Additionally, some phenophases in that study showed no significant correlation with altitude. In our study, the range between the lowest and highest phenological station was almost 1,000 m (Doksany—155 m a.s.l.; Filipova Hut—1,102 m a.s.l.). According to Estrella et al. (2009), higher population densities or size of urban areas are correlated with advancement in onset dates because of the influence of heat islands. Not all stations in this study were further away than 10 km from a settlement larger than  $10 \text{ km}^2$ . This area was determined as a limit from which the impact of increased temperature from the settlement is negligible (Zhang et al. 2004), and this effect also should be taken into an account.



## Conclusion

Our results contribute to the coherent pattern of plant phenological responses across Europe. In short, spring phenophases have advanced and those in autumn have delayed. The most substantial shifts in advancement of spring phenophases were revealed for shorter-lived, early-successional species, which might be related to their life histories as pioneer species. This shift could bring an advantage to these species in the form of a better ability to track the changing climate (Körner and Basler 2010). In addition to commonly considered plant phenophases, we provide comprehensive multi-species data on the timing of fruit/seed ripening. Such data are still very rare. An interesting finding of our study is a marked shift in fruit ripening in coniferous species, which largely exceeded values found for deciduous trees. We are not aware of any comparable study dealing with conifers and their fruit ripening phenology, but undoubtedly, this phenomenon merits further attention. Along with the timing, we also analyzed the change in duration of all phenophases. Similarly to the trends in means, rather shorter-lived species prolonged or compressed the duration of phenophases the most, but the trends were not as uniform as in mean values. The species that shifted the duration of phenophase and the mean timing were not always the same. As a consequence of advanced spring and delayed autumn phenophases, the growing season has extended on average by 23.81 days during the 35-year time period.

The timing of phenophases is a crucial mechanism for coexistence of plant species in ecosystems, which leads to reduction of competition for resources (Rathcke and Lacey 1985). Decoupled synchronisation can promote the disruptions of relationships on intra- and interspecific levels through a wide range of species and trophic levels (Adamík and Král 2008; Visser and Holleman 2001).

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