

# Timing of bud burst and tree-leaf development in a multispecies temperate forest

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Received 31 December 2005; received in revised form 14 July 2006; accepted 28 September 2006

## Abstract

Timing of bud burst and leaf unfolding in trees growing in a mixed species stand was recorded during nine years (1997–2005) in primeval old-growth forests preserved in the Białowieża National Park (E Poland). Performance of five main woody species (producing over 98% of foliage) growing in the most diversified oak–lime–hornbeam *Tilio-Carpinetum* habitat were observed. Despite 2–3-week, interyear shifts in dates of bud burst onset, the order of bud burst by different species remained constant (from *Coryllus avellana* L., through *Carpinus betulus* L., *Acer platanoides* L., *Quercus robur* L., to *Tilia cordata* Mill.) among years. Depending on the year, the median bud burst dates of *Coryllus* and *Tilia* differed by 13–26 days. These differences tended to be smaller in the late (13–17 days) than in the early (20–26 days) springs, though the relationship was not significant. Leaf spread dates were much more synchronous than bud burst dates (span of 9 and 24 days, respectively), as the earliest commencing species – *Coryllus* and *Carpinus* – developed leaves at slower rates. Within a species, individual trees were developing leaves consistently early or late. The high repeatability across years, despite strong environmental variation, suggests existence of genetic differences. Leaves appeared earlier and grew faster in warmer springs. This variation was strongest influenced by weather variation in March and April, the temperature sums accumulated from March 1 were the best predictors of the actual burst dates. This appears to be the first multi-year study of timing of tree-leaf development in a multispecies deciduous forest in Europe.

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**Keywords:** Białowieża forest; Primeval forest; Bud burst; Phenology

## 1. Introduction

Spring appearance of leaves on deciduous trees influences critically numerous processes in temperate forests—from carbon flux and energy balance (references in Jenkins et al., 2002), via development of ground vegetation (e.g. Faliński, 2001), eclosion of folivorous insects' larvae (e.g. Buse and Good, 1996; van Dongen et al., 1997), to timing of birds' breeding (review in Visser et al., 2004) and their nest site choices (e.g. Tomiałojć, 1993). Thus, the knowledge of timing of tree bud burst, its spatial and temporal variation, and of mechanisms behind this variation, appears crucial for understanding most of seasonal phenomena in the deciduous forests, as well as for predictions of forests' reactions to changing climate (review in Harrington et al., 1999). One would therefore expect to find a large body of published multi-year data on

timing of bud burst gathered in various mixed species deciduous forest of Europe. Unfortunately it is not so, Lechowicz (1984) failed to find any detailed phenological records for a single European forest and situation has not apparently improved since then (Schwartz, 1998; Jenkins et al., 2002). In consequence, the question of: how synchronous is leaf emergence in different tree species growing within the same stand remains without an answer. Observations in natural conditions, free of direct human interference, repeated in the same places over several years, can also provide answers to the questions of extent of interyear variation in phenological synchronisation among tree species, consistency of leafing out sequence by different species across years, as well as, of repeatability of leaf emergence sequence of individual trees among years.

We attempt to answer these questions with the data collected in primeval old-growth forests preserved in the Białowieża National Park (E Poland). The local trees are probably well adapted to prevailing climatic conditions, as they all of native origin, descendants of individuals which naturally colonised the

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area in the post-glacial period (Faliński, 1986, 2001). We describe temporal patterns of bud burst and leaf unfolding in five woody species growing in a mixed stand recorded over 9 years first, continue with checking how this interannual variation in leafing phenology was related to the year-to-year variation in spring temperatures and, finally, we discuss possible mechanisms behind the recorded patterns.

## 2. Study area and methods

### 2.1. Study area

Situated on the Poland/Belarus border, the Białowieża Forest is located in mixed forest zone, on the boundary of central and eastern Europe (the Białowieża village co-ordinates are: 52°41'N and 23°52'E). The forest has Norway spruce *Picea abies* Karst. component in almost all types of stands (Faliński, 1986).

Primeval oldgrowth stands in the Białowieża Forest retain some features which are distinct among European temperate forests. They are multi-storey (up to 5–6 layers oak–lime–hornbeam *Tilio-Carpinetum* forest), strongly diversified as regards the age and size of trees (up to 400–500 years old, reaching 55 m height and 720 cm circumference) and species rich. The oak–lime–hornbeam stands alone may be composed of a dozen or so tree species, including lime *Tilia cordata* Mill., pedunculate oak *Quercus robur* L., hornbeam *Carpinus betulus* L., maple *Acer platanoides* L., elms *Ulmus* spp., birches *Betula* spp., aspen *Populus tremula* L., and ash *Fraxinus excelsior* L. More details and photos are given in Tomiałojć et al. (1984), Faliński (1986, 1991) and Tomiałojć and Wesołowski (1990, 1994, 2004).

The climate is subcontinental: mean annual precipitation 624 mm (425–940), long-term average annual temperature +6.6 °C, average January temperature –4.8 °C (–16.8 to 1.8). Snow cover (up to 95 cm deep) lasts up to 92 days; morning ground-frosts occur as late as mid-May, during the 1970s even to mid-June. Snow melts between c. 10 March (early spring) and 20 April (exceptionally late)-based on a 49-year-long series, see Faliński (1986, 2001) and Jędrzejewska et al. (1997) for more information. Mean annual temperatures in the last 200 years fluctuated, without a clear long term trend (Jędrzejewska and Jędrzejewski, 1998).

### 2.2. Data collection

We gathered phenological observations in the most diversified oak–lime–hornbeam *Tilio-Carpinetum* habitat. We recorded leaf development in four most numerous deciduous species in this forest type (*Carpinus betulus*, *Tilia cordata*, *Acer platanoides*, *Quercus robur*-jointly over 90% of trees, Wesołowski, 1996), as well as, *Coryllus avellana* L. The latter species, though morphologically a bush, reaches there height of 8–10 m, and looks like a small subcanopy tree. Jointly, these five species produce over 98% of deciduous tree foliage in the oak–hornbeam habitat (Rowiński, 2001).

To avoid any phenological bias sample trees we selected in a leafless period, before onset of study (in March of 1997). We

chose ten sites, 50–200 m apart, within one of permanent study areas (plot W, Tomiałojć et al., 1984). Within each site, we picked up one individual of every observed species (healthy tree, crown in the main canopy layer of a given species), selecting trees growing close to one another (within 10–40 m). This way any possible microhabitat variation among sites affected equally all species. We assessed leaf development of the same trees during the whole study (1997–2005), except two *Carpinus* (broken in 2002 and 2005) replaced by the individuals closest to them.

For practical reasons the observations sites were situated close (50–500 m) to the forest edge. To see whether this localisation, could have an influence on the observed leaf flush phenology, in 1998 we replicated all observations in another group of 10 sites within an oak–hornbeam area localised c. 1.5 km from the forest edge (plot CW + CE, Tomiałojć et al., 1984). After finding, that leaves developed at the same rate in both plots (Table 1) we restricted observations to the 50 trees in plot W.

Each spring we were beginning observations in the period when *Coryllus* leaf buds were strongly swollen/begun to break and continued them till shoots on all sample trees developed small unfolded leaves. Every second afternoon, using a 20–60× magnifying scope, we assessed development of apical leaf buds on a three-grade scale (Fig. 1). We classified a bud as

- (0) undeveloped, all stages from sleeping bud, to a bud with broken scales, tips of leaves visible but still forming a single bud tip;
- (1) broken-from small leaves with bases still hidden in bud scales but tips detached from the bud axis, till small leaves with folded blades;
- (2) developed, small unfolded leaves.

We assessed development stage of ten apical leaf buds, casually selected in the southern part of crown of a sample tree. On each occasion the buds were chosen anew. For each observation day we summed values for individual buds within a tree to get a leaf development score for individual trees (ranging 0–20). After a tree reached the maximum score we discontinued its observations. Finally, to arrive at leaf development index for

Table 1  
Comparison of leaf development advancement at the forest edge (plot W) and in the forest interior (plot C) in 1998

	Species plot									
	Coryllus		Carpinus		Acer		Quercus		Tilia	
	W	C	W	C	W	C	W	C	W	C
8 April	58	59	0	0	0	0	0	59	0	0
20 April	99	98	23	16	0	0	0	98	0	0
2 May	200	200	200	193	200	196	119	98	113 <sup>a</sup>	62 <sup>a</sup>
6 May	200	200	200	200	200	200	144	142	182 <sup>b</sup>	167 <sup>b</sup>

For each plot values of species leaf development indices (sum of leaf development scores of 10 sample trees) on different dates are shown. The index varies between 0 (all buds in all trees closed) and 200 (small flattened leaves on all shoots)—see Section 2 for details. a, b: Even on days with the most disparate results the advancement scores of individual trees did not differ significantly (Man–Whitney test:  $Z = -1.52$ ,  $p = 0.13^a$  and  $Z = -0.98$ ,  $p = 0.32^b$ ).

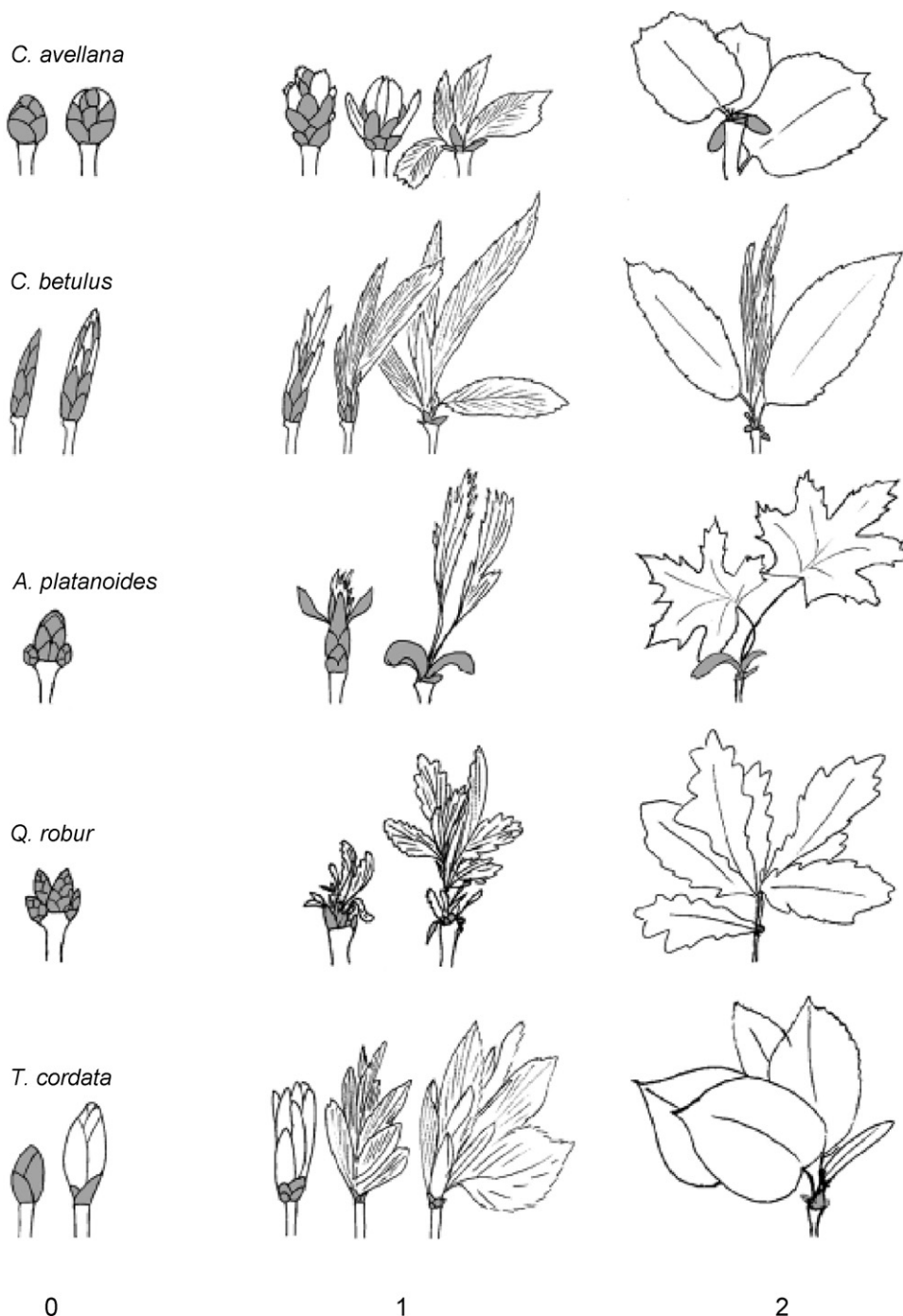


Fig. 1. Stages of bud/leaf development of individual species classified as 0 (undeveloped), 1 (broken) or 2 (developed).

a tree species, we added up tree scores for each observation day. This produced an index, which values ranged from 0 to 200 (small leaves on all shoots of all trees).

Temperature data origin from the local weather station in Białowieża village, c. 1 km from the study area (Wesołowski and Tomiałojć, 1997; Rowiński, 2001, unpublished data).

### 2.3. Data analysis

Following earlier work (reviewed in Hunter and Lechowicz, 1992; Hänninen, 1995; Jenkins et al., 2002) we use temperature

sums to analyse impact of warmth accumulation on leaf development. We assume that the buds were always fully chilled, as the mean daily temperatures in the preceding November–December in all seasons remained below 10 °C for 90–100% of time, including 16–41 of days with mean temperatures below zero, and winter conditions (subzero temperatures, often combined with deep snow cover), preventing bud development, prevailed also in January and February. Therefore, the trees in the Białowieża Forest experienced regularly c. 4 months of chilling temperatures, what well exceeds the longest period (>2000 h, i.e. >83 days) found in the literature (Kozłowski et al., 1991).

We assumed that bud burst occurred after a fixed thermal time (year-to-year variation in the timing of bud burst has been satisfactorily accounted for by yearly differences in thermal time alone in several studies (Cannell and Smith, 1986; Hunter and Lechowicz, 1992).

Initially we used two temperature thresholds, and summed temperatures of days with mean value >0 and >5 °C, from January 1 to the median onset of bud burst. However, after realising that these two temperature sums were completely redundant ( $r_s = 0.96$ ,  $p \ll 0.00001$ ,  $n = 450$ ) we used only one temperature threshold (>0°) in the final analysis. As winter conditions prevailed in January and February (see above), we used also two later dates – February 1 and March 1 – as the onset dates of temperature sum accumulations.

To check which periods of temperature sum accumulation best predicted the median date of bud burst onset, similarly to (Hickin and Vitum, 1976; in Hunter and Lechowicz, 1992), we compared the difference between the observed and predicted median dates of bud burst (standard error of prediction in days). To predict the bud burst dates we used medians of yearly temperature sums, accumulated over appropriate periods. The multi-year median date served as the null model. To be useful, bud burst dates calculated with help of the temperature sums, must have a lower standard error that the null model.

All statistical procedures follow the formulae given in STATISTICA for Windows (Anonymous, 1996). To avoid problems with non-normality and data transformation, non-parametric tests are used throughout. All probability values shown in the text are two tailed.

### 3. Results

#### 3.1. Across species patterns

Buds started to burst in the end of March/beginning of April in the early seasons, but in the late springs the onset of bud burst

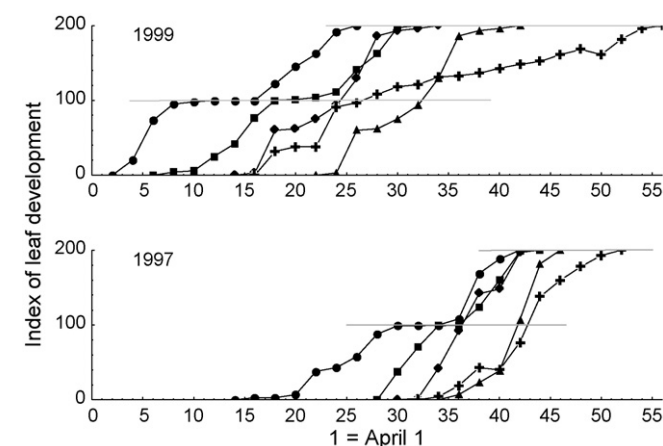


Fig. 2. Pattern of leaf development by different species in the earliest and latest season within the study period. ●: *Coryllus*; ■: *Carpinus*; ◆: *Acer*; +: *Quercus*; ▲: *Tilia*. The index of leaf development shows a cumulative score of leaf growth in all sample trees. It ranges from 0 (no growth) to 200 (small leaves on all shoots of all trees). The method of index calculation is given in Section 2.2.

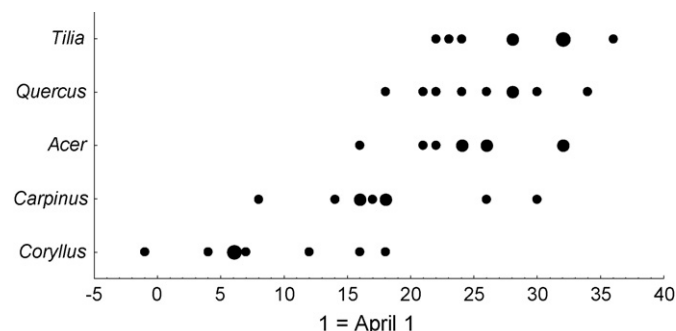


Fig. 3. Distribution of dates of onset of bud burst by different tree species at Białowieża National Park over nine seasons. Varying size of dots denotes the number of seasons (1–3) in which the onset of bud burst was recorded at any given date. The species varied significantly in timing of onset of development, these differences were consistent among seasons (Friedman’s ANOVA:  $\chi^2 = 34.1$ ,  $p < 0.00001$ ; Kendall coefficient of concordance = 0.95).

did not occurred before mid-April. Small leaves developed on all trees by the end of May–first days of June (Fig. 2). The dates of bud burst onset varied significantly across years, they moved over a period of 14 (*Tilia*)–22 days (*Carpinus*)—Fig. 3. Nevertheless, every spring the individual species begun leaf development in the same order (Figs. 2 and 3): from earliest *Coryllus*, through *Carpinus*, *Acer*, *Quercus*, to the latest *Tilia*. In the same order the species reached also stages of full bud burst and of leaf unfolding (Table 2). The differences of bud burst in *Tilia* and *Carpinus* tended to be smaller in the late (13–17 days) than in the early (20–26 days) springs, though the relationship was not significant ( $r_s = -0.42$ ,  $p = 0.26$ ). The late species developed leaves faster than the early ones (Fig. 4). In consequence, despite a 24 day span in the initiation of development, small leaves appeared in all species within 9 days (Table 2).

The species differed significantly in thermal requirements for leaf development. Temperature sums to bud burst were over twice higher in *Tilia* than in *Coryllus* (Table 3). Similarly, temperatures during leaf development were much higher in *Tilia* than in *Coryllus* (Table 4). Though there was a substantial interyear variation in heat accumulated before bud burst (maximum/minimum ratio 1.2–1.8), the temperature sums, were nevertheless more precise predictors of actual bud burst dates than the median dates alone (Table 5). In all tree species

Table 2  
Dates of leaf development by different tree species at Białowieża National Park

Species	Bud burst onset	Full bud burst	Leaf spread
<i>Coryllus</i>	8 (4–22)	16 (7–28)	29 (22–40)
<i>Carpinus</i>	20 (12–30)	25 (18–33)	32 (23–42)
<i>Acer</i>	26 (18–34)	30 (21–36)	32 (25–42)
<i>Quercus</i>	28 (20–38)	31 (23–44)	34 (27–48)
<i>Tilia</i>	32 (24–39)	36 (27–42)	38 (29–45)
Friedman’s	$\chi^2 = 35.5$	$\chi^2 = 34.5$	$\chi^2 = 33.9$
ANOVA <sub>9,4</sub>	$p < 0.00001$	$p < 0.00001$	$p < 0.00001$

Dates are expressed as April days (1 April = 1, 1 May = 31, etc.). Shown median (minimum – maximum) values of yearly medians for the onset and end of bud burst, as well as, for the end of leaf spread.



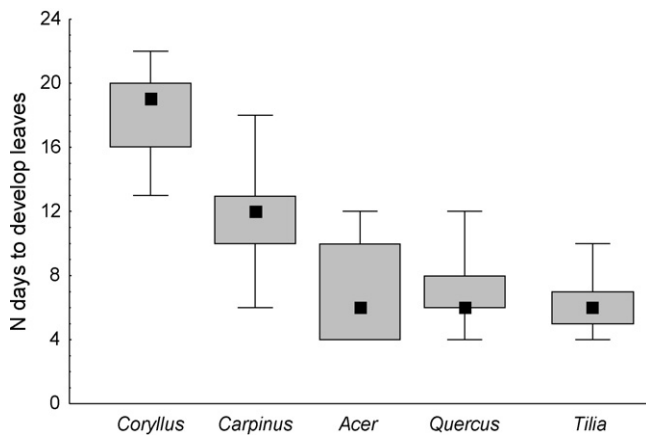


Fig. 4. Variation in the length of leaf development (=number of days from onset of bud burst to appearance of small unfolded leaves on all shoots) in individual trees of different species at Białowieża National Park. Shown are medians (squares), 25–75% values (boxes) and ranges (whiskers). The interspecific differences were consistent across seasons (Friedman's ANOVA:  $\chi^2 = 29.9$ ,  $p < 0.00001$ , Kendall coefficient of concordance = 0.83).

the temperature sums accumulated from March 1 produced the most precise (smallest standard errors) predictions of the real dates. Across years, the March temperature sums did not show relationship with the bud burst dates, if anything they tended to be larger in the late seasons (*Quercus*,  $r_s = 0.50$ ,  $p = 0.17$ ). In all

Table 3

Temperature sums to median bud burst dates in different tree species at Białowieża National Park

Species	Temperature sum accumulated		
	1 January	1 February	1 March
<i>Coryllus</i>	205 (187–273)	191 (146–231)	148 (106–195)
<i>Carpinus</i>	301 (271–390)	282 (238–348)	239 (220–277)
<i>Acer</i>	351 (326–430)	339 (270–387)	291 (264–326)
<i>Quercus</i>	363 (344–454)	351 (297–411)	323 (291–356)
<i>Tilia</i>	423 (371–479)	411 (354–441)	359 (326–407)
Friedman's	$\chi^2 = 35.5$	$\chi^2 = 35.5$	$\chi^2 = 35.5$
ANOVA <sub>9,4</sub>	$p < 0.00001$	$p < 0.00001$	$p < 0.00001$

Shown median (minimum – maximum) values of yearly medians.

Table 4

Average daily temperatures during leaf development of different tree species at Białowieża National Park and relationship between temperatures and the length of leaf growth period

Species	Daily temperature (°C)	$r_s$	$p$
<i>Coryllus</i>	9.3 (8.5–13.3)	–0.51	0.160
<i>Carpinus</i>	13.2 (8.0–17.2)	–0.92	0.0004
<i>Acer</i>	14.5 (9.9–17.2)	–0.77	0.015
<i>Quercus</i>	15.3 (10.5–17.0)	–0.48	0.192
<i>Tilia</i>	15.0 (9.5–16.8)	–0.82	0.006

Shown are mean (minimum – maximum) values of average daily temperatures during the leaf growth period, as well as, Spearman's correlation coefficients and their probabilities, between the average temperatures and the median number of days necessary to develop leaves in individual years/species. Daily temperatures during leaf development differed consistently across species (Friedman's ANOVA:  $\chi^2 = 19.46$ ,  $p < 0.0007$ , Kendall coefficient of concordance = 0.54).

Table 5

Standard errors of prediction in days for temperature sums used to forecast median date of bud burst of tree species

Species	Median	Temperature sum accumulated (date)		
		1 January	1 February	1 March
<i>Coryllus</i>	2.3	1.9	1.4	<b>1.1</b>
<i>Carpinus</i>	1.8	1.1	1.2	<b>0.6</b>
<i>Acer</i>	1.7	1.0	1.2	<b>0.5</b>
<i>Quercus</i>	1.8	1.1	1.2	<b>0.8</b>
<i>Tilia</i>	1.7	0.9	1.0	<b>0.6</b>

The median date serves as a null model. Bold entries show the lowest standard error (most precise prediction) for each species.

Table 6

Repeatability of bud burst onset by individual trees within a species and difference between median onset dates of the earliest and latest individuals

Species	Concordance coefficient	$\chi^2$	$p$	Difference (days)
<i>Coryllus</i>	0.45	36.58	<0.00003	8
<i>Carpinus</i>	0.41	33.0	<0.0002	4
<i>Acer</i>	0.48	38.56	<0.0001	4
<i>Quercus</i>	0.87	70.45	<0.000001	18
<i>Tilia</i>	0.60	48.35	<0.000001	7

Shown are values of Kendall's coefficient of concordance, as well as  $\chi^2$  values and probabilities of Friedman's ANOVA by ranks ( $n = 9$ , 9 d.f.).

species leaves appeared to grow faster in warmer weather, though the relationship was significant only in some of them (Table 4).

### 3.2. Within species patterns

In every species the onset of bud break of individual trees was highly repeatable among seasons (Table 6). Even if difference between the earliest and latest trees was only 4 days, as in *Carpinus* and *Acer*, some trees were nevertheless developing leaves consistently before the others (Table 6). These differences did not depend on tree localisation within the study area, as the spatial distribution of the early and late individuals of different species did not coincide (median onset ranks, Kendall's coefficient of concordance = 0.14,  $r_s = -0.07$ ,  $p = 0.71$ ). In all species but *Quercus*, the difference between the early and late individuals was much smaller than the time necessary to develop leaves (cf. Table 2 with Fig. 4), so they grew leaves to large extent synchronously. This was not true in *Quercus*, where buds in the latest individuals started to break 18 days after the first ones (Table 6), i.e. only after the earliest leafing trees had already developed leaves.

## 4. Discussion

Variation among the observed trees was minimised by design—they all were healthy mature individuals of local origin, growing next to one another in the same patch of forest, affected by the same weather fluctuations. This way numerous sources of variation, such as differences in age (Ununger et al., 1988), provenance (e.g. Myking and Heide, 1995; Kramer, 1995;

Leinonen and Hänninen, 2002), soil fertility (Wielgolaski, 2001; Faliński, 2001), humidity (Friedel et al., 1993; Kramer et al., 2000; Wielgolaski, 2001), elevation or climate (e.g. Kramer, 1995; Spano et al., 1999), known to affect timing of leaf development were removed. Despite the standardisation, there were consistent interspecific phenological differences. The large, 2–3-week, interyear shifts in dates of bud burst by individual species did not affect their order of bud burst onset. Every spring *Coryllus* started the earliest and *Tilia* was the latest species to begin bud burst. Thus, all species moved their onset dates in parallel, what suggests that they all perceived the environmental variation in a similar fashion, but they responded to it in a species-specific way. The same pattern of leaf development – repeatable order of bud burst by different tree species in consecutive springs despite large variation of bud burst dates across years – was also recorded in S Finland (Linkosalo, 2000).

Also within a species, individual trees were developing leaves consistently early or late. This was not due to a microhabitat variation, as distribution of early and late individuals of different species did not coincide. Such high constancy of reactions indicates, that the reaction thresholds of various individuals differed. This could be to some extent due to the genetic differences among trees, especially the large differences between early and late leafing *Quercus* (up to 18 days) would be difficult to explain by variation in environmental factors alone.

Our results confirm the large body of data showing that both dates of bud burst onset and rate of leaf growth of forest trees are under strong temperature control (reviewed in Hunter and Lechowicz, 1992; Hänninen, 1995)—also in the Białowieża Forest leaves appeared earlier and grew faster in warmer springs. The interyear variation of bud burst dates was strongest influenced by weather variation in March and April, the temperature sums accumulated from March 1 were the best predictors of the actual burst dates. The temperature sums necessary to accumulate before bud burst differed – depending on tree species – by 20–80% between the extreme years. Contrary to some results (e.g. Perry and Wang, 1960; Hänninen, 1990; Heide, 1993; Häkkinen et al., 1998), this variation was not related to the photoperiod. The temperature sums probably did not vary to compensate for chilling deficit (Cannell and Smith, 1986). This could be a problem in a mild oceanic climate, but with harsh local winters the Białowieża Forest trees were probably always adequately chilled. Another reason for this variation could stem from a discrepancy between our methods of temperature sums calculations and rules of warmth accumulation used by the trees. They could have fixed temperature thresholds (temperature sums) for bud burst, which appeared variable only by our standards. However, the fact that early and late individuals of the same species regularly accumulated different temperature sums before bud burst, indicates that their temperature requirements probably differed (i.e. each tree had its own required temperature) or that the particular trees “interpreted” the same environmental cues in different ways.

Onset of bud burst by different species in the Białowieża Forest was asynchronous, depending on the year, the median bud burst dates of *Coryllus* and *Tilia* differed by 13–26 days.

Lechowicz (1984) found the same amount of asynchrony in bud burst onset in a mixed deciduous forest in Quebec. He found that the early leafing genera had only narrow-diameter xylem vessels (diffuse porous wood, e.g. *Acer*, *Carpinus*), while the genera with large diameter vessels (ring porous wood, *Quercus*), in which cambial activity had to precede the onset of bud burst were late leafing. However, some trees with diffuse porous wood (e.g. *Tilia*) developed nevertheless leaves late. The Białowieża observations generally fit this pattern, *Carpinus* was earlier than *Acer* and *Quercus* and *Tilia* was the latest of all.

Lechowicz (1984) concluded that the timing of leaf emergence by different trees had no clear adaptive value in contemporary forest environments, that it constituted legacy of selection regimes faced by individual species in their ancient environments. This true, one would expect to find a constant order of bud burst of the same species in different areas. This is not the case, though. Whereas bud burst of *Quercus* preceded that of *Tilia* in the Białowieża Forest, in North Germany both species developed leaves at the same time (Kramer, 1994), in England and in Austria their burst order was reversed (Lechowicz, 1984; Sparks and Carey, 1995). Though these results must be treated with caution due to methodological inconsistencies, they nevertheless suggest that the timing of bud burst may be more flexible, prone to selective pressures, than Lechowicz (1984) thought.

Timing of bud burst in trees has attracted much attention and generated an impressive number of publications (see Lechowicz, 1984; Hänninen, 1995; Wielgolaski, 2001 for reviews). However, the studies were mostly limited to modelling work, to attempts of explaining and predicting timing of bud burst, with some (as a rule climatic) environmental variables. Unfortunately, the published data pertain mostly to the results of modelling exercises, the real in situ observations are only infrequently reported. As a consequence, in spite of numerous publications, it is difficult to get the actual information from individual localities, on timing of bud burst or temperature sums even for the commonest European trees. Therefore it is currently impossible to map distribution of bud burst dates of any species across the continent. We are unable to answer whether, and if so, in which fashion, temperature sums to the bud burst onset differ among the geographical regions. We do not know if the co-occurring species develop leaves in the same order in all areas. Neither can we tell whether synchrony of leaf development by different species changes geographically or not. We are convinced that answers to these questions are necessary to understand timing of tree leafing, its adaptive value, as well as, to verify the models. Therefore we encourage the readers to provide the missing information, to publish not only the highly transformed results of statistical testing or modelling but also the initial observations.

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