

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

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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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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 Tomiałoć et al. (1984), Faliński (1986, 1991) and Tomiałoć and Wesolowski (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, Wesolowski, 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, Tomiałoć 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, Tomiałoć 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 ^a	62 ^a
6 May	200	200	200	200	200	200	144	142	182 ^b	167 ^b

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 $Z = -0.98$, $p = 0.32^b$).

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