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# GROWTH AND DEVELOPMENT OF SPECIES AND HYBRIDS OF THE GENUS *POPULUS* L. IN THE RIGHT-BANK FOREST-STEPPE OF UKRAINE

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## Abstract

The growth and development of vegetative and generative organs of *Populus alba* L., *P. balsamifera* L., *P. bolleana* Lauche, *P.* × *canescens* (Ait.) Smith., *P. deltoides* Bartr. ex Marsh., *P. nigra* L., *P. nigra* cv. Italica (Du Roi) Moench, P. *simonii* Corr., *P. tremula* L., and European-American *P. deltoides* × *P. nigra* hybrids 'I-45/51', 'Blanc du Poitou', 'Gelrica', 'Marilandica', 'Robusta', 'Serotina', 'Tardif de Champagne', and *P.* × *hybrid*a clones 'Weresina' and 'Witschtejna' were studied outdoor for seven years under current climate change. The development of most *Populus* species and hybrids started in the second half of March – beginning of April when the phase of bud swelling was reached in correspondence of a significant temperature sum from 68 to 112 °C, depending on the species/hybrid considered. In most species, flowering began on April 20th and lasted 9 to 16 days, temperature sum of 93–139 °C, depending on the species. The duration of linear shoot growth was shorter in native species of the genus *Populus* (118–130 days) than in introduced species (135–140 days). Fruiting began when the temperature sum reached 217–234 °C in *P. tremula*, while in *P. balsamifera* it required 413 °C. The other species required an intermediate temperature sum (299–329 °C) to reach the same phase, which was accumulated in the first ten-day period of June. Discolouration of leaves depended on the date of first autumn frosts and during the study period was shifted by two to three weeks later. After analyzing the timing of phenological phases of growth and development, species and hybrids were assigned to phenological groups characterized by early, mid or late beginning and end of the vegetation period. The knowledge of thermal requirements for key phenological stages is expected to be useful for modelling and predicting growth, flowering and fruiting of poplars, which is crucial to create efficient and productive bioenergy plantations and to take anti-allergic measures during fruiting in the Right-Bank Forest-Steppe of Ukraine.

**Key words**: development, growth, phenology, poplar, thermal time.

## Introduction

The seasonal development cycle of plants reflects the interaction of their genotype with the environment. Seasonal cycles play an important role in many sectors of the economy, in particular, decorative gardening, landscaping, phytomelioration, and forestry. Studies of growth and development cycle of introduced plants in connection with climate change are particularly relevant. In the annual cycle of plant development, the periods of entry and exit from deep dormancy and the end of vegetation are essential. The characteristics of seasonal development determine the indicators of ecological plant resistance, i.e. winter hardiness and drought resistance, which define the ability of the species to survive and reproduce in various growth conditions (Lapin 1967, Sergeeva 1971, Sabirova et al. 2018). The results of long-term phenological observations demonstrate successful plant adaptation to soil and climatic conditions.

Phenological observation makes it possible to have an approximate idea of the degree of morpho-physiological periodicity compliance in the annual cycle of development of a particular tree species (Lapin 1967, Sergeeva 1971). Even a short-term (2–3 years) phenological observation provides sufficient material for preliminary assessment of the adaptation of trees and shrubs of the same genus but of different geographical origins (Lapin 1967). Information on the phenological rhythms of growth and development of a particular species is essential for planning and managing new tree plantations.

In Ukraine, the rhythms of development of *Populus* were investigated by Redko (1975), Sluchyk (2000), Litvin et al. (2009), and Danylchuk (2013). In Russia, the seasonal growth rhythm of poplars was examined by Demidova and Durkina (2013), and Medveva and Srodnykh (2014). In other areas with a cold temperate climate, phenological studies of species, hybrids and clones of the genus *Populus* were conducted in Scandinavia by Stener and Westin (2017), in Belgium by Broeck et al. (2003), in Estonia by Lutter et al. (2016), in Iran by Lashkarbolouki et al. (2011) and in Canada by Huybregts et al. (2007).

In Donetsk, seasonal rhythms of development of *Populus* species have been studied by Moskalevskyj and Dem'janenko (2014). The time course of flushing of vegetative and generative buds of six poplar clones ('Strilopodibna', 'Kanadska × Balzamichna', 'Slava Ukrayini', 'Guliver', 'Volosystoplidna' and 'Novoberlinska-3') in Kyiv was analyzed by Khoma and Kutsokon (2019). In Ivano-Frankivsk, the influence of technogenic pollution of urban ecosystems on growth, development and morphometric parameters of shoots of *P.* × *berolinensis* Dippel. and *P. simonii* Corr. was studied by Sluchyk (2000). The influence of heavy metals on the growth of *P. nigra* cv. Italica (Du Roi) Moench, *P. deltoides* Bartr. ex Marsh., *P. simonii*, *P. candicans* Ait., *P. bolleana* Lauche and Euro-American hybrids in Kryvyi Rih region was investigated by Danylchuk (2013). The phenology of 10 species and clones of poplar in the town of Ovruch in Zhytomyr region was studied by Redko (1975). The phenology of the development of black and balsam poplars hybrids in the forests of the green zone of Kyiv was analyzed by Litvin et al. (2009). Zalesny et al. (2009) studied hybrids of poplar *Aigeiros* × *Tacamahaca* in the USA (*P. deltoides* × *P. suaveolens* ssp. *maximowiczii*; *P. nigra* × *P. suaveolens* ssp. *maximowiczii*) and Euro-American hybrids.

In Scandinavia, field studies on shoot growth of hybrid aspen (*P. tremula* L. × *P. tremuloides* Michx.) and poplar clones (*P. trichocarpa* Torr. & A. Grey, *P. balsamifera* L., *P. maximowiczii* A. Henry and their hybrids) showed considerably higher growth for hybrid aspen than for poplars (Stener and Westin 2017). The researchers link the data obtained with the genetic features of aspen.

Broeck et al. (2003) found out that the flowering time of *P. nigra* and the male clone of *P. nigra* cv. Italica were not synchronized, but *P. nigra* and *P.* × *canadensis* freely interbred during flowering, which is a potential threat to native plantings of *P. nigra* in Belgium.

In Estonia, Lutter et al. (2016) investigated the phenology of hybrid genotypes of *P. tremula* of northern and southern origin and found out that the genotypes of southern origin were more adapted to climate change as they had a 27-day longer growing season and a tremendous increase in annual shoots.

Lashkarbolouki et al. (2011), in a 22-year-long phenological study, established the phases of the beginning of vegetation, flowering, fruiting and leaf fall of seven *P. deltoides* clones in Iran, and identified the genotypes with different duration of the growing season and productivity.

In the province of Alberta in Canada, the phenology of native and introduced poplars (*P. balsamifera*, *P. davidiana, P. tremuloides*) was assessed to study the occurrence of spontaneous hybridization between them (Huybregts et al. 2007).

The characteristics of seasonal growth of native *P. tremula* L. and introduced *P. alba* L., *P. laurifolia* Ldb., *P. tristis* Fish., *P. deltoides*, *P. nigrosuaveolens* Bogd. in order to obtain poplar in the conditions of the Far North of Russia were studied by Demidova and Durkina (2013). Medvedeva and Srodnykh (2014) reported about the phenological development of *P. alba*, *P. berolinensis*, and *P. alba* × *P. bolleana* in the city of Yekaterinburg (Russian Federation).

At the biological research station of Bila Tserkva National Agrarian University (Bila Tserkva NAU), the formation of a collection of plants of the genus *Populus* began in 2007. The first cuttings of Euro-American hybrid poplars were obtained from the National University of Bioresources and Nature Management and planted by the Associate Professor I. D. Vasylenko (Ishchuk 2017). In the spring of 2013, the collection was supplemented with introduced and hybrid poplars from the Kryvyi Rih Botanical Garden, and in 2017, with hybrid poplars from the Ukrainian Order ‘Badge of Honor’ Research Institute of Forestry and Agroforestry named after G. M. Vysotskyi of the State Agency of Forest Resources of Ukraine and the National Academy of Sciences of Ukraine (Kharkiv).

Currently, the collection includes 25 species and hybrids, most of which are represented by male individuals aged 1 to12.

Due to global climate change, the timing of phenological events is shifting (Parmesan and Yohe 2003). In Europe, especially during the early spring, global warming changes the phenology of trees (Cleland 2007, Shevchenko 2014), which can lead to different reactions both in individual plants and at the population level. Temperature and photoperiod drive the beginning of the shoot development and growth as well as the acclimatization process (Polgar and Primack 2011). As climate-induced changes in phenology become more apparent over time, the need to quantify these changes is becoming increasingly urgent.

The research aims to find out the difference between the rhythms of development and growth, including flowering and fruiting, of species and hybrids of the genus *Populus* and to establish their dependence on the sum of significant temperatures.

The study is based on collection and

analysis of multi-year phenological observations and meteorological data and is intended to continue a long time into the future. This knowledge is expected to be useful for establishing bioenergy plantations and designing a functional plan of anti-allergic measures in the Right-Bank Forest-Steppe of Ukraine. The data obtained will also help to reduce the risk of spontaneous hybridization of native and introduced poplar species and clones.

## Plant Material and Study Sites

We name species and hybrids of the genus *Populus* according to the consensus document on poplar biology (OECD 2000). The International Poplar Commission (IPC) has recognized male specimens of *P. nigra* cv. Italica as the standard for phenological observations and all species and hybrids of the genus are compared with it.

The objects of the research were native juvenile individuals that have not entered the period of flowering and fruiting, pregenerative and generative individuals aged 50 to 80 of the species *P. alba*, *P. nigra*, and *P. tremula*, grown in the urban tree plantations of Bila Tserkva. Among the introduced species, the objects of the research were those introduced since centuries, such as *P. balsamifera*, *P. × canescens*, *P. bolleana, P. deltoides, P. simonii,* and *P. nigra* cv. Italica, aged 60 to 120. Their adult fruiting individuals are widely represented in the plantings of the State Arboretum 'Oleksandriya' of the National Academy of Sciences of Ukraine and Bila Tserkva area. Besides, species and hybrids that were more recently introduced (*P. suaveolens* Fisch., *P. trichocarpa* Torr. et Gray, *P. × euramericana* cv. I-45/51, *P. × euramericana* cv. Blanc du Poitou, *P. × euramericana* cv. Gelrica, P. × *euramericana* cv. Marilandica, *P. × euramericana* cv. Robusta, P. × *euramericana* cv. Serotina, *P. × euramericana* cv. Tardif de Champagne, and *P. × hybrida* clones 'Weresina' and 'Witschtejna') and were mainly represented by young plants up to 12 years old at the biological research station of Bila Tserkva NAU, were also the objects of the research.

Various genetic types, such as greyzem forest, chernozem, sod-meadow, chernozem and meadow, silt-gley and swampy soils, represent the soil cover of the territory. Grayzem forest soils prevail and are characterized by a low degree of saturation, as well as CA+ and MD+. As a result, the process of humification and nitrification is slow. The amount of organic soil (humus) in the surface layer with a thickness of 10–20 cm is 2.7 %. In the horizon of 50–60 cm, it is reduced to 1 %. The boiling line of carbonates is located at a depth of 120–150 cm. In terms of mechanical components, these are medium-loamy soils.

## Methodology

We carried out phenological observations during 2012–2018 according to the methodology approved by the Council of Botanical Gardens of the USSR (Lapin 1975) and some modifications according to Weih (2009) and Ghelardini et al. (2014).

The average dates of all phenological phases studied for 7 years (2012–2018) and calculated as the arithmetic mean of the numerical values are represented in the research.

The phase of generative buds swelling was assumed for the beginning of vegetation since generative buds are the first to start vegetation in species of the genus *Populus*. The date of generative buds swelling was recorded after their size was increased by 3–5 mm. The scales covering the buds begin to disperse, and green stripes become visible between them. Therefore, we considered this phase to be the beginning of vegetation. We evidenced the opening phase of the vegetative buds when the integumentary scales parted, and the green tips of the leaves looked noticeably from the top of the bud. In most species, it occurred after or simultaneously with flowering.

We documented the phase of flowering during the period of pollination of male catkins and full opening of female catkins. The fruiting date was considered to be the beginning of splitting of the capsules and appearance of fluff. The end of fruiting was marked by complete fluff release and beginning of abscission of catkins. The features of the seed maturation were yellowing, splitting of the capsules and appearance of fluff.

We evidenced the phase of the linear growth of shoots at the beginning of May. The dynamics of the seasonal growth of shoots was determined by the method of Molchanov and Smirnov (1967). The length of the shoots of a sample of mature trees and 1–8-year-old seedlings was estimated with a measuring ruler every ten days from May 1st till September 1st. Every time ten shoots in the lower, middle and upper zones of the crown of a sample plant were measured. The lignification of shoots was documented by the presence of a protective cork tissue under the bark, which, unlike the epidermis, was darker and had the same density along the entire length.

We evidenced the phase of changing leaf colour from green to yellow after the first autumn frosts in September-October. The phase of leaf fall was determined in October-November. The beginning of any phenological phase was defined as the date when its diagnostic signs were visible in at least 1/3 of a plant's organs.

Having analyzed the periods of vegetation during the years 2012–2018, we defined three phenological groups of species and clones of the genus *Populus*, namely with early (March 1–20), mid (March 21–April 10) and late (April 11–May 1) beginning of vegetation. Similarly, three groups of species with early (August 28–September 30), mid (October 1–25) and late (October 26–November 15) end of vegetation were identified. Based on the timing of the beginning and end of vegetation periods, five phenological groups were distinguished in the studied taxa: (EM) species with early beginning and mid-end, (EL) early beginning and late end, (MM) mid start and mid-end, (ML) mid beginning and late end, and (LE) late beginning and early end.

The sum of significant temperatures (starting with +5 °C) was calculated based on average daily temperatures (data from Bila Tserkva meteorological station) to detect the temperature threshold for the phenological phase of development and growth of the studied species. Average sums of temperatures for each phenological phase during 2012–2018 were identified using the software Statistica and are presented in the research findings.

## Results

### Climate conditions in the study period

The climate of the Right-Bank Forest-Steppe of Ukraine is moderately continental and relatively mild, with an average annual temperature of 8.4 °C and fluctuations in some years from 5.8 °C to 8.5 °C (Shevchenko 2014). However, over the years of research (2012–2018), the average annual temperature fluctuated between 8.8–9.9 °C, which is higher than the long-term average by 0.4–1.5 °C (Table 1, Fig. 1). During the research period, the winter seasons of 2012, 2013 and 2018 with the minimum air temperature of –25.4 °C were the coldest ones, whereas the overall maximum temperature was +32.9 °C. During the study period, the registered number of frost days was in the range of 110 and 163 (on the average 137). There were 63 days on average when the temperature remained below zero throughout the day. Soil temperature always equal to or below 0 °C was recorded from December to March to a depth of 0.4 m. Late spring frosts occurred in 2013 (May 2–4, to –2.5 °C) and 2017 (May 10–11 on the soil surface to –7.9 °C). The average daily air temperature was always above +5 °C from April 6–8 and dropped below 5 °C from October 26–28. The average length of the growing season was 210 days.

**Table 1. Indicators of air temperature, precipitation and relative humidity recorded.**

| Year | Month | | | | | | | | | | | | Year average |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | |
| Average monthly air temperature, ºC | | | | | | | | | | | | | |
| 2012 | -4.3 | -9.9 | 2.2 | 11.8 | 18.2 | 20.3 | 22.4 | 19.7 | 16.4 | 10.2 | 4.5 | -5.2 | 8.9 |
| 2013 | -4.0 | 0.3 | 0.2 | 9.9 | 18.5 | 20.7 | 19.6 | 18.9 | 12.4 | 9.5 | 6.5 | -0.9 | 9.3 |
| 2014 | 1.8 | -2.0 | -3.9 | 8.5 | 16.2 | 17.2 | 21.1 | 20.5 | 14.2 | 6.7 | 1.8 | -2.0 | 8.8 |
| 2015 | -1.3 | -1.1 | 4.1 | 9.4 | 16.3 | 19.6 | 20.9 | 20.6 | 17.6 | 6.8 | 4.6 | 1.7 | 9.9 |
| 2016 | 2.5 | -1.4 | 2.8 | 12.4 | 14.7 | 19.8 | 21.6 | 20.4 | 15.5 | 6.4 | 3.7 | -0.3 | 9.8 |
| 2017 | -1.5 | -0.5 | 3.1 | 10.3 | 14.9 | 19.7 | 20.3 | 21.7 | 16.3 | 8.4 | 3.3 | -1.1 | 9.6 |
| 2018 | -2.3 | -4.2 | -2.1 | 13.3 | 18.4 | 20.1 | 20.5 | 21.5 | 16.2 | 9.9 | -2.1 | -3.1 | 8.8 |
| 2012–2018 average | -1.3 | -2.6 | 0.9 | 10.8 | 16.7 | 19.6 | 20.9 | 20.5 | 15.5 | 8.3 | 3.2 | -1.6 | 9.3 |
| Long term average | -4.6 | -2.1 | 1.6 | 8.4 | 14.8 | 17.8 | 19.0 | 18.4 | 14.9 | 7.8 | 2.4 | -2.0 | 8.4 |
| Average monthly precipitation, mm | | | | | | | | | | | | | |
| 2012 | 32.0 | 27.0 | 23.0 | 38.0 | 45.0 | 25.0 | 69.0 | 29.0 | 91.0 | 37.0 | 29.0 | 138.0 | 583.0 |
| 2013 | 40.0 | 39.5 | 92.3 | 29.6 | 87.1 | 20.7 | 29.6 | 68.0 | 155.5 | 5.7 | 83.6 | 64.2 | 550.7 |
| 2014 | 40.3 | 33.2 | 49.1 | 50.1 | 118.1 | 76.5 | 93.2 | 48.0 | 37.6 | 14.5 | 63.5 | 17.7 | 678.2 |
| 2015 | 16.6 | 34.1 | 81.4 | 15.3 | 37.6 | 32.8 | 82.4 | 2.4 | 36.5 | 31.3 | 75.0 | 25.7 | 662.6 |
| 2016 | 21.5 | 25.1 | 48.1 | 65.8 | 107.5 | 50.1 | 29.9 | 23.0 | 3.1 | 50.6 | 72.4 | 35.6 | 532.7 |
| 2017 | 22.6 | 18.1 | 63.1 | 22.7 | 42.9 | 18.8 | 83.0 | 16.0 | 33.2 | 79.8 | 71.3 | 28.4 | 499.9 |
| 2018 | 32.6 | 34.6 | 74.0 | 8.1 | 22.8 | 58.7 | 128.4 | 23.9 | 47.9 | 22.0 | 43.2 | 54.0 | 550.2 |
| 2012–2018 average | 29.4 | 30.2 | 61.6 | 32.8 | 65.6 | 40.4 | 73.5 | 30.0 | 57.8 | 34.4 | 62.4 | 51.9 | 579.6 |
| Long term average | 35.0 | 33.0 | 30.0 | 47.0 | 46.0 | 73.0 | 85.0 | 60.0 | 35.0 | 33.0 | 41.0 | 44.0 | 562.0 |
| Average monthly humidity, % | | | | | | | | | | | | | |
| 2012 | 95.0 | 75.0 | 73.0 | 73.0 | 60.0 | 68.0 | 67.0 | 72.0 | 67.0 | 82.0 | 76.0 | 77.0 | 75.0 |
| 2013 | 86.0 | 77.0 | 71.0 | 66.0 | 62.0 | 72.0 | 72.0 | 70.0 | 84.0 | 79.0 | 80.0 | 83.0 | 72.0 |
| 2014 | 82.0 | 77.0 | 74.0 | 84.0 | 72.0 | 72.0 | 71.0 | 66.0 | 67.0 | 69.0 | 90.0 | 81.0 | 65.0 |

| Year | Month | | | | | | | | | | | | Year average |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | |
| 2015 | 81.0 | 78.0 | 71.0 | 58.0 | 60.0 | 60.0 | 65.0 | 59.0 | 68.0 | 69.0 | 81.0 | 80.0 | 73.5 |
| 2016 | 80.0 | 75.0 | 72.0 | 62.0 | 75.0 | 72.0 | 66.0 | 66.0 | 63.0 | 78.0 | 83.0 | 79.0 | 72.5 |
| 2017 | 82.0 | 76.0 | 71.0 | 56.0 | 59.0 | 61.0 | 63.0 | 64.0 | 66.0 | 82.0 | 85.0 | 80.0 | 70.4 |
| 2018 | 81.0 | 87.0 | 86.0 | 58.0 | 56.0 | 64.0 | 77.0 | 66.0 | 71.0 | 78.0 | 82.0 | 87.0 | 74.4 |
| 2012–2018 average | 83.4 | 77.6 | 74.0 | 65.3 | 63.4 | 67.0 | 68.7 | 66.1 | 69.4 | 76.7 | 82.4 | 81.0 | 71.8 |
| Long term average | 86.0 | 85.0 | 82.0 | 68.0 | 64.0 | 66.0 | 67.0 | 68.0 | 73.0 | 80.0 | 87.0 | 88.0 | 76.0 |

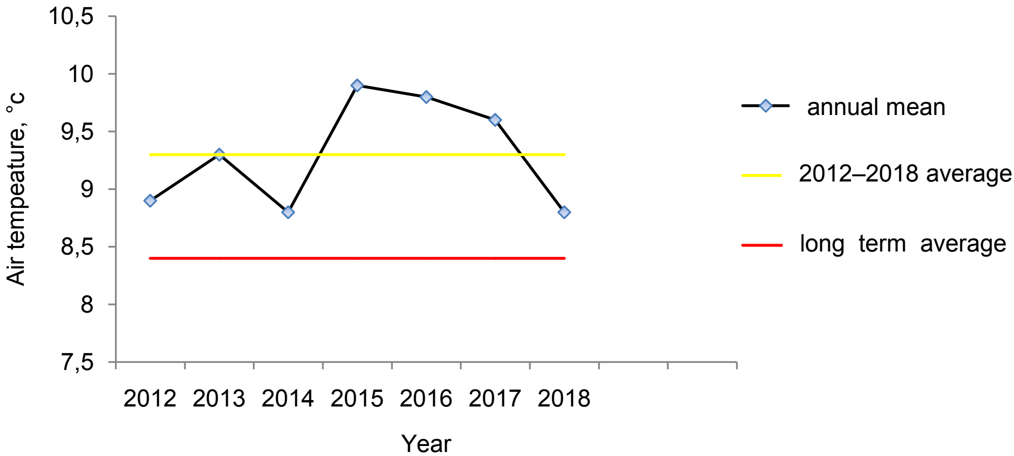


**Fig. 1. Fluctuation of average annual temperature in the study years (2012–2018) and its relation to the average one in Bila Tserkva.**

The average annual precipitation in the study region is 580 mm, about 80 % of which falls as rain. Precipitation that was lower than average annual amount insufficient precipitation was observed in 2016 and 2017, with annual precipitation being 532.7 mm and 499.9 mm accordingly. We evidenced the best highest amount of precipitation supply in 2014 (678 mm) and 2015 (662 mm). However, even in years with higher amount of precipitation, the distribution of precipitation by month during the year was uneven. We also registered the driest summer periods in 2015–2017 with the minimum amount of precipitation in May-September (191.7 mm, 213.6 mm and 193.9 mm). The snow cover lasted for an average of 60 days, with a maximum thickness of 20 cm, and was not stable. Winters of 2017–2018 were characterized by a thin snow cover and a decrease in frosts days (Ishchuk and Ishchuk 2018).

## Growth and development of *Populus* species and hybrids

During 2012–2018, we followed the seasonal development progress of species and hybrids. We defined the following phases of development: swelling and budding of vegetative and generative buds, flowering, linear shoot growth, fruiting, woodiness of shoots, leaf colour change and leaf abscission. The timing of phenological phases of development and growth of vegetative organs of trees is shown in Figure 2.

According to the methodology of phenological observations (Lapin 1975), the starting point of woody plant vegetation is considered to be the phase of swelling of vegetative buds.

In *P. tremula* and *P.* × *canescens*, the appearance of inflorescences and the discharge of the integumentary scales occurred much earlier than the vegetative buds' swelling and bud bursting. In most species of the genus *Populus*, the beginning of the swelling phase of vegetative buds occurred from March 12 to March 25 on average, depending on species and weather conditions. In native species, the vegetation started first in *P. tremula* and *P.* × *canescens* (on average on March 3rd), while *P. nigra* was the last species to start flushing on March 15th. Among the introduced *Populus,* the earliest bud swelling was in *P. deltoides* (on March 25th), while the latest was in *P.* × *hybrida* 'Witschtejna' (on April 5th). In most species of the genus, *Populus* leaf budding was recorded from April 12 to April 28. The first leaves appeared in *P. balsamifera* and *P. alba* (April 17–20 on average). On April 22–26, leafing occurred in *P. nigra* cv. Italica, and then in the other species until the end of April.

After emergence from the bud, the leaf blade of poplars grows by dividing and stretching of cells in the basipetal direction. However, these processes take place with different intensity depending on the influence of external factors, species, leaf age, and tissue considered. Crit-

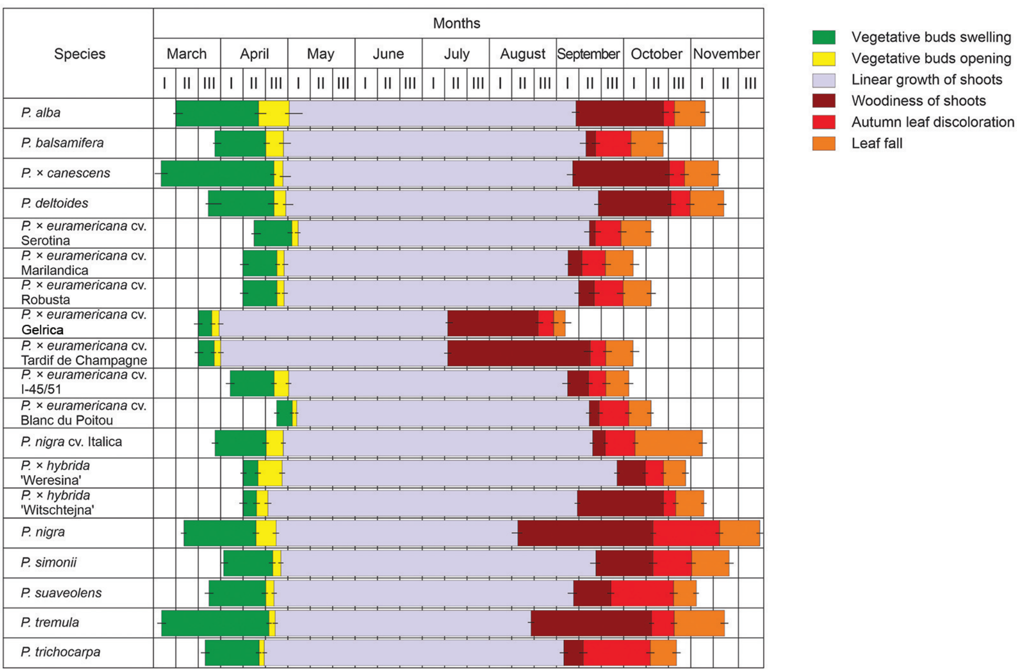


**Fig. 2. Seasonal development of vegetative organs.**

ical physiological processes occur most actively during leaf growth, which is due to the predominance of cell division over their extension. According to our observations, leaf growth is very intensive, especially during 10–15 days in late April-early May. The end of leaf growth occurred on average on May 10–15, in 20–25 days after leaf flushing depending on the species and weather conditions.

Most introduced species and hybrids enter this phase before mid-May. When the leaves are entirely separated, the stipules fall off. With the cessation of growth, the period of leaf ageing begins. In species with early vegetation period, it occurred on average on May 12–15, while in the rest of the species on May 20–25.

Predicting the linear growth phase is very important for identifying species that are promising for creating short-rotation poplar plantations for bioenergy. According to the results obtained, it was concluded that in the study area the linear growth of shoots in species of the genus *Populus* with early vegetation period begins on average on April 22–26, while in hybrids with late vegetation period, linear shoot growth starts on May 1–5.

The study of annual growth in seedlings of species and hybrids of the genus *Populus* showed that intensive growth of shoots occurred in May-June. In the second half of July and in August, the growth energy of all species and hybrids decreases, and at the end of August, it stops.

Euro-American hybrid 'Gelrica' finished its growth in 100 days, which was faster if compared to a maximum of 140 days in the *P.* × *hybrida* 'Weresina'. In most indigenous species of the genus *Populus*, the growth of shoots lasted for 118–130 days, while it was longer in introduced species (135–140 days) (Fig. 1). In native species, shoot growth rate peaks at the end of May-June, while in introduced species, and especially Euro-American hybrids, bud growth peaks later in June-July, and slows down in August.

Linear shoot growth was completed in July-September, however not simultaneously in all species and hybrids. Partial lignification of the shoots in the native species was observed at the end of June-July. Complete lignification of the shoots occurred in September and some species before the beginning of November.

As seen in Table 2, *P. trichocarpa* and clones of Euro-American hybrids 'Serotina', 'Marilandica', 'Tardif de Champagne', 'Robusta', 'Gelrica', 'Blanc du Poitou', *P.* × *hybrida* 'Weresina' and *P.* × hybrida 'Witschtejna' were characterized by the most massive increase at the young age. For other species, the average growth which ranges from 50 to 80 cm per year.

Variations in air temperatures determine the changes in rhythms of the plant life cycle, i.e. bud swelling and burst, beginning of flowering, and fruiting. The calendar dates of certain phenological phases are closely related to temperature conditions, which are the environmental cues for adjustment of biological rhythms of development and which can shift their timing by several days. However, it is possible to trace some trends in the flowering time of poplar species (Ishchuk 2019).

Based on the analysis of average daily temperatures and the timing of phenological phases in species and clones during 2012–2018, the average sum of significant temperatures above a threshold for the beginning of each phase of generative development was identified. Thus, depending on the species, the swelling of generative buds occurred when a temperature sum ranging from 68 to 112 °C was accumulate, bud opening occurred when

**Table 2. Growth dynamics of the aboveground part of juvenile (1–3 years old) plants (Biological Research Station of Bila Tserkva, NAU).**

| Name of the species and hybrids | $H_{2013}$, cm | $H_{2014}$, cm | $H_{2015}$, cm | $\Delta H_{2014}$, cm | $\Delta H_{2015}$, cm | Height, cm | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | *M* | *m* | σ | *V* |
| *P. alba* | 23.8 | 58.2 | 132.1 | 34.4 | 73.9 | 71.3 | 7.1 | 5.8 | 8.7 |
| *P. balsamifera* | 28.0 | 63.4 | 131.9 | 35.2 | 68.5 | 74.4 | 7.4 | 6.0 | 4.2 |
| *P. × canescens* | 26.3 | 62.9 | 135.4 | 36.6 | 72.5 | 74.8 | 7.4 | 6.8 | 7.3 |
| *P. deltoides* | 25.6 | 58.3 | 115.6 | 32.7 | 57.3 | 66.5 | 6.7 | 5.4 | 6.6 |
| P. × *euramericana* cv. Serotina | 28.5 | 92.0 | 189.9 | 63.5 | 97.9 | 103.5 | 10.4 | 11,2 | 5.4 |
| P. × *euramericana* cv. Marilandica | 32.5 | 91.8 | 195.1 | 59.3 | 103.3 | 106.5 | 10.7 | 8.6 | 7.1 |
| *P. × euramericana* cv. Robusta | 33.6 | 90.0 | 200.3 | 56.4 | 110.3 | 108.0 | 10.8 | 8.7 | 9.3 |
| *P. × euramericana* cv. Gelrica | 32.9 | 87.5 | 190.3 | 54.6 | 102.8 | 103.6 | 10.3 | 8.4 | 4.7 |
| *P. × euramericana* cv. Tardif de Champagne | 30.8 | 84.5 | 188.4 | 53.7 | 103.9 | 101.2 | 10.1 | 8.2 | 9.1 |
| *P. × euramericana* cv. I-45/51 | 31.9 | 95.4 | 199.6 | 63.5 | 104.2 | 109.0 | 10.9 | 8.8 | 8.3 |
| *P. × euramericana* cv. Blanc du Poitou | 28.5 | 88.4 | 196.2 | 59.9 | 103.8 | 104.4 | 10.4 | 8.4 | 6.2 |
| *P. × hybrida* 'Weresina' | 36.7 | 102.8 | 198.3 | 66.1 | 95.5 | 112.6 | 11.3 | 9.1 | 11.4 |
| *P. × hybrida* 'Witschtejna' | 37.7 | 104.3 | 186.4 | 66.6 | 82.1 | 109.5 | 10.0 | 8.3 | 10.7 |
| *P. nigra* cv. Italica | 32.3 | 75.7 | 139.5 | 43.4 | 63.8 | 82.5 | 8.3 | 6.7 | 7.6 |
| *P. nigra* | 25.7 | 54.3 | 125.9 | 28.6 | 71.6 | 68.6 | 6.9 | 5.5 | 4.8 |
| *P. simonii* | 26.7 | 57.2 | 122.1 | 30.5 | 64.9 | 68.7 | 6.9 | 5,8 | 6.2 |
| *P. suaveolens* | 37.1 | 81.5 | 173.0 | 44.4 | 91.5 | 97.2 | 9.7 | 7.9 | 4.7 |
| *P. tremula* | 22.4 | 52.4 | 108.3 | 30.0 | 55.9 | 61.0 | 6.1 | 4.9 | 5.9 |
| *P. trichocarpa* | 38.9 | 109.5 | 194.2 | 70.6 | 84.7 | 114.2 | 11.4 | 9.2 | 7.7 |

Note: *M* is the arithmetic mean value, *m* is the error of the average value, σ is the mean-square deviation, *V* is the coefficient of variation.

a temperature sum from 84 to 128 °C was reached, while flowering began when a temperature sum of 93 to 140 °C was accumulated. The average sums significant temperatures for fruit set and fruit ripening ranged from 128 to 151 °C and from 299 to 394 °C respectively, while for fruit fall the sum needed was in the range 342–413 °C (Fig. 3). The only exception was *P. tremula*, which requires the lowest sum of threshold effective temperatures for bud swelling (22 °C), opening of generative buds (45 °C), flowering (54 °C), fruit ripening (226 °C) and fruit fall (245 °C).

The knowledge of thermal requirements for flowering and fruiting may enable the development of predictive models for forecasting the periods of poplar pollen and fluff spread, which is especially important for reducing the risk of allergic reactions in the human population. In this study, *P. tremula* was the first species to begin flowering in a few days between late March and the first ten days of April. *P. × canescens, P. alba,* and *P. nigra* followed in the last ten days of April. At the beginning of the last ten days of April,

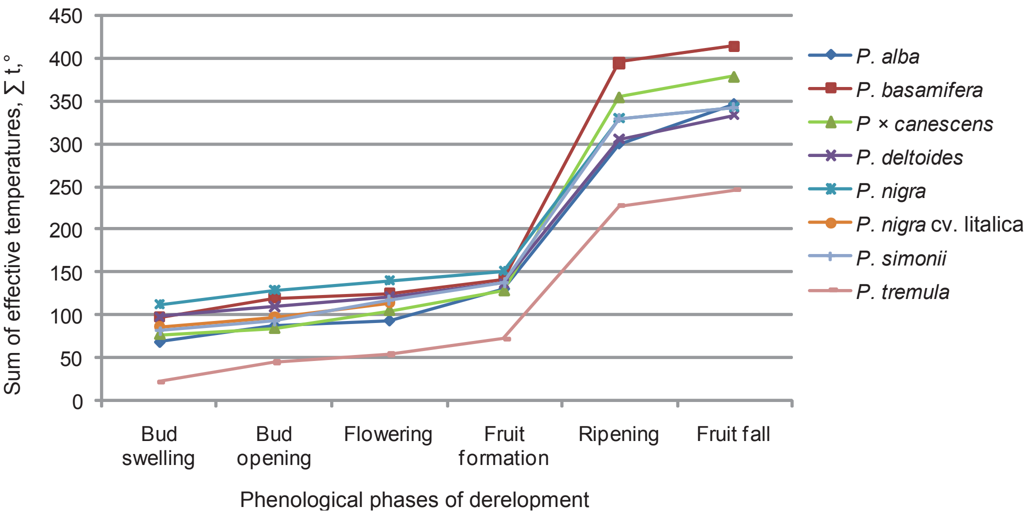


**Fig. 3. Average indicators necessary for the beginning of phases of generative organs development.**

*P. simonii, P. deltoides,* and *P. nigra* cv. Italica began to bloom almost simultaneously, while *P. balsamifera* started to bloom from April 25th. However, the leafing of the shoots began first in *P. balsamifera* (Fig. 4).

According to the studies of Starova (1980) and Barna (2002), the period from pollination to fertilization in plants of the genus *Populus* is not visually noticeable and lasts for 1 or 2 days. In the present study, flowering lasted on average from 6.9 days in *P. simonii* to 10 days in *P. tremula* (Ishchuk 2019). Juvenile plants only represent hybrid poplars in our collection, so we have not studied the biology of flowering and fruiting in those hybrids.

The issues of introgressive hybridization between introduced and native poplars, raised by some researchers from Belgium (Broeck et al. 2003) and Canada (Huybregts et al. 2007), seem not to be much relevant for Ukraine at present, because the native species, *P. alba,* and *P.* × *canescens* complete the flowering before introduced species start flowering, while in the case of *P. tremula* there is only a short period overlap.

In the genus *Populus*, the beginning of fruiting is considered to coincide with the beginning of capsules splitting and fluff's appearance. The end of fruiting is defined as the moment of complete fluff release and the beginning of abscission of fruit catkins. The signs of seed maturation are yellowing, splitting of the capsules and appearance of fluff. The timing of boxes' dehiscence is also extended, but much less than the timing of flowering. The fruit matures at the end of May, almost simultaneously in *P. nigra, P. alba, P.* × *canescens.* On June 15–20, they mature in *P. simonii* and *P. balsamifera* and are the latest.

In May, during 2012–2016 and 2018, the ten days average daily temperature was 2–4 °C higher than the long-term average of the month, so the timing of fruit maturation and fruiting lasted less. Among the species, the lowest sum of significant temperatures was required by *P. tremula* (226 °*C*), the highest sum was required by *P. balsamifera* (413 °*C*). To start fruit-

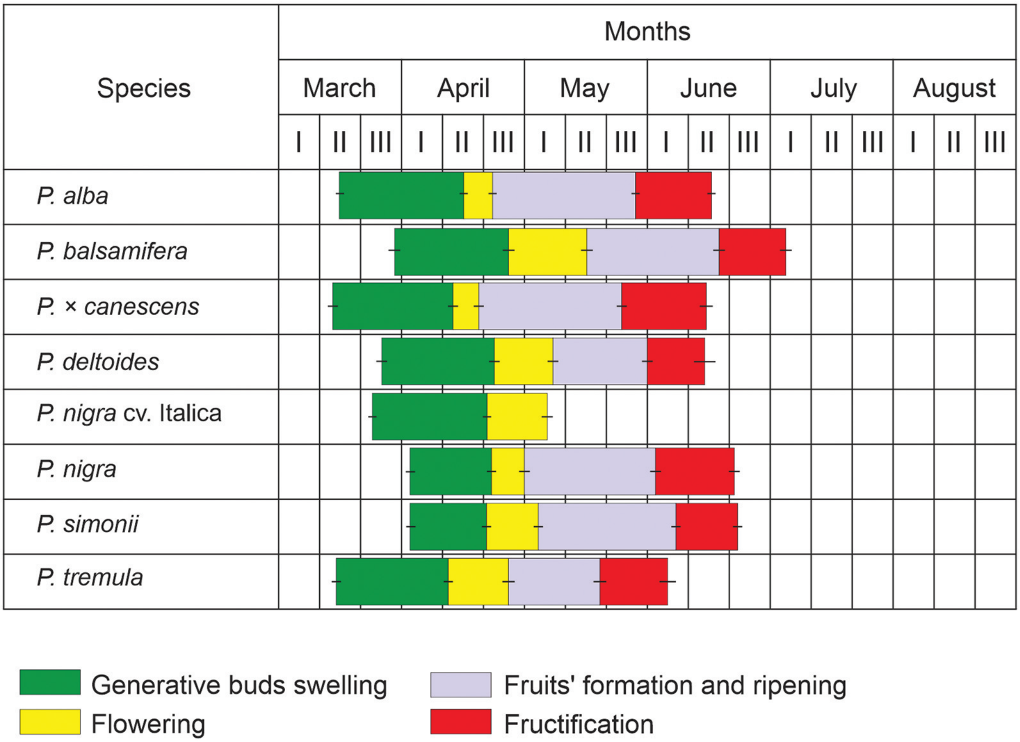


**Fig. 4. Seasonal development of reproductive organs of introduced species and hybrids.**

ing *P. alba* required a temperature of 299 °C, for *P. deltoides* – 305 °C, for *P. nigra, P. simonii* – 329 °C, and 354 °C for *P. × canescens.* Fruiting occurred between late May and the first ten days of June. It should be noted that in the study of Sluchyk (2000) and Danylchuk (2013), these indicators were higher by 30–50 °C in polluted urban systems.

According to our observations, the leaves change colour with the first frosts. In the past few years, there has been almost no frost in the research area of Bila Tserkva in September. Therefore, the change in leaves colour occurred in October and by the end of the month they fell off.

Based on the analysis of the timing of the start and end dates of the growing season of poplar species and hybrids in the period of 2012–2018, five phenological groups have been defined (Table 3, last column).

Euro-American hybrids 'Gelrica', 'Marilandica', 'Tardif de Champagne', and 'I-45/51' completed vegetation by the end of September. At the beginning of October, the vegetation period for hybrids 'Blanc du Poitou', 'Robusta' was finished. In mid-October, leaf fall was observed in *P. balsamifera, P. trichocarpa*, *P. × hybrida* 'Witschtejna', and *P. × hybrida* 'Weresina'. Other species of *P. suaveolens, P. trichocarpa, P. nigra* cv. Italica*,* completed vegetation by the end of October. Only at the beginning of November, defoliation was observed in *P. alba, P. tremula, P. × canescens,* P*. deltoides, P. simonii,* and *P. nigra*.

**Table 3. Average start and end dates of vegetation of species and hybrids.**

| Species and hybrids | Vegetation | | | Phenological group |
|---|---|---|---|---|
| | Start, date | End, date | Duration, days | |
| *P. tremula* | 3.03 | 20.10 | 231 | EM |
| *P. × canescens* | 3.03 | 25.10 | 236 | EM |
| *P. alba* | 10.03 | 20.10 | 224 | EM |
| *P. nigra* | 15.03 | 10.11 | 240 | EL |
| *P. balsamifera* | 28.03 | 1.10 | 209 | MM |
| *P. deltoides* | 25.03 | 25.10 | 214 | MM |
| *P. × hybrida* 'Weresina' | 10.04 | 15.10 | 181 | MM |
| *P. × hybrida* 'Witschtejna' | 10.04 | 12.10 | 185 | MM |
| *P. trichocarpa* | 28.03 | 15.10 | 202 | MM |
| *P. nigra* cv. Italica | 23.03 | 01.11 | 223 | ML |
| *P. simonii* | 1.04 | 28.10 | 20 | ML |
| *P. suaveolens* | 26.03 | 27.10 | 216 | ML |
| *P. × euramericana* cv. Serotina | 1.05 | 25.09 | 148 | LE |
| *P. × euramericana* cv. Marilandica | 15.04 | 20.09 | 158 | LE |
| *P. × euramericana* cv. Robusta | 16.04 | 28.09 | 165 | LE |
| *P. ×euramericana* cv. Gelrica | 25.04 | 28.08 | 125 | LE |
| *P. × euramericana* cv. Tardif de Champagne | 26.04 | 20.09 | 147 | LE |
| *P. × euramericana* cv. I-45/51 | 22.04 | 20.09 | 151 | LE |
| *P. × euramericana* cv. Blanc du Poitou | 1.05 | 30.09 | 153 | LE |

Note: EM – with the early start and mid-end, EL – an early start and late end, MM – mid start and mid-end, ML – mid start and late end, LE – late start and early end.

## Discussion

The research results on the timing of the phenological phases of growth and development of species and hybrids of the genus *Populus* in Bila Tserkva area are consistent with the data obtained by Litvin et al. (2009), who studied the phenology of poplars in Kyiv. When adapting to climatic and environmental conditions, the phenological phases of hybrids can be reduced or prolonged.

In general, the duration of the growing season of *P. balsamifera, P. simonii, P. suaveolens, P. trichocarpa, P. nigra* and *P. nigra* cv. Italica in our research was similar to the data of Litvin et al. (2009). Due to climate change resulting in the warming that was observed during 2012–2018 (Table 1, Fig. 1), the duration of the growing season in poplar increased by 7–10 days if compared to Redko (1975) studies, which were conducted in the mid-1960s in Kyiv area.

Khoma and Kutsokon (2019) studied the phase of budding indoors on cut branches. According to them, the delay of this phase is explained by insufficient light in the room. The photoperiod's effect on the duration of the growing season is confirmed in the studies of Gill et al. (2015) and Way and Montgomery (2014).

According to Medvedev and Srodnykh (2014), the most stable phenological development in Yekaterinburg was shown by *P. alba*, which vegetation period lasted only for 148 days. Hybrid species *P. berolinensis* are characterized by a more extended vegetation period, namely 153 days. Species of the genus *Populus* are winter-hardy, but leaves and young non-woody shoots can often be damaged by spring and autumn frosts (Ishchuk and Ishchuk 2018). In the course of the research, we noted an increase in air temperature. In September of 2012, 2015–2018, the air temperature was even higher than the annual mean temperature, and autumn frosts, that usually occur in this season (Chirkov 1986), were absent. During these years, the phase of leaf discolouration was shifted by 2–3 weeks later.

A more accurate indicator for analyzing phenological phases is the sum of significant temperatures accumulated by each species of poplar at the beginning of each phase. The results of the calculations of the sum of significant temperatures in the research conducted in Bila Tserkva area almost coincided with similar experiments carried out by Redko (1976) in the city of Kyiv for the phases of swelling and opening of generative buds, flowering and fruiting in *P. alba, P. nigra,* and *P. nigra* cv. Italica.

The data obtained on the growth of shoots of Euro-American hybrids 'Serotina', 'Marilandica', 'Robusta', 'Tardif de Champagne', 'I-45/51', 'Blanc du Poitou' coincide with the data recorded by Litvin et al. (2009), who studied the development of clones of these plants in the city of Kyiv. At the same time, Zalesny et al. (2009), who explored the behaviour of poplar hybrids *Aigeiros* × *Tacamahaca* from the northern regions of the United States, transplanted to more southern latitudes, recorded a delay in bud growth in the spring and an early stop in the fall, which led to a decrease in productivity. In our research, shoot growth on 1- to 3-year-old seedlings was most intense in May-June. In Euro-American hybrids, the increase was much higher than in pure species. Among the species, the introduced *P. suaveolens* and *P. trichocarpa* were identified as the most promising for cultivating plantations. Long-term observations of *P. trichocarpa* have confirmed that this species is promising for its stability, growth energy and productivity in the conditions of the Far North of Russia (Demidova and Durkina 2013)

The duration of the growing season depends on biological characteristics of the plant, climate zone and weather conditions of the growing year. This vegetation period for poplars is much more extended than that for other species of woody plants in temperate climates. The daylight factor also plays an essential role here. In this study, the vegetation end in certain species and hybrids of the genus *Populus* was observed at the end of September. However, the majority of species completed the vegetation in the second half of October or in November.

Based on the meta-analysis Gill et al. (2015) concluded that the autumn leaf ageing phase had been significantly delayed at 25–49° north latitude. Moreover, the city of Bila Tserkva, where we conducted the study, is located at 49°47′44″ north latitude. At this latitude, plants are more sensitive to temperature. In more northern latitudes, photoperiod affected the ageing of leaves. The absence of constant links between air temperature and leaf ageing time indicates that various factors can affect autumn ageing. The date of the first autumn frosts is variable in temperate and boreal ecosystems and does not always correspond to a linear cooling trend (Tuskan et al. 2006, Way and Montgomery 2014). Our observations also confirm this fact.

## Conclusions

We found out that despite significant differences in the temperature regime in individual years, each species and hybrid of the genus *Populus* is characterized each year by approximately the same amount of sufficient (above +5 °C) temperature sums at which it is possible to predict the start and end of the flowering, seed maturation and fruiting phases. For species it is possible to calculate the sum of significant (above +5 °C) temperatures needed to reach the studied phenological phases. During the study years, the sum of significant temperatures for each phase ranged from 5–20 °C, depending on the study type and year. However, the development phases timing varied from 5 to 10 days, and the duration of the flowering and fruiting phases was 7–12 days, depending on the study type and year.

We defined that most species development starts in the second half of March-beginning of April with the phase of bud swelling when a sum of significant temperatures of 68–112 °C, depending on the species, has been accumulated. Budburst and leaf emergence was recorded in the second half of April in correspondence with an accumulation of a temperature sum of 45–118 °C, depending on the species.

Fruiting began when the temperature sum reached 217–234 °C in *P. tremula*, while in *P. balsamifera* the start of fruiting required 413 °C. The other species (*P. nigra, P. simonii, P. deltoides, P*. × *canescens*) required an intermediate temperature sum (299–329 °C) to reach the same phase, which was accumulated at the beginning of June.

The analyses showed that in native species linear growth of shoots lasts for 118–130 days, while it is longer in introduced species (135–140 days). The Euro-American hybrid 'Gelrica' finished its growth in 100 days, which was faster if compared to a maximum of 140 days in the *P.* × *hybrida* 'Weresina'.

Discolouration of leaves depended on the date of first autumn frosts and during the research was shifted by two to three weeks later. We defined the phenological groups of species with early, mid and late beginning and end of vegetation period after analyzing the timing of phenological phases of growth and development of each taxa.

Thus, taking into account the sum of significant temperatures accumulated over a certain period, it may be possible to model and predict the timing of growth, development, flowering, and fruiting phases of plants of the genus *Populus*. These indicators could be considered when creating bioenergy plantations of poplars and in order to develop anti-allergic measures.

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