Original Paper *Journal of Forest Science, 72, 2026 (4): 202–211*

https://doi.org/10.17221/6/2026-JFS

Soil temperature and weather factors as key drivers of flowering phenology and nectar production in black locust (*Robinia pseudoacacia* L.) in Hungary

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Citation: Porcsin A., Ábri T., Déri H., Zajácz E., Bolla B., Szakálosné Mátyás K., Rédei K., Keserű Z. (2026): Soil temperature and weather factors as key drivers of flowering phenology and nectar production in black locust (*Robinia pseudoacacia* L.) in Hungary. J. For. Sci., 72: 202–211.

Abstract: The black locust (*Robinia pseudoacacia* L.) is the second most planted tree species worldwide, and the most common in Hungary. Phenotypic traits, particularly flowering patterns, are well-established indicators of the species' response to climate change. This study examined four forest subcompartments across three Hungarian regions: Northern-Central, Eastern and Southern-Central. The aim was to identify climatic factors correlating with the onset and duration of the flowering period. Additionally, the relationships between these factors and nectar weight and sugar concentration were defined. Results indicate a strong negative correlation between precipitation levels and flowering time: lower accumulated and average precipitation during the spring months of the preceding year was associated with a delayed flowering period in the following year ($r = -0.922$, $r = -0.918$, $P = 0.05$). However, when examining the 14-day period ($r = 0.829$) before blooming or examining from 1 January ($r = 0.929$, $r = 0.890$), the results indicate that other environmental factors may play a more dominant role. Furthermore, the number of chill and heat days was found to affect the starting date ($R^2 = 0.819$, $R^2 = 0.765$).

Keywords: apiculture; cultivars; flowering date; phenological plasticity; weather factors

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Supported by the Ministry of Culture and Innovation of Hungary from the National Research, Development and Innovation Fund, financed under the TKP2021-NKTA funding scheme (Project No. TKP2021-NKTA-43).

Black locust (*Robinia pseudoacacia* L.) is native to North America, primarily the Appalachian Mountains and the Ozark Plateau (Huntley 1990). Its initial introduction to Europe was in the 17th century (Vítková et al. 2017). The species is highly adaptable to diverse soil types with the exception of compacted clayey soils and waterlogged areas (Rédei 2020). In terms of its ecological requirements, black locust exhibits significant drought tolerance in Europe. It still maintains an economically optimal yield with only 500–550 mm of total annual precipitation, whereas in its native range it requires 1 020–1 830 mm (Nicolescu et al. 2020). Furthermore, because its original area is located 5–10° further south than its range in Europe, it is susceptible to late spring frosts (Bartha et al. 2008).

Flowering phenology is regulated by endogenous genetic mechanisms alongside various environmental drivers (Hasna et al. 2024; Wang et al. 2025). Key factors include the length of the dormant period and preceding meteorological conditions, such as temperature, light conditions, and precipitation (Kozma et al. 2003; Lakatos et al. 2008).

Most research investigating and modelling the primary drivers of the flowering period of black locust has focused on cumulative daily maximum or average air temperature (Walkovszky 1998; Lee et al. 2007; Alilla et al. 2022). Other studies have attributed the onset and duration of the flowering to genetic factors (Halmágyi, Keresztesi 1975) or environmental conditions such as topography and elevation (Fritsch 2012). In temperate trees, satisfying chilling requirements is essential for breaking dormancy. According to Cesaraccio et al. (2004), black locust needs approximately five months – 157 chilling days – to initiate spring flowering. The plant's sensitivity to air and soil temperatures is significantly influenced by the accumulation of these chill days, defined by some authors as days with an average temperature below 5 °C from 1 November until flowering onset (Murray et al. 1989; Lee et al. 2007). Additionally, several models have attempted to predict the onset date of flowering by correlating the accumulated thermal sum with the number of days elapsed from 1 January (Carbonari, Epifani 2025; Lee et al. 2007) or other pre-flowering dates (Lee, Hong 2005; Byeong Mee et al. 2008).

Taking into account the above literature, this study examined environmental variables of air temperature, including cumulative and average precipitation, as well as soil temperature at various depths. These factors were calculated for four periods – specifically, 7 or 14 days prior to bloom, from 1 January until the onset of flowering, and during the previous year's spring (March, April, May), summer (June, July, August) and autumn (September, October and November) seasons to the average starting date of flowering for the individual stands. Furthermore, we differentiated between the average flowering period (from the appearance of flower buds to petal fall) and the intensive flowering period (when bees can collect most of the nectar).

The interplay of the factors mentioned above also affects nectar production (Kozma et al. 2003; Lakatos et al. 2008). Specifically, soil moisture and nutrient availability are key determinants; adequate hydration ensures that nutrients are soluble enough for root absorption, directly influencing nectar traits (Fazekas, Péntek 2016, Denisow et al. 2025). Researchers typically monitored how accumulated air temperature and precipitation affect herbaceous plants on an hourly basis (Petanidou, Smets 1996; Takkis et al. 2018). There are species that show a delayed reaction to temperatures in terms of nectar weight (Takkis et al. 2015); therefore, this paper explores the correlation between these weather factors and soil temperature prior to the measurements, and their impact on the nectar quantity (mg) and sugar concentration (%) of the black locust.

MATERIAL AND METHODS

To examine the relationship between the onset of flowering, nectar production, and related environmental factors, a multi-year field investigation was conducted from 2023 to 2024 across four locations in Hungary. The Isaszeg 8/C (47°33'09.3'N, 19°23'45.0'E) and 8/E (47°33'04.8'N, 19°23'51.6'E) subcompartments are situated within the Gödöllő Arbo-Park, in the northern lower hillside of Hungary. Additional study sites included an eastern location near Debrecen (47°36'33.5'N, 21°37'31.8'E), and a southern site in Kecskemét (46°53'35.4'N, 19°44'12.6'E, Land Registry Number: 0743/2) (Figure 1).

The planting network was 2.5 × 1.0 m in all subcompartments. Designated sample trees were systematically monitored using standardised protocols

https://doi.org/10.17221/6/2026-JFS

Figure 1. Locations of the studied subcompartments marked with red dots

(Table 1), and individual phenological observations were performed using binoculars. Meteorological and soil temperature data were obtained from different monitoring networks: the ICP Forests Level II intensive monitoring system (station number M08) for weather and soil temperature data at Kecskemét-Méheslapos (Manninger, personal communication); the Boreas monitoring system for the two Isaszeg sites; and the National Meteorological Service (station number 64711) for the Debrecen 17/C subcompartment. Potential deviations in results may arise from the distinct warming rates characteristic of the different soil types at these locations.

Average and intensive flowering periods. Flower density was categorised into five distinct classes based on the visual extent of inflorescence within the tree crown (Csiha et al. 2013):

- I. extent: No inflorescence is visible in the crown;
- II. extent: Flowering is visible on 1/3 of the crown;
- III. extent: The inflorescence can be seen on 2/3 of the crown;
- IV. extent: Flowers are visible throughout the entire crown;
- V. extent: More than one flower is present on each branch.

Five flowering stages were differentiated:

- 1st stage: Only green buds in a closed stage are visible;
- 2nd stage: The white ends of the flowers are visible at the end of the buds;
- 3rd stage: Most flowers are white and the buds have opened;
- 4th stage: The flowers are fully open and the entire inflorescence is white;
- 5th stage: Wilted flowers appear in the crown, white and brown colours are mixed, petals begin to fall, and scattered fallen flowers appear on the ground.

The average flowering period (AFP) was defined as the duration from phenological stage 1 to stage 5. The intensive flowering period (IFP) was calculated as the sum of days when the trees exhibited both a flowering extent of III–V and were in the 3rd or 4th phenological stages, since this period coincides with the peak nectar-collecting activity of honeybees (*Apis mellifera*) (Giovanetti, Aronne 2013).

Descriptive statistics have been compiled for the two years and four subcompartments. To analyse the experimental data (n = 9), we used the number of days elapsed from 1 January. Throughout this analysis, the term 'average' refers specifically to the

Table 1. The initial data of the observed subcompartments

Subcompartment	Year of planting	Number of trees	Average height (2025) (m)	Diameter at breast height (2025) (cm)	Forestry climate type (2000–2025 period)*	*FAI* over the examined years (2023–2024)*	Forest site type**
Isaszeg 8/C	2002	58	16.5	15.9	sessile oak – Turkey oak	7.87	Chromic Cambisol
Isaszeg 8/E	2004	44	14.2	15.9	sessile oak – Turkey oak	7.87	Chromic Cambisol
Debrecen 17/C	2002	30	16.7	15.4	sessile oak – Turkey oak	8.72	Lamellic Luvisol
Kecskemét-Méheslapos (0743/2)	2000	46	12.6	15.2	forest-steppe	9.92	Brunic Arenosol

*Based on Führer et al. 2011; **based on the World Reference Base for Soil Resources (IUSS Working Group WRB 2022); *FAI* – forestry aridity index

arithmetic mean. We examined the correlation between the days passed from 1 January until the onset of the AFP and IFP and the following variables:

- Cumulative average and maximum air temperature from 1 January (°C).
- Cumulative average soil temperature from 1 January (°C).
- Cumulative and average precipitation from 1 January (mm).

We measured the different weather factors for 7-day and 14-day periods prior to the starting date of the AFP and IFP, such as:

- Average and maximum air temperature (°C).
- Cumulative and average maximum air temperature (°C).
- Average soil temperature (°C).
- Average and maximum temperature of the 0–20 cm and 30–50 cm deep soil layers (°C).
- Cumulative precipitation (mm).

We also studied the correlation between the accumulated and average precipitation of the spring months in the previous and the actual years of flowering, as well as the cumulative and average precipitation and average soil temperature in the autumn months. For the statistical analysis, we calculated the Pearson correlation coefficients in Microsoft Excel (Version 365).

The study also examined chill days – defined as the number of days with an average air temperature below 5 °C from 1 November until the onset of the AFP (Murray et al. 1989) – and heat days, defined with an average air temperature above 35 °C during the previous growing season (1 April – 31 October). To study these relationships, linear regression analysis was conducted using Microsoft Excel (Version 365) to assess the relationship between the number of chill days and the onset of the average flowering period.

Measuring nectar properties. Nectar production was measured by the capillary method of Péter (1978). While the standard protocol involves a 24-hour exclusion of insects using mesh bags, the tree height in our study areas required an alternative sampling strategy: the flowers were collected at dawn, preceding the onset of daily honeybee (*Apis mellifera*) activity. This arrangement has its disadvantages over the original in terms of reliability. Nectar weight was measured on an analytical balance (mg) and its sugar concentration (%) was determined using a handheld refractometer (MASTER-500, 0–90 % Brix, Atago, Japan). An average of 63 flowers was measured per clone (range: 10–208 pieces/stem tree/day). The nectar was collected in one glass pipette by a group of 5 flowers. Data were obtained from 11 trees in 2022, 8 in 2023 and 17 in 2024.

For the statistical analysis, meteorological data from the 24 hours preceding the measurements were recorded, including: average, maximum and minimum air temperatures; accumulated and average precipitation and average soil temperature (0–20 cm depth). Additionally, we registered the average and maximum air temperatures and precipitation for the preceding 7-day interval, as well as the average and maximum air temperature for the 14 days prior to the collection of the flowers. The collection of the flowers and the nectar measurements took place on the same day. Pearson correlation coefficients were calculated ($P = 0.05$) to assess the correlation between these weather factors and nectar properties (Microsoft Excel, Version 365).

RESULTS AND DISCUSSION

Weather data. The flowering period and nectar production of black locust were studied across four different stands between 2023 and 2024. Regarding the weather conditions, the following observations were made: 2023 had a higher amount of precipitation and higher accumulated air temperatures compared to 2024. This trend remained consistent for both air and soil temperatures [Table S1 in the Electronic Supplementary Material (ESM)]. As shown in Table S2 in the ESM, the number of chill days and heat days was also lower in 2024 than in 2023.

Average and intensive flowering periods (AFP and IFP). Across both study years and all four research areas, the Average Flowering Period (AFP) lasted between 14 and 27 days. Within this timeframe, the Intensive Flowering Period (IFP) ranged from 6 to 14 days. In all four study areas, flowering began approximately 3–4 weeks later in 2023 than in 2024 (Table S3 in the ESM). A prolonged drought occurred in the summer of 2022 (Table S1 in the ESM), followed by significantly higher precipitation in the spring of 2023. In 2024, a phenological anomaly was observed at Isaszeg. Specifically, at Isaszeg 8/C, a double flowering occurred: the first period lasted from 14–17 April 2024 to 28–30 April 2024, the second period started two days after, at 01–03 May 2024 and ended at 18–20 May 2024 (Table S3 in the ESM). The first IFP lasted 10 days, while the second lasted only 8 days. In the Isaszeg 8/E subcompartment, flowering commenced between 17 and 20 April 2024, but the trees remained in the first flowering stage for 9–10 days. Data from both flowering phases in Isaszeg 8/C were included in the analysis, as this dataset highlights the short-term plasticity of black locust in response to weather fluctuations (Mantovani et al. 2014; Wilczyński et al. 2026). The spring, summer and autumn months were analysed separately, as Nagy (2007) showed that weather conditions in different seasons affect the onset of the flowering period differently. Weather factors significantly associated with the onset of the AFP and IFP are shown in Table 2.

Studying the different chosen and calculated weather factors, a new component needs to be taken into account: time. Most weather variables from the previous year exhibited a strong negative correlation with the time elapsed until the onset of the AFP and IFP, which supported the others' findings (Walkovszky 1998; Lee et al. 2007). Out of these climatic factors, the strongest negative correlation was observed between the onset of the AFP and the cumulative and average precipitation of the previous year's seasonal precipitation (Table 2). It indicated that water scarcity may delay the flowering period in the following season. Furthermore, the higher average soil temperature of the different layers in the previous year can bring the onset earlier.

There is a strong positive correlation between the days passed from 1 January to the onset of the AFP and IFP, and both cumulative average (AFP: $r = 0.793$, IFP: $r = 0.888$) and maximum air temperatures (AFP: $r = 0.943$, IFP: $r = 0.924$). These findings highlight a complex interplay between air temperature, precipitation and the flowering phenology. Specifically, reduced precipitation and lower soil temperatures appear to delay the initiation of the flowering period. Regarding soil temperature, an early study by Daubenmire (1949) reported findings similar to ours. Additionally, the impact of soil temperature on flowering phenology was previously investigated by Llorens and Peñuelas (2005) in Mediterranean shrubs. The sensitivity of *R. pseudoacacia* L. to water availability is also supported by the observations of Li et al. (2022) and Wang et al. (2023).

However, the average temperatures of the various soil layers exhibit an increasingly strong posi-

Table 2. Relationship between the starting date of the average flowering period and weather factors (Pearson correlation coefficients)

	AFP starting date (*r*)	IFP starting date (*r*)
Weather factors prior to flowering		
Cumulative precipitation of the III-IV-V months in the previous year (mm)	–0.922	–
Average precipitation of the III-IV-V months in the previous year (mm)	–0.918	–
Cumulative and average precipitation of the VI-VII-VIII months in the previous year (mm)	–0.880	–
Average soil temperature of the IX-X-XI months in the previous year (°C)	–0.672	–
Cumulative precipitation of the III-IV-V months in the year of the measurement (mm)	0.798	–
Average precipitation of the III-IV-V months in the year of the measurement (mm)	0.786	–
Cumulative average soil temperature in the III-IV months of the year of the measurement (°C)	–0.927	–
Average soil temperature in the III-IV months of the years of the measurement (°C)	–0.930	–
From 1 January		
Cumulative air temperature (°C)	0.793	0.888
Cumulative maximum air temperature (°C)	0.943	0.924
Cumulative average soil temperature from (°C)	0.913	0.949
Cumulative precipitation (mm)	0.929	0.966
Average precipitation (mm)	0.890	0.940
14-day period prior to the starting date		
Average soil temperature (°C)	0.785	0.840
Average soil temperature of the 0–20 cm deep soil layer (°C)	0.673	0.843
Average soil temperature of the 30–50 cm deep soil layer (°C)	0.839	0.829
Cumulative precipitation (mm)	0.829	0.912
7-day period prior to the starting date		
Average maximum temperature (°C)	–0.893	0.704

AFP – average flowering period; IFP – intensive flowering period; all of the weather factors shown in Table 2 are significant at the 0.05 level (2-tailed)

tive correlation with the proximity to the starting date. Within the 14-day period preceding the starting date, higher temperatures were associated with a delayed onset. Since flowering can stagnate during its initial two stages, this delay may represent an energy-saving and safety mechanism to mitigate the risk of late frosts.

Chill days and heat days show a strong correlation with the starting date (R^2 = 0.719, R^2 = 0.765) (Figure 2).

As illustrated in Figure 2, a lower number of chill and heat days is associated with an earlier onset of flowering. According to Murray et al. (1989), until a specific chilling requirement is met, the increased accumulated maximum air and average soil temperatures driven by climate change maintain a positive correlation, thereby advancing the flowering period. However, these relationships transition into strong positive correlations when observed from 1 January, or in the 7- and 14-day

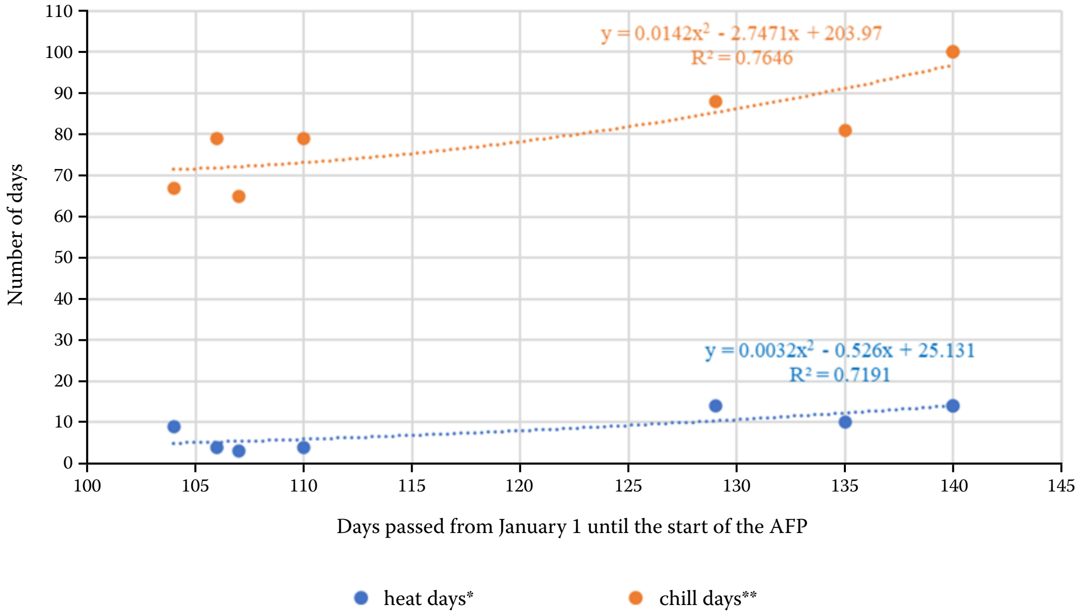

Figure 2. Correlation between the number of chill and heat days and the starting date of the average flowering period (AFP)

*Number of days where the average air temperature was > 35 °C, in the previous year, from IV. 1. – X. 31.; **number of days where the average air temperature was < 5 °C from Nov 1 until the onset of the AFP; orange line – polynomial regression function ($y = 0.0142x^2 – 2.7471x + 203.97$) for chill days; blue line – polynomial regression function ($y = 0.0032x^2 – 0.526x + 25.131$) for heat days

long periods preceding the onset. The only exception was accumulated precipitation, which remained positive across both intervals. This discrepancy may stem from the chilling requirements during winter months and the number of heat days in the preceding growing season. Our analysis suggests that if the species does not meet its chilling requirement, the thresholds for cumulative and average soil and air temperatures and accumulated precipitation in the examined year will grow. Nevertheless, these higher temperature thresholds can be reached earlier in the year due to climate change. Our results align with the findings of previous research (e.g. Carbonari, Epifani 2025; Kozma et al. 2003; Lakatos et al. 2008), indicating that precipitation and chill days act as equalising factors on the analysed timeframe.

Nectar traits. In this study, a total of 0.00–4.54 mg (with an average of 1.37 mg) of nectar was collected per sub-sample, with each sub-sample consisting of pooled nectar from five flowers. The nectar sugar concentration varied between 0% and 60%. Detailed data are presented in Tables S4 and S5 in the ESM.

Influence of meteorological factors on nectar parameters. The effects of some weather factors on the nectar traits were analysed separately for each subcompartment, with the exception of Isaszeg 8/C and 8/E, which were examined together. Table 3 presents only those meteorological factors that showed significant results in at least two of the three subcompartments.

Nectar weight (mg). The results of the nectar weight may indicate that while the stem trees reacted in the same way and mostly the same strength to the different weather factors at the Debrecen 17/C and the Kecskemét-Méheslapos stands, the two Isaszeg subcompartments reacted differently in most cases. This can be attributed to the fact that while the higher average and maximum air temperature did not occur with decreased precipitation at Isaszeg, we can assume that in the observed period, there was less precipitation alongside higher temperatures at Debrecen and Kecskemét.

Higher temperatures increased nectar weight at the two Isaszeg subcompartments, but decreased it at the Debrecen 17/C and the Kecskemét-Méheslapos one, where the precipitation levels were lower (Table S5 in the ESM). The literature review showed that the relationship between nectar weight and air temperature is complex. Higher temperatures caused higher nectar volume, sugar content and concentra-

Table 3. Impact of weather conditions on average nectar sugar concentration (%) and nectar weight (mg·flower^{-1}): A Pearson correlation analysis (*P* = *0.05*)

Correlation between average nectar weight (mg·flower^{-1}) and various weather factors								
Isaszeg 8/C and 8/E (*n* = 48)	0.436*	0.312*	0.420*	0.178	0.510*	0.544*	0.464*	0.531*
Debrecen 17/C (*n* = 18)	–0.674*	–0.594*	–0.417	–0.717*	–0.645*	–0.492	0.488	–0.438
Kecskemét-Méheslapos (0743/2) (*n* = 25)	–0.630*	–0.520*	–0.686*	–0.692*	–0.695*	–0.597*	0.627*	–0.561*
Correlation between average sugar concentration (%) and various weather factors								
Sub-compartment	A	B	C	D	E	F	G	H
Isaszeg 8/C and 8/E (*n = 48*)	0.580*	0.627*	0.334*	0.492*	0.266	0.430*	0.240	0.466*
Debrecen 17/C (*n* = 18)	0.592*	0.566*	0.221	0.441	0.590*	0.727*	–0.600*	0.404
Kecskemét-Méheslapos (0743/2) (*n* = 25)	0.245	0.270	0.179	0.147	0.107	0.273	–0.113	–0.105

*Correlation is significant at the 0.05 level (2-tailed); A – average air temperature of the previous day (°C); B – maximum air temperature of the previous day (°C); C – minimum air temperature of the previous day (°C); D – soil temperature in the top layer (0–20 cm depth) (°C); E – average air temperature over the 7-day period preceding measurement (°C); F – maximum air temperature over the 7-day period preceding measurement (°C); G – average precipitation over the 7-day period preceding measurement (mm); H – average maximum air temperature over the 14-day period preceding measurement (°C)

tion but only if the plants were not under drought stress (Scheid-Nagy Tóth 1991; Petanidou and Smets 1996; Takkis et al. 2015), because higher temperatures enhance the photosynthetic rate**,** resulting in increased nectar weight (Southwick 1984, Cawoy et al. 2008). However, nectar production only occurs within a specific temperature range, and slows down or stops at both excessively low and excessively high temperatures (Halmágyi, Keresztesi 1975, Petanidou, Smets 1996, Takkis et al. 2015, 2018).

Sugar concentration (%). Air temperature showed a mostly strong or moderate positive correlation with nectar sugar concentration in the Isaszeg and Debrecen areas (Table 3). In contrast, a moderate correlation with soil temperature was observed only in the Isaszseg stands. Such a relationship between air temperature and sugar concentration has previously been pointed out by Descamps et al. (2021) and McCombs et al. (2022). Additionally, the Debrecen 17/C subcompartment showed a strong negative correlation between the average precipitation of a 7-day period prior to the measurements and the sugar concentration. This finding can be attributed to the fact that the other two subcompartments did not have significant rainfall in that period. As Pusey (1999) and Bubán et al. (2003) showed, the precipitation during the week before the measurement increased nectar weight, as the nectar became more diluted.

CONCLUSION

The phenology of flowering is regulated by a complex interaction between air temperature, soil temperature and precipitation. In our study, we demonstrated that black locust (*Robinia pseudoacacia* L.) possesses significant short-term plasticity in response to weather fluctuations. Our results highlight the complex relationship between environmental factors and the onset of the flowering period (AFP and IFP). Lower temperatures and reduced precipitation in the previous year may delay flowering in the following year, whereas within the current year, they may accelerate its onset. This occurs because if the winter dormancy period is disturbed – for instance, if the chilling requirement is not met – a higher temperature threshold is required to trigger flowering. Today, however, due to climate change, these higher thresholds can be reached earlier in the year, further modifying the species' phenological responses. In the period immediately preceding flowering, the temperature of various soil layers plays a critical role alongside precipitation and air temperature. Furthermore, less extreme weather – specifically the decrease in the number of cold and hot days – plays a balancing role in regulating the onset of the flowering period.

Climate change causes an increase in extreme weather conditions, such as premature spring warming followed by abrupt temperature drops, which significantly affect the flowering of black locust due to its sensitivity to late frosts.

In the future, the species is expected to further advance its flowering phenology, assuming sufficiently low temperatures for dormancy or adequate spring precipitation do not occur. This early bloom poses a critical challenge for beekeepers, as bee colonies are often still insufficiently developed in late spring. While elevated temperatures may enhance nectar weight and sugar concentration, prolonged drought spells may reduce the overall amount of collectable nectar. Consequently, the combination of shifted blooming periods and diminished nectar production may lead to substantial economic losses for the beekeeping industry.

Acknowledgement: We thank Miklós Manninger for his insightful advice, and Tilla Takács, Csilla Póvikné Török, and Imre Sass for their valuable assistance in data collection.

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Received: January 19, 2026
Accepted: March 30, 2026