



Seasonal variability in flower lifespan in common chicory (*Cichorium intybus* L.)

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ABSTRACT

Flower opening and closure is a crucial process in pollinator attraction. The duration of flower lifespan, the time between flower opening and closure, represents a trade-off between pollinator attraction and the cost of flower maintenance caused by increased respiration and transpiration rates, particularly when ambient temperature is high. Moreover, flower lifespan can decrease rates of autonomous self-pollination. We examined whether flower lifespan in common chicory (*Cichorium intybus*) is determined by pollinator availability and/or by abiotic factors such as temperature and day length. Plants were investigated in one study site in East Slovakia during the summer and autumn seasons of 2016 and 2019, respectively. Individual flower opening and closure and pollinator availability were recorded during the flowering season and across various hand-pollination treatments including self-pollination, cross-pollination, no pollination and an unmanipulated control. Flower lifespan was positively correlated to time of the season as well as to lower pollinator abundance. Unpollinated flowers remained open for a longer period than self-pollinated, cross-pollinated and control flowers. The time of the season has stronger impact on flower lifespan than the onset of pollination. Findings in this study indicate that seasonal changes characterized by daytime temperature, day length and pollinator availability need to be taken into account in research of flowering time.

1. Introduction

The primary function of entomophilous flowers is reproduction which requires pollinator attraction, but flowers are simultaneously exposed to various environmental factors such as temperature or heat and water stress (Caruso et al., 2019; Strauss and Whittall, 2006; van der Kooi, 2016; van der Kooi et al., 2019). These factors seem to affect the metabolic costs of flowering and reproductive success. Flowering is energy consuming, thus floral longevity represents a trade-off between time available for pollen reception/removal and physiological costs required for flower maintenance (Ashman and Schoen, 1994). For instance, in *Clarkia tembloriensis* prolonged flowering periods resulted in proportionally more nectar sugar production and consequently in a reduced amount of seed production (Ashman and Schoen, 1997). Additional costs associated with flowering include increased respiration

and transpiration rates as a result of flower maintenance (Galen, 2000; Galen et al. 1999; Vemmos and Goldwin, 1994), which can be particularly significant in arid environments (Caruso, 2006; Galen et al., 1999; Teixido and Valladares, 2013).

Flowering costs can be partly mitigated by flower opening and closure (van Doorn and van Meeteren, 2003), which can either occur repetitively or only once. It is hypothesized that repetitive flower closure can protect plants from florivory (Kemp and Ellis, 2019; Prokop and Fedor, 2016; Tagawa et al., 2018), and/or protect reproductive organs against unfavourable environmental conditions (Abdusalam and Tan, 2014; Bynum and Smith, 2001; Liu et al., 2017; Prokop et al., 2019). Moreover, flower closure seems very sensitive to pollination (e.g., Ashman and Schoen, 1994; Castro et al., 2008; Fründ et al., 2011; Proctor and Harder, 1995; Prokop and Neupauerová, 2014; van Doorn and Kamdee, 2014), but also to environmental variables such as light

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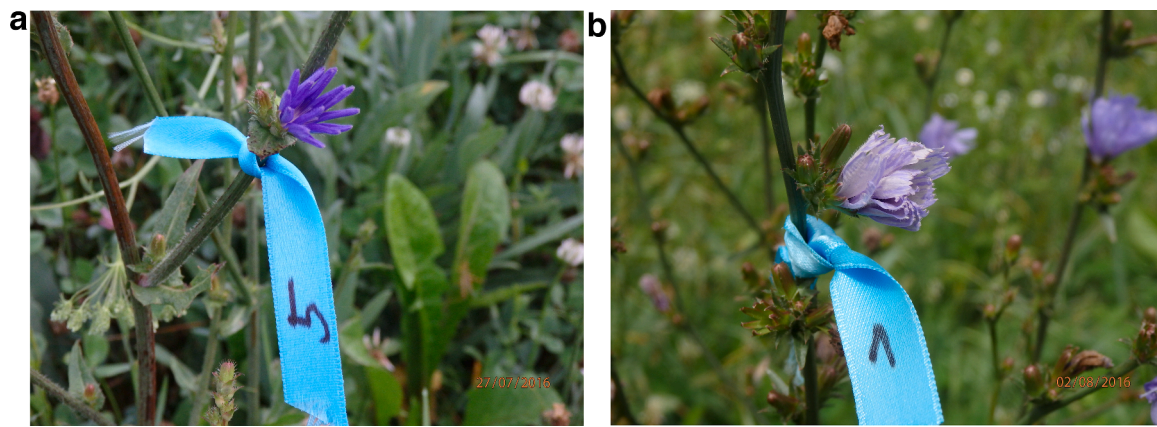


Fig. 1. a) Partially open and b) fully closed capitulum of common chicory

(van Doorn and van Meerten, 2003; Maguvu et al., 2018). Flowers are not expected to have a fixed lifespan, because the deposition of pollen induces senescence. For instance, in the orchid *Calypto bulbosa*, pollen receipt had a significant impact on shortening the flower lifespan (Proctor and Harder, 1995), and in *Convolvulus arvensis* a shortened flower lifespan was associated with higher seed production (Prokop and Neupauerová, 2014).

Both pollinator availability and light intensity or temperature may vary depending on the time of day and year (Vesprini and Pacini, 2010). Therefore, a changing environment may impose different costs on flower maintenance for plants with longer blooming periods across the reproductive season (Primack, 1985). In particular, when maintenance costs are high, selection should favour short-lived flowers (Primack, 1985; Schoen and Ashman, 1995; Ashman and Schoen, 1996). Short flowering periods are beneficial in this case because of their reduced physiological costs (e.g., water loss) particularly in dry environments, where the cost of flowering may be higher (e.g., Teixido and Valladares, 2013). To better understand the functional significance of flowering, two factors are worth considering: annual climatic variation (seasonality) and pollinator availability.

Linnaeus (1751) compiled a list of 44 plant species with regular flower opening and closure periods at particular times of the day. This periodicity was used in “floral clocks” or *horologium florum*, a book in which plant species are arranged in sequence according to their flowering times indicated by the time of the day. *Cichorium intybus* was one of the species of Linnaeus’ floral clock (Linnaeus, 1751). Interestingly, Linnaeus (1751) provided only the opening time (4–5 AM) at the latitude of Uppsala (60° N), but not the flower closure time in this species. Fründ et al. (2011) investigated floral movements of the certain species of Linnaeus’ floral clock, but common chicory was not included in their study, because it was considered an “unusual Cichorioideae species in the dataset” (Fründ et al., 2011, p. 898). This species has a prolonged flowering period, beginning in the summer and ending in the autumn (from 75 to 102 days, data from Ukraine, Adamchuk et al., 2017). The end of the flowering period occurs when mean daily temperatures decrease, and when both day length and pollinator availability are reduced (Parker, 1981; McCall and Primack, 1992), suggesting that flowering may be shaped by various environmental pressures. In this study we investigated whether the flower lifespan of common chicory is influenced by these environmental factors under natural conditions in Slovakia. First, we predicted that high pollinator availability correlates with shorter flower lifespan. Second, we predicted that flowering exposure periods are shorter under conditions with high temperature and prolonged day light periods.

2. Materials and methods

2.1. Study species

Common chicory is a perennial plant from the family Asteraceae, commonly occurring in roadsides or as garden weed. It is 90 to 180 cm tall and produces conspicuous blue, insect-pollinated capitula (Fig. 1). Capitula are arranged along the length of a more or less hairy stem; they have a diameter of about 25–39 mm (M = 33 mm, SE = 0.5, N = 50) and their flower lifespan lasts a single day (Barcaccia et al., 2016; Rick, 1953). Flowers are open between 5:30 AM and 7:30 AM and flowers close around noon (Barcaccia et al., 2016; Dinakaran and Sundaraj, 1960) or about 2:00 or 3:00 PM (Knuth and Muller, 1908). In the early morning, still closed capitula were marked with blue ribbons (Fig. 1). Although common chicory is generally considered self-incompatible (e.g., Barcaccia et al., 2016), it was observed that certain individuals exhibit a low degree of self-compatibility (Cichan, 1983). After flower closure, the petals change colour from blue to white (Linnaeus, 1751, pers. obs.).

2.2. Observations of flower opening times and pollinators

A survey on flower opening and abiotic factors (day length, temperature) was carried out between August 2nd and September 24th, 2016. Additional research on flower closure, abiotic factors, and pollinator abundance was carried out between August 19th and September 22nd, 2019. The study site had an area of 150 m² and was located on private land in East Slovakia, near Honce (48° 40' 4.44" N 20° 24' 19.8" E). The dominant plants in the study area included dandelion (*Taraxacum* spp.), red clover (*Trifolium pratense*), ribwort plantain (*Plantago lanceolata*), meadowgrassess (Poaceae), buttercups (*Ranunculus* spp.), common yarrow (*Achillea millefolium*) and common chicory (*C. intybus*). The study area is commonly mown three times per year, except in the years when the research was carried out; during this time, the vegetation in the target area was left uncut. Although mowing regimes may affect selection opportunities for specific local flower closure times, we did not observe any apparent differences in flower lifespan compared with plants from uncut roadside areas. Only windless (wind speed < 10 km/h), rainless and sunny days (cloudiness < 20%) were chosen for observations to eliminate the influence of potentially confounding factors. Daylight temperature was measured in the shade twice during a day (06:00 AM and 12:00 PM) directly in the study area. Average temperature varied between 18°C and 24°C in August and between 11°C and 18°C in September. Daytime was calculated in minutes as the time between sunrise and sunset. In August, daytime varied between 806–898 minutes, whereas in September it was about 722–775 minutes. Daily observations were conducted on 20 capitula, each from a different plant. About 30% of all available plants in the study area were investigated.



Fig. 2. Experimental plants covered with white tissue

Capitula were checked each hour between 06:00 AM and 14:00 PM in 2016, and every 30 minutes in 2019 to include additional data about pollinators. Time of capitulum opening (Fig. 1a) and closure (Fig. 1b) was recorded. The presence of pollinators on focal capitula was recorded during 30 minute intervals. Pollination was defined as the presence of an insect visitor inside the capitulum for at least 3 seconds (Patiño et al.,

2002). However, because a single plant simultaneously produces multiple capitula within one day (15 – 25, Barcaccia et al., 2016), it is highly likely that a pollinator visiting neighbouring flowers could move onto the focal flower outside the recording interval. We therefore also recorded the presence of pollinators on neighbouring capitula of the same plant (Dramstad and Fry, 1995).

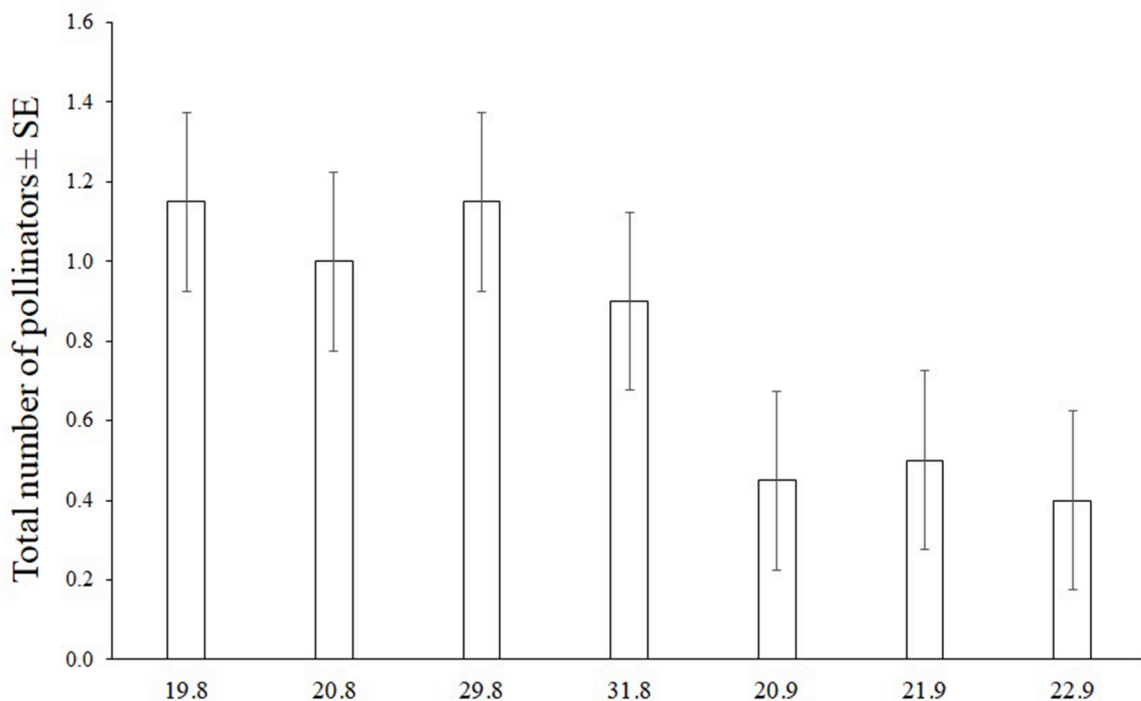


Fig. 3. Combined total number of pollinators observed on capitula during the season

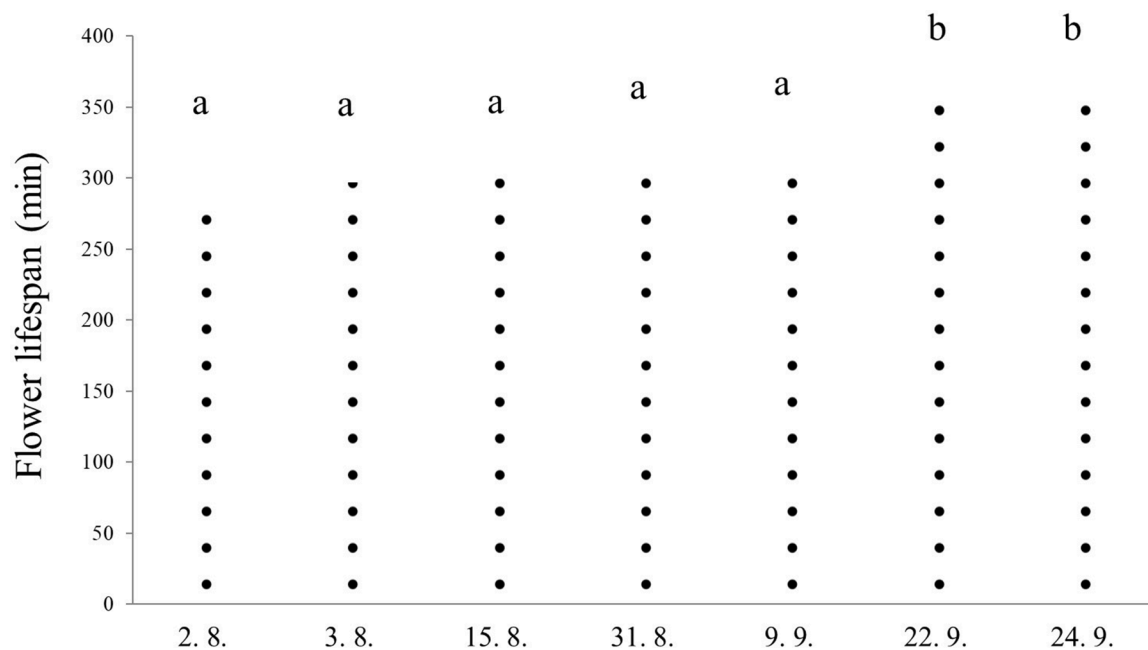


Fig. 4. Differences in flower lifespan with respect to time of season in 2019. Dot plots marked with "a" significantly differ from plots marked with "b" ($P < 0.001$).

2.3. Controlled pollination experiment

A controlled pollination experiment was performed in the study area described above from August 19th to August 26th, 2019 during sunny (cloudiness $< 20\%$), rainless and windless days (wind speed < 10 km/h). Early in the morning of the day of the experiment, individual flower heads from different plants with closed capitula were randomly assigned to 1 of 4 treatments: cross-pollination ($N = 15$), self-pollination ($N = 15$), all visitors excluded ($N = 15$), and unmanipulated control ($N = 15$). All flowers, except the control group were covered with a white tissue that resembled a fine mesh, gently attached to the capitulum stem with a ribbon (Fig. 2), which prevented any contact between the pollinator and the flowers (Prokop and Neupauerová, 2014). Capitula receiving the cross-pollination and self-pollination treatments were hand pollinated with a fine brush at 09:00 AM when the flower heads were open. For cross-pollination, we used pollen from freshly collected capitula from plants outside the experimental plot. Control capitula were individually marked with a ribbon, similar to the flower heads from other treatments. The capitula were checked every 30 minutes until closure and the time of flower closure was recorded.

2.4. Statistical analyses

Data on flower lifespan from observations of flower closure in 2016 and 2019 as well as flower lifespan exposure data from controlled pollination experiments were not normally distributed (Kolmogorov-Smirnov test, $d = 0.13, 0.14$ and 0.21 , all $P < 0.01$, respectively) and were therefore Box-Cox transformed, which resulted in normality (Kolmogorov-Smirnov test, $d = 0.05, 0.92$ and 0.15 , all $P > 0.15$, respectively). A one-way ANOVA with a Fisher LSD post-hoc test was used for comparison of means between groups. The Pearson correlation coefficient was used to examine associations between temperature, day length and flower lifespan. Relationships between flowering exposure time (dependent variable), time of season and pollinators (predictors) were analysed with multiple regression. The total number of observed pollinators dropped as the season progressed (Kruskal-Wallis ANOVA, $H_6 = 12.32, N = 140, P = 0.055$, Fig. 3), hence, the effect of the season needed to be controlled for. Predictors in the multiple regression analyses were residuals of the regression derived from time of season (dependent variable) regressed on total number of pollinators seen on

focal and on neighbouring plants (independent variable). In addition, total number of pollinators (dependent variable) was regressed on time of season (independent variable). This approach allowed us to analyse the data while controlling for the effect of season and pollinator abundance. Multicollinearity in a multiple regression analysis was examined with the variance inflation factor (VIF). The VIF values for pollinators (while controlling for time of season) and for the time of the season (while controlling for pollinators) were both low (both $VIF = 1.09$), meaning that the variance of a regression coefficient was not inflated due to multicollinearity. A generalized Linear Mixed Model (GLMM) with identity link function and normal distribution was used for analysis of experimental data, where flower lifespan was defined as dependent variable. Individual plants were included as a random effect that controls for variation in spatial position. The analyses with non-transformed data yielded the same results as the analysis with transformed data. We therefore conclude that the interpretation of results was not negatively influenced by data transformation (Changyong et al., 2014). All the statistical tests were performed using the SPSS program version 25.

3. Results

Seasonal variability in flower closure (2016). The mean flowering exposure time (measured from the opening of the capitulum in the morning until capitulum closure) ranged from 240 to 449 minutes. ($M = 313$ min, $SE = 4.01, N = 135$). However, time of season significantly influenced flowering time (ANOVA, $F_{6,128} = 9.5, P < 0.001$). Subsequent post-hoc tests showed that the capitula observed between August 2nd and September 9th were open for a significantly shorter time than capitula observed at the end of the season (22 and 24 September 2016, Fig. 4).

Both temperature and day length were significantly negatively correlated with mean flower exposure time ($r = -0.99$ and $-0.87, P < 0.001$ and $0.01, N = 7$ observation days). This finding suggests that lower temperatures and shorter day length were associated with longer flower exposure time. It was not possible to disentangle these two influencing factors, because temperature was significantly and positively correlated with day length ($r = 0.83, P = 0.02, N = 7$ observation days). These results indicate that flower closure in chicory is significantly influenced by seasonal variability.

Correlation between pollinator availability and flower closure (2019).



Fig. 5. Example of a pollinator (*Scaeva pyrastris*, Diptera: Syrphidae) frequently visiting the common chicory

The most frequently observed pollinators were syrphid flies (Diptera: Syrphidae) (Fig. 5), honeybees (*Apis mellifera*) and occasionally flesh flies (Sarcophagidae). Bumblebees (*Bombus* spp.) were never observed on common chicory flowers.

A multiple regression model with the combined number of pollinators and time of season (independent variables) and flower lifespan (dependent variable) was significant. The time of season had a positive influence on flower lifespan ($\beta = 0.78$, $P < 0.001$), and conversely, the combined number of pollinators had a negative impact on flower

lifespan ($\beta = -0.13$, $P = 0.025$). These results suggest that flower lifespan was longer in autumn than in summer and when the presence of pollinators was low.

Controlled pollination experiment. Results from the Generalize Linear Mixed Model (GLMM) showed that flowering exposure time was significantly influenced by the effect of treatment ($F_{3,56} = 288.7$, $P < 0.0001$). Flower lifespan was longer for unpollinated capitula, followed with self-pollinated capitula and cross-pollinated capitula. Flowering time of control capitula was shorter than that of capitula in the

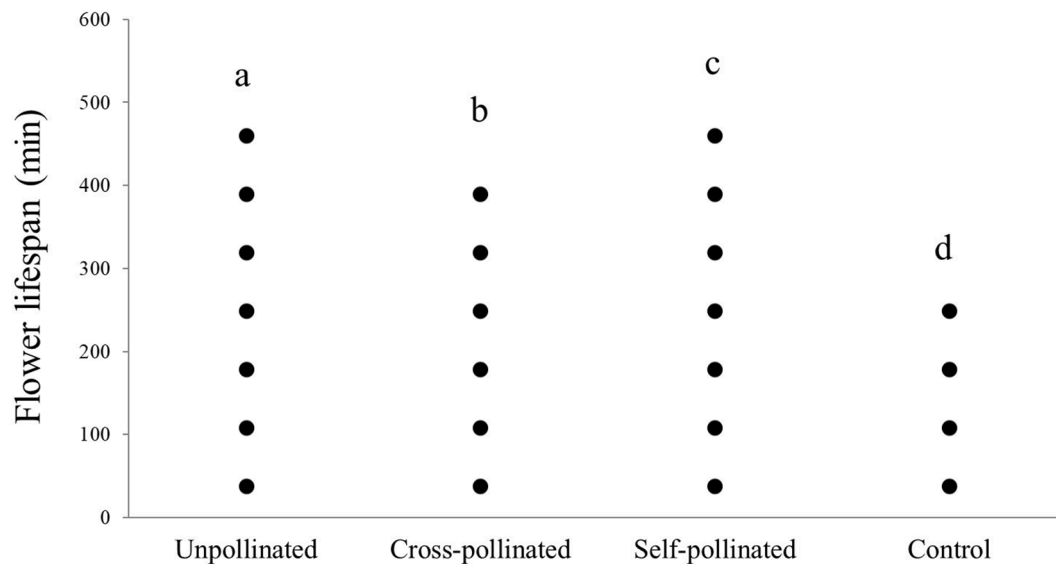


Fig. 6. Differences in mean flower lifespan (untransformed data) with respect to treatment (N = 15 per each treatment). The different letters denote significant differences based on Fisher LSD post-hoc test (all differences are significant at $P < 0.01$ and less).

treatment groups (Fig. 6).

4. Discussion

Findings from this study indicate that both pollinator availability as well as time of season, characterized by shorter day length and decrease in temperature, influenced flower lifespan in the common chicory.

Our first prediction suggested a negative relationship between pollinator availability and flower lifespan (Fründ et al., 2011; Proctor and Harder, 1995). Both empirical and experimental evidence support this prediction. Results from our field surveys showed that flower lifespan was negatively correlated with pollinator availability. This finding supports the idea that natural selection favours a synchronization between flowering and pollinator abundance (Waser, 1979). In fact, mismatches between flowering and pollinator activity may have negative fitness consequences for a plant (Herrera, 1990; Rafferty and Ives, 2012). Our experiment clearly confirmed the idea that cross-pollination reduces flowering exposure time more than self-pollination or than the absence of pollination, presumably because the species is largely self-incompatible (Cichan, 1983). Self-compatibility can lead to rapid inbreeding which can have detrimental effects on seed viability (Charlesworth & Charlesworth 1987; Darwin, 1876; Marr et al., 2000). Self-pollination shortened flower lifespan in comparison with the absence of pollination (Aizen, 1993). Earlier senescence of self-pollinated flowers can limit opportunities or pollen transfer and can be a selective force of mating systems (Weber and Goodwillie, 2007). Whether the earlier senescence of self-pollinated flowers has any specific adaptive value in the common chicory requires further work.

The ultimate explanation for a reduced flowering time may lie in the cost of flowering (Primack, 1985), because flower maintenance is energetically costly in terms of nectar production, respiration rates and/or water balance which ultimately decreases reproductive success (Ashman and Schoen, 1994, 1997; Castro et al., 2008; Nobel, 1977). Control flower buds showed a very apparent reduction in flowering time compared with all other treated flower buds. A probable explanation is that control flowers were visited by various pollinators that pollinated flower buds more effectively than in the manually pollinated flowers (Prokop and Neupauerová, 2014). Potential pollinators included beetles (Coleoptera), bees (Hymenoptera), flies (Diptera) and butterflies (Lepidoptera) (Knuth and Muller, 1908). Likewise, Fründ et al. (2011) observed that plants in cages with pollinators showed reduced flowering times compared to flowers without pollinators. Prokop and

Neupauerová (2014) used the same experimental approach as was used here in the species *Convolvulus arvensis* and obtained similar results to those presented in this study. No other studies, however, investigated flower lifespan under natural seasonal changes which may also influence flowering exposure time.

The second prediction dealt with the influence of the time of season on flower lifespan, characterized by changes in abiotic variables, particularly temperature and/or day length. Both of these external factors are important regulators of biological processes, often setting the circadian clock (Van Doorn and Kammdee, 2014). Because day length and temperature were mutually correlated, we were unable to disentangle their possible effects, but we used time of season as a proxy of apparent changes in temperature and light. Results in this study strongly suggest that time of season has a stronger effect on flower closure than pollinator availability; however, both factors were significantly correlated with flower lifespan.

Given that the cost of flower maintenance can be higher in arid environments (e.g., Caruso, 2006; Teixido and Valladares, 2013), early flower closure in the afternoon may be beneficial particularly during summertime, when the ambient temperatures are high. Summer afternoon temperatures in Slovakia commonly reach 30 to 36°C which may increase transpiration rates. The presence of large floral displays and fast flower senescence seem to represent a trade-off between high summer temperatures and pollinator attraction in autumn when temperatures are lower and pollinators are less abundant. Furthermore, high temperatures cause damages in photosynthetic membranes and consequently decrease photosynthetic activity and viability of female reproductive organs (Polowick and Sawhney, 1988; Prasad et al., 2008; Ristic et al. 2007). Thus, it seems to be beneficial to have short flower opening periods, when daily temperatures are high. Correspondingly, high temperatures increase pollinator activity (McCall and Primack, 1992; Vicens and Bosch, 2000), which suggests that plants respond differently to environmental changes than to their pollinators. Longer flowering times may be a compensation strategy for pollen limitation when pollinators are scarce due to temperatures limiting pollinator availability. Pollinator scarcity is a factor involved in the selection of longer flowering periods (Ashman and Schoen, 1994; Castro et al., 2008; Prokop and Neupauerová, 2014) in the autumn season when temperatures are lower and the cost of flower maintenance is lower than during summertime.

In closing, flower lifespan of the common chicory is simultaneously influenced by biotic and abiotic factors. Flowering is shorter during the

summer season when both pollinator presence and cost of flower maintenance are high. As the blooming season progresses, flower lifespan increases, ambient temperature decreases and pollinators become scarce. Based on the fact that time of the season influences flower senescence more strongly than pollinator availability, we suggest that laboratory experiments are required to disentangle the effects of abiotic factors and possible circadian rhythm on flower lifespan.

CRedit authorship contribution statement

Pavol Prokop: Supervision, Conceptualization, Methodology, Writing – original draft, Writing – review & editing. **Dominika Molnářová:** Investigation, Methodology. **Jana Fančovičová:** Conceptualization, Visualization. **William Medina-Jerez:** Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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