

FACTORS DETERMINING THE DIURNAL DYNAMICS OF BLOOMING OF CHOSEN PLANT SPECIES

Bożena Denisow

Department of Botany, Laboratory of Horticultural Plants Biology, University of Life Sciences in Lublin
Akademicka 15, 20-950 Lublin, Poland
e-mail: bozena.denisow@up.lublin.pl

Received: 16.10.2008

Abstract

The paper attempts to synthesize the determinants which may influence the diurnal rhythm of blooming. Additionally, I tried to explore and bring together topics that concern blooming and have always been considered separately because of their origin in different disciplines. The following species were included: *Hydrangea arborescens* L. subsp. *discolor* (Raf.), *H. paniculata* Sieb., *Viburnum opulus* L., *Chaenomeles japonica* Lindl., *Knautia arvensis* L., *Adonis vernalis* L., *Aster saggitifolius* Willd., *Taraxacum officinale* L. *Chelidonium majus* L. The taxons were observed in Lublin (51°08' – 51°18' N and 21°27' – 21°41' E) in the years 2001-2007. The blooming of species was determined at least for two vegetation seasons. During observations all flowers developed in one-hour intervals were counted. The diurnal dynamics of blooming differs among species and is modified by different endogenous and exogenous factors. The endogenous determinants of diurnal dynamics of blooming are morphological diversity of flowers (fertility or sterility) within species or heterostyly. The different pattern of blooming succour different mechanisms which prevent self-pollination (*Chaenomeles japonica* Lindl., *Knautia arvensis* L.). The abiotic factors, such as day length and temperature during the vegetation season, influence the change in the process of diurnal dynamics of blooming (e. g. *Taraxacum officinale*, *Chelidonium majus*)

Key words: diurnal dynamics of blooming, endogenous and exogenous factors, heterostyly

INTRODUCTION

Blooming is a part of the plant breeding system. The male reproductive structures of the flower release pollen and take part in pollination. In consequence, fertilization occurs. The process is of great importance for successful sexual reproduction and the ensuing development of seeds and fruits depend on flowering at the right time. Flowers may open only once or may repeat

the process (Szafer and Wojtusiakowa, 1969; Faegri and van der Pijl, 1979; Cresswell, 1994). In consequence of blooming, the presentation of attractants is possible. These strategies have been selected during evolution to optimize reproductive success at minimal metabolic costs and are closely connected with pollinators' activity (van Dorn, 1997). Diurnal or nocturnal patterns are known, and thus flowers may open systematically (*Ribes nigrum* L. or *Robinia pseudoacacia*) or with different intensity during the day (*Prunus* sp., *Malus* sp.) – (Jabłoński and Szklanowska, 1997). In many species from Brassicaceae, opening occurs early in the morning (Denisow, 2004). Some species are nocturnal, e.g. *Oenothera* spp. Exogenous and endogenous factors influence blooming and the interdependent regulation by genetic, physiological, biochemical factors is known. The endogenous mechanism and its periodicities are modified by external factors of various kinds, mainly meteorological. Weather conditions modify the blooming in the season. Long-term studies have proven that mostly temperatures influence the process of flower opening. The temperature decrease is usually connected with rainfall and can even stop blooming (Jabłoński and Szklanowska, 1997). The intensity of blooming increases during warm, dry and sunny weather. However, even less predictable factors, such as nutrients or wind, can also modulate flowering time, depending on the species (Ausin et al. 2005).

Jabłoński and Szklanowska (1997) emphasize that the diurnal rhythm of blooming is species related. Other studies, however, show that the dynamics of blooming is influenced by environmental conditions during the day or even the night before (Cruden et al. 1984; Klepacz-Baniak and Czekońska, 2006). This paper attempts to synthesize, on the basis of the author's own study, the

determinants which may influence the diurnal rhythm of blooming. Additionally, I tried to explore and bring together topics that concern blooming and have always been considered separately because of their origin in different disciplines.

MATERIALS AND METHODS

The observations were carried out in the period 1997-2007 in Lublin, Poland. The localization of the species was described by ATPOL net units which belong to 86 squares of 10 km long sides (Zając, 1978). The blooming of each species was determined at least for two vegetation seasons (Tab. 1). The species from different botanical families were included.

Table 1
Species included in the study.

Species	Localization	Years of study
<i>Hydrangea arborescens</i> L. subsp. <i>discolor</i> (Raf.),	FE2765	2001–2004
<i>H. paniculata</i> Sieb.,	FE2765	2001–2004
<i>Viburnum opulus</i> L.	FE2765	2002–2003
<i>Chaenomeles japonica</i> Lindl.	FE2765	1997–1999
<i>Knautia arvensis</i> L.	FE2766	2004–2007
<i>Adonis vernalis</i> L.	FE2833	2004–2005
<i>Aster saggitifolius</i> Willd.	FE2765	2002–2003
<i>Taraxacum officinale</i> L.	FE2773	2004–2006
<i>Chelidonium majus</i> L.	FE3707	2003–2005

The observations of diurnal dynamics of blooming were made during the full bloom stage. In one-hour intervals, all opened flowers were counted and marked in order to exclude a second time counting. For *Hydrangea arborescens* L. subsp. *discolor* (Raf.), *H. paniculata* Sieb., *Viburnum opulus* L., *Chaenomeles japonica* Lindl., the counts were made on marked randomly chosen branches in 4 replications. In the case of the remaining taxons, the counts were made on 1 m² plots. The observations were made during different weather conditions, sunny and dry as well as cloudy with lower temperatures. The morphological differences in flower structure were taken under consideration, and simultaneous observations were made separately for each morph. For taxons with a long period of blooming, the observations were made in the successive months of the blooming period.

The means and standard deviation are given. Flower morphs within species were used as single units and one-way ANOVA was applied and significance of differences between means were analyzed by Duncan's test at $\alpha = 0.05$.

RESULTS AND DISCUSSION

Flower opening can be evaluated in different aspects. The observations of diurnal dynamics of blooming are usually connected with detailed experiments on plants' flow production and make the information on pollen and nectar distribution more complete.

In the course of a 2-4-year study, the character of diurnal dynamics of blooming differed among species. Within species, the time of the day when flowers open depends on flower morphology. Moreover, taxons with a long period of blooming change the diurnal pattern in the vegetation season. With no doubt, the main strategy taxons represent is to attract pollinators at the most effective moment for pollination.

The blooming pattern in morphologically different flowers

The first strategy is to attract pollinators by flowers which lose their sexual function and become sterile. Morphologically different flowers were found on *Hydrangea arborescens* L. subsp. *discolor*

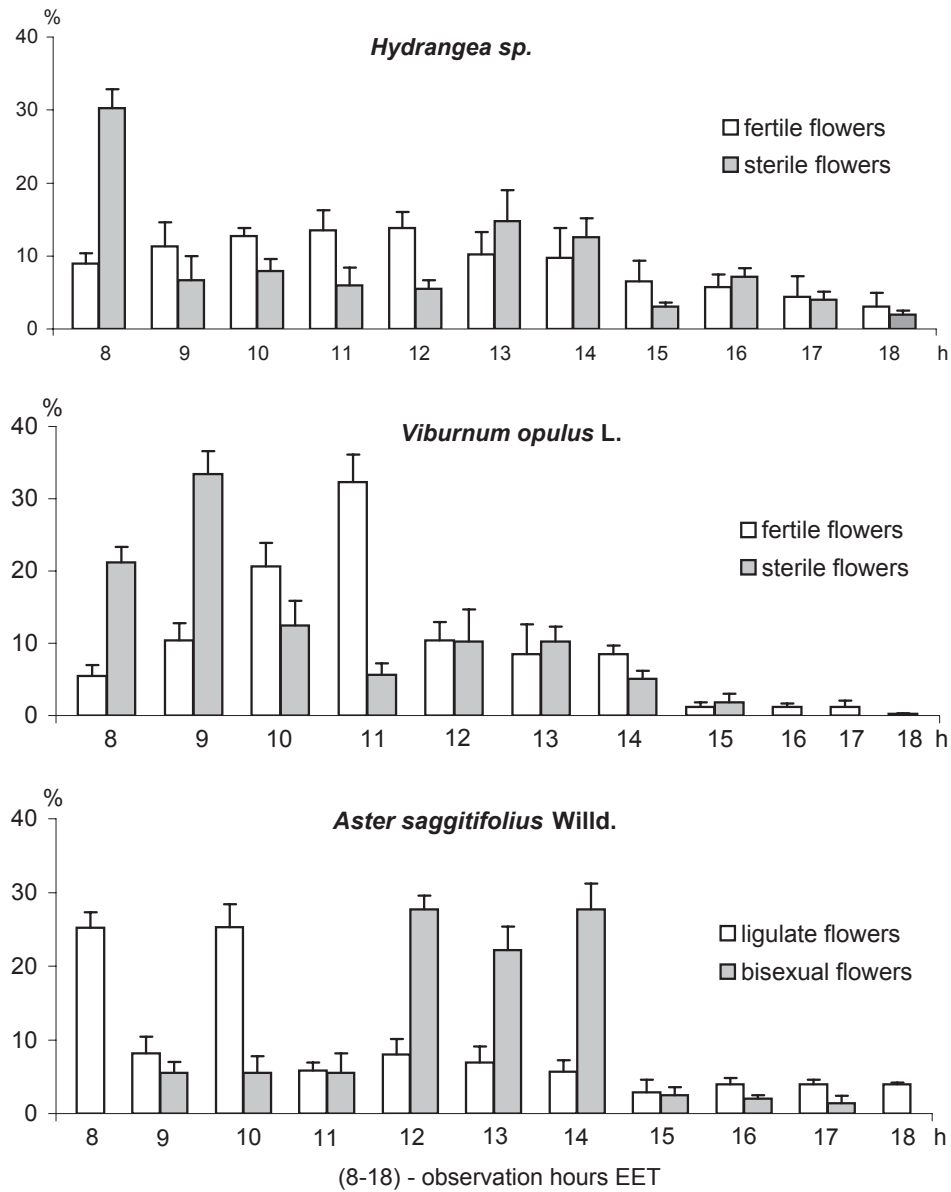


Fig. 1. Diurnal dynamics of blooming of *Hydrangea* sp., *Viburnum opulus* and *Aster sagittifolius* depending on flowers morphology (mean values from the years of study are given). For *Hydrangea* spp. values are means from *H. arborescens* ssp. *discolor* and *H. paniculat*. Vertical bars indicate s.d. around the means. The mean number of flowers at a given hourly period is expressed in % of a total number of flowers bloomed daily.

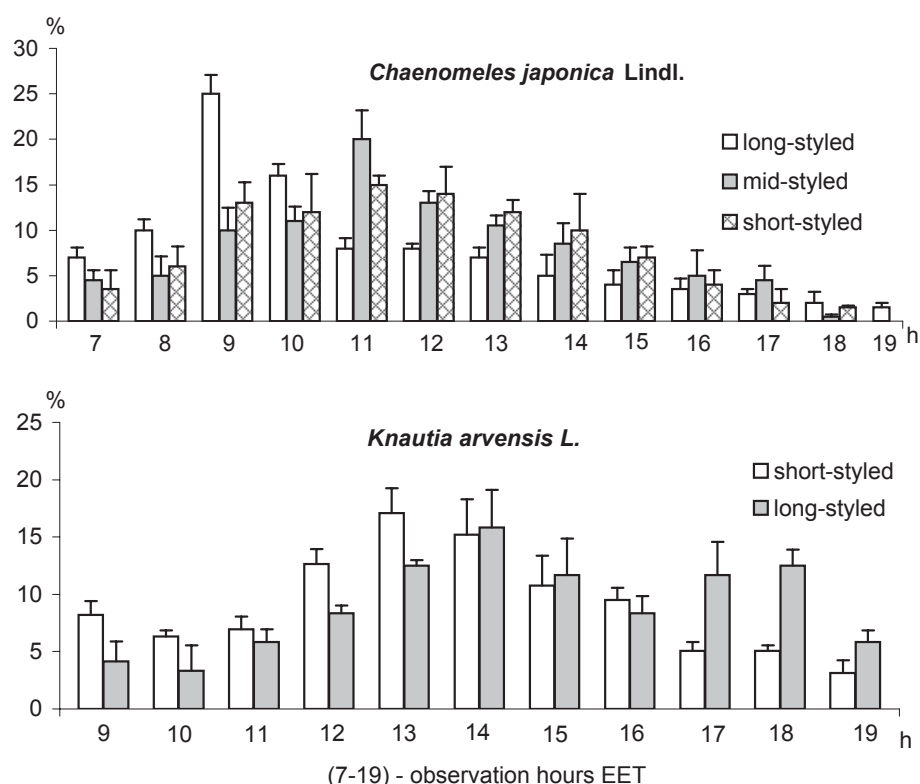


Fig. 2. Influence of heterostyly on diurnal dynamics of blooming of *Chaenomeles japonica* and *Knautia arvensis* (mean values from the years of study are given). Vertical bars indicate s.d. around the means. The mean number of flowers at a given hourly period is expressed in % of a total number of flowers bloomed daily.

(Raf.) McClintock, *H. paniculata* Sieb., *Viburnum opulus* L., and in the highly specialized inflorescence of Asteraceae. If sterile flowers are present they are usually peripheral in inflorescences and the peak of blooming of these sterile flowers is always earlier than it is for fertile ones (Fig. 1). In *Hydrangea* spp. sterile flowers bloom most intensely one hour earlier than bisexual ones and no significant differences were found between species. The peripheral flowers of *Viburnum opulus* develop 2-3 hours earlier than sterile ones. The outer enlarged sterile flowers with the visual function in the capitulum of *Aster saggitifolius* open 2-4 hours earlier than the inner, bisexual florets with the reproductive function. According to Proctor et al. (1996), the function in composites (Asteraceae), apart from luring insects, is associated with gynomonocy.

The different pattern of flower development during the day is associated with heterostyly. The example is *Chaenomeles japonica* Lindl. with tristylous flowers; long-styled, mid-styled and short-styled, as well as *Knautia arvensis* with distyly. Each form represents an alternative rhythm of blooming during the day (Fig. 2). In *Chaenomeles japonica* the process of pollen dehiscence in flowers with short styles and sufficiently developed anthers starts just after perianth

opening. Then, long-style flowers with the receptive stigma are opened. They bloom most intensively 1-2 hours earlier than mid-styled and short-styled flowers. The differences between flower types were significant ($F=5.7$ $df=1$, $P=0.05$ long-styled versus mid-styled; $F=8.2$ $df=1$, $P=0.05$ long-styled versus short-styled).

In general, additional characteristics are associated with different heterostyly morphs. Heterostyly is connected with the position of sexual organs, pollen morphology, number of pollen grains per anther and stigma morphology (Ganders, 1979). Furthermore, there is variation in the degree of secreted nectar in flowers with heterostyly (Denisow, 2002). As assumed by Shore and Barrett (1984), the features of heterostyly are controlled by a supergene: the cluster of tightly linked and co-adapted genes that are inherited as a single unit and carry out related functions. Adaptation has a value with respect to the functioning of the mating system and enforces outcrossing between the morphs and is strictly connected with the relationship of self-incompatibility. Also, the morphological differences cause relative differences in the attractiveness for pollinators and potentially influence the pollination process. Additionally, a different character of flower blooming strengthens the effect of heterostyly.

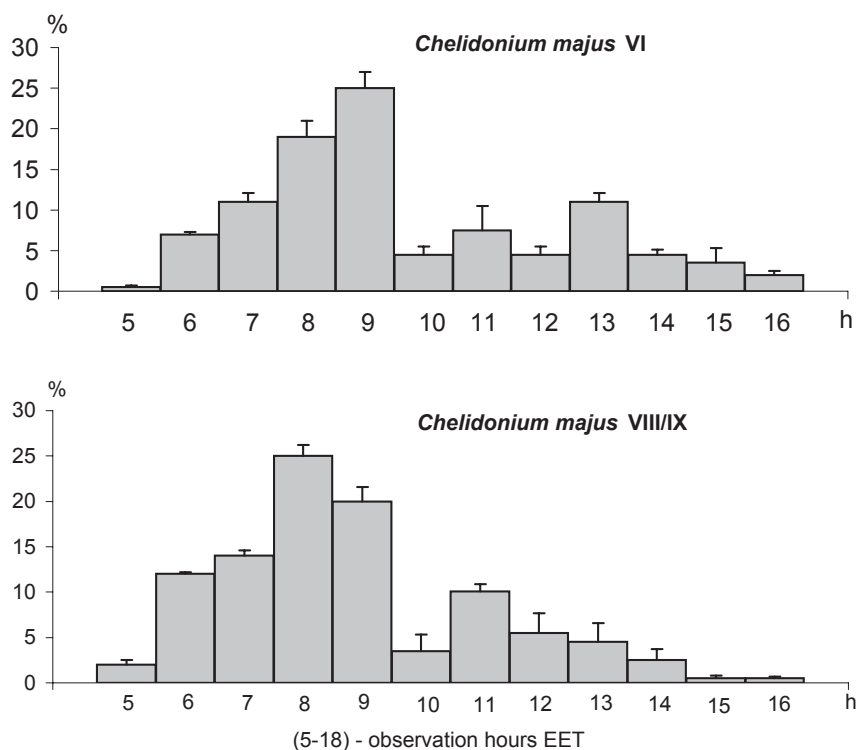


Fig. 3. Diurnal dynamics of *Chelidonium majus* blooming depending on the season (mean values from the years of study are given). Vertical bars indicate s.d. around the means. The mean number of flowers at a given hourly period is expressed in % of a total number of flowers bloomed daily.

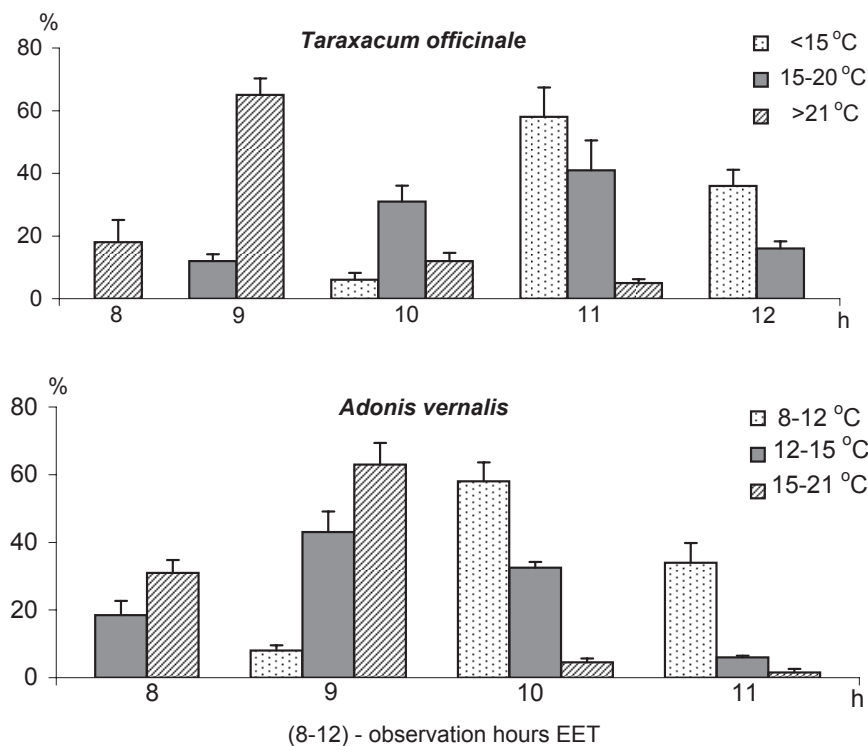


Fig. 4. Diurnal dynamics of blooming of *Taraxacum officinale* and *Adonis vernalis* depending on temperature (mean values from the years of study are given). Vertical bars indicate s.d. around the means. The mean number of flowers at a given hourly period is expressed in % of a total number of flowers bloomed daily.

Seasonal changes in the diurnal pattern of blooming

Another strategy to attract pollinators at the time most suitable for pollination is the harmonization of flower opening with insects' activity during the day and during the period of blooming. The activity of pollinators changes in the course of the season and it is connected with abiotic, mainly meteorological factors (Herrera, 1997).

In the conditions of south-eastern Poland, *Chelidonium majus* L. blooms between May and September (Fig. 3). In spring the peak intensity of diurnal flowering was at 8.00 h when mean day temperature was between 12-24°C and relative humidity 41-65%. In autumn (September), when mean day temperatures were lower (10-20°C) and relative humidity higher (50-80%), they opened an hour later at 9.00. The statistical differences between the spring and autumn pattern were significant ($F=4.5$, $df=1$, $P=0.05$). Such phenomenon was also observed for *Berteroa incana* and *Lamium album* (Denisow, 2004; Denisow and Bożek, 2008). The reaction is associated with the endogenous interaction between day length, temperature and humidity at the moment of anthesis mentioned by Rodkiewicz et al. 1994; van Dorn and van Meeteren 2003.

The mechanism which controls the opening of flowers has a molecular base. Schaffer et al. (2001) found that in *Arabidopsis* the expression of several genes depends on the time of day and is surprisingly similar to the characteristic of the endogenous rhythm of flower opening. Genetic and molecular analyses have revealed distinct but linked pathways that are responsible for detecting the major seasonal cues of day length and cold temperature, as well as other local and environmental signals. The balance of signals from these pathways is integrated by a common set of genes to determine when flowering occurs. Many of these same genes regulate flowering in different species (Putterill et al. 2004). Molecular studies indicate that plants perceive daylength through the degree of coincidence of light with the expression of the gene which encodes a clock-regulated transcription factor that controls the expression of floral-inductive genes in a light-dependent manner (Yanovsky and Kay, 2003).

A different reaction of flowering in relation to changes in relative humidity and temperature was observed in *Taraxacum officinale* and *Adonis vernalis* (Fig. 4). Generally, an increase in relative humidity and temperature decreases results in inflorescence or flower closing.

The capitulum of *Taraxacum officinale* reopened up to 4 times. The higher the temperature, the earlier the time of wilting within this temperature range. Flowers of *Adonis vernalis*, an early blooming perenn-

nial, start to close again when temperature drops below 7°C, even during sunny weather, and usually open flowers prematurely closed their corollas. The flowers reopened up to 3 times and did not open thereafter, even when temperature increased up to 21°C. Finally, they wilted. Flower opening of *Anemone*, *Crocus* and *Tulipa* is also controlled by a temperature rise, as reported by Horowitz et al. (1975), van Dorn and van Meeteren (2003). The physiological mechanism of flower opening and closing in relation to the thermal factor was described by Wood (1953). The physiological changes are rapid and cause a high rate of cell development. The mechanism causes a different growth rate on two sides of the perianth. Optimum temperatures for the growth of mesophyll cells situated in the outer and inner parts of petals are different. Even small environmental temperature changes can cause an unequal growth of both sides of the petals. The reaction in petal movements according to external temperature changes correlate with flower opening. In some plants, the full opening of the flower depends not only on temperature but also on the simultaneous action of other factors. In *Portulaca grandiflora* the opening is controlled by the direct effects of temperature, light and humidity (Kauzo and Suto 1998). With no doubt, flowers that avoid opening at times of low temperature and high humidity avoid wetting by rain or dew and are adapted in a high degree to effective pollination, as during low temperatures and rainy weather pollinators are not active. As assumed by Corbet (1991), temperature evaluation inside flowers creates the 'microgreenhouse' effect caused by radiation transmitted through the corolla. The radiation by petals may be even significant for pollinator visitation, pollen, ovule and seed development. In the species that open in the afternoon or at night, e.g. *Oenothera* spp., the movement is correlated with decreasing temperature and light intensity, and with an increase in humidity (Arnold, 1959).

CONCLUSIONS

1. The diurnal dynamics of blooming differ among species and are modified by different endogenous and exogenous agents; thus all these factors ought to be taken under consideration during observation of blooming.
2. The endogenous determinants of diurnal dynamics of blooming are morphological diversity of flowers (fertility or sterility) within species or heterostyly.
3. The abiotic factors, such as day length and temperature during the vegetation season, influence the change in the process of diurnal dynamics of blooming (e. g. *Taraxacum officinale*, *Chelidonium majus*)

REFERENCES

- Arnold C. G., 1959. Blütenöffnung bei *Oenothera* in Abhängigkeit vom Licht-Dunkelrhythmus. *Planta*, 53: 198-211.
- Ausin I., Alonso-Blanco C., Zapater M., 2005. Environmental regulation of flowering. *Int. J. Dev. Biol.* 49: 689-705.
- Corbet S. A., 1991. Applied pollination ecology. *Trends Ecol. Evol.* 6: 3-4.
- Cresswell J.E. 1994. Secondary pollen presentation: form, function, evolution. *J. Ecol.* 82: 86.
- Cruden R. W., Hermanutz L., Shuttleworth J. 1984. The pollination biology and breeding system of *Monarda fistulosa*. *Oecologia*, 64: 104-110.
- Denisow B., 2002. The blooming and melliferous value of tristylous flowers of Japanese quince (*Chaenomeles japonica* Lindl.). *J. Apic. Sci.* 46 (2): 15-22.
- Denisow 2004. Dynamic of blooming and insects visits on several (Brassicaceae=Cruciferae Juss.) species. *J. Apic. Sci.* 48 (2): 13-21.
- Denisow B., Bożek M., 2008. Blooming and pollen production of two *Lamium* sp. *J. Apic. Sci.* 52 (1): 25-32.
- Faegri K., van der Pijl L., 1979. The principles of pollination ecology. Pergamon Press.
- Ganders R. F. 1979. The biology of heterostyly. *NZ J. Bot.* 17: 607-635.
- Herrera, C. M. 1997. Thermal biology and foraging responses of insect pollinators to the forest floor irradiance mosaic. *Oikos*, 78: 601-611
- Horovitz A., Galil J., Zahory D. 1975. Biological flora of Israel. *Israel J. Bot.* 24: 26-41.
- Jabłoński B., Szklanowska K., 1997. Wpływ niektórych czynników pogody na kwitnienie, nektarowanie, pylenie i oblot przez owady zapylające entomofilnych roślin uprawnych. W: *Biologia kwitnienia, nektarowania i zapylania roślin*. / The influence of some weather factors on blooming, nectar secretion, pollen presentation and pollinators forage on entomophilous crop plants. [In:] *Blooming biology, nectar secretion and plants pollination*. LTN, Lublin.
- Kauzo I., Suto K., 1998. Experimental factors controlling flower opening and close in a *Portulaca* hybrid. *Ann. Bot.* 82: 67-70.
- Klepacz-Baniak J., Czekońska K., 2006. Dzienny rozkład wykorzystywania pyłku kwiatowego przez pszczołę miodną (*Apis mellifera* L.). / Daily distribution of pollen collection by honeybee foragers (*Apis mellifera* L.). *Acta Agrobot.* 59 (1): 271-278.
- Proctor M., Yeo M., Lack A., 1996. The natural history of pollination. Harper Collins Publishers.
- Putterill J., Laurie R., Macknight R., 2004. It's time to flower: the genetic control of flowering time. *Bioessays*, 26 (4): 367-373.
- Rodkiewicz B., Śnieżko R., Fyk B., Niewęgłowska B., Tchurzewska D., 1994. Embriologia Agiospermae – rozwojowa i eksperymentalna. / Developmental and experimental embryology of Agiospermae. Wydawnictwo UMCS, Lublin.
- Shore J. S Barrett S. C. H. 1984. The genetics of distyly and homostyly in *Turnea ulmifolia*. *Heredity*, 55: 167-174.
- Schaffer R., Lagraf J., Accerbi M., Simon V., Larson M., Wisman E., 2001. Microarray analysis of diurnal and circadian-regulated genes in *Arabidopsis*. *The Plant Cell*, 13: 113-123.
- Szafer W., Wojtusiakowa 1969. Kwiaty i zwierzęta – zarys ekologii kwiatów. Polskie Wydawnictwo Naukowe, Warszawa.
- van Dorn W. G. 1997. Effects of pollination on floral attraction and longevity. *J. Exp. Bot.* 48: 1615-1622.
- van Dorn W. G., van Meeteren U., 2003. Flower opening and closure: a review. *J. Exp. Bot.* 54 (389): 1801-1812.
- Wood WML. 1953. Thermonasty in tulip and crocus flowers. *J. Exp. Bot.* 4: 65-77
- Yanovsky M. J., Kay S. A., 2003. Living by the calendar: how plants know when to flower. *Nat. Rev. Mol Cell Biol.* 4 (4): 265-275.
- Zajac A., 1978. Założenia metodyczne „Atlasu rozmieszczenia roślin naczyniowych w Polsce”. / Methodological assumption of Distribution Atlas of Vascular Plants in Poland. *Wiad. Bot.* 22 (3): 145-155

Czynniki modyfikujące dzienny rytm kwitnienia wybranych gatunków roślin

Streszczenie

W pracy analizowano czynniki modyfikujące dzienny rytm kwitnienia kilku gatunków należących do różnych rodzin z klasy dwuliściennych. Uwzględniono *Hydrangea arborescens* L. subsp. *discolor* (Raf.), *H. paniculata* Sieb., *Viburnum opulus* L., *Chaenomeles japonica* Lindl., *Knautia arvensis* L., *Adonis vernalis* L., *Aster sagittifolius* Willd, *Taraxacum officinale* L., *Chelidonium majus* L. rosnące na terenie Lublina (51°08' – 51°18' N oraz 21°27' – 21°41' E). Badania prowadzono w latach 2001–2007, a każdy z taksonów obserwowano przez co najmniej dwa sezony wegetacyjne. Obserwacje dziennej dynamiki kwitnienia wykonywano notując w odstępach jednogodzinnych wszystkie rozkwitłe pąki. Okazało się, że w obrębie jednego gatunku sposób rozkwitania kwiatów w ciągu dnia uwarunkowany jest wieloma czynnikami. Gatunki, które posiadają kwiaty morfologicznie zróżnicowane, wykazują odrębny rytm dobowego kwitnienia każdej z postaci. Sposób kwitnienia wspomaga systemy reprodukcyjne gatunków oraz mechanizmy przeciwdziałające samopylności np. heterostylię (*Chaenomeles japonica*, *Knautia arvensis*). Długość dnia znacznie modyfikuje przebieg dobowego kwitnienia w okresie sezonu wegetacyjnego w przypadku *Taraxacum officinale* oraz *Chelidonium majus*.