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RESEARCH ARTICLE

Traits of the pollination process in *Gladiolus imbricatus* and *Iris sibirica* (*Iridaceae*)

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Abstract. Results of a study of self-pollination in two of Ukrainian flora's threatened species, *Gladiolus imbricatus* and *Iris sibirica* (*Iridaceae*), are presented. To confirm or refute the occurrence of self-pollination in *G. imbricatus* and *I. sibirica*, an experiment was conducted on pollen germination on their stigmas. It has been found that in *G. imbricatus* pollination with autogenous pollen grains on the last day of flowering leads to the growth of pollen tubes in the cases of both hand and natural pollination. However, pollen grains on the stigma of an isolated *I. sibirica* flower were not detected on the first or last day of flowering, which means the absence of a mechanism of autonomous pollen transfer within the meranthium. Ungerminated pollen grains were also found on the stigma after autogenous hand pollination. It has been experimentally confirmed that in the absence of pollinators at the end of the flowering phase in *G. imbricatus*, as well as in some other members of the genus, self-pollination and self-fertilization are possible, which contribute to the well-being of populations and species. With regard to *I. sibirica,* it has been found that the autogamous self-incompatibility inherent in this species prevents inbreeding, maintaining heterozygosity in plant populations, allowing plants' better adaptation to different environmental conditions.

Keywords: *Gladiolus imbricatus*, *Iris sibirica*, pollen grains, pollen tubes, pollination, self-incompatibility, self-pollination, threatened species

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Introduction

The pollination process is the subject of a number of disciplines, such as botany, ecology, zoology, horticulture and agriculture. The study of pollination processes, in particular the ability to self-pollinate in the family *Iridaceae* Juss., is of great interest to researchers and these processes are best studied in members of the family from South Africa, which is the center of diversity of genera and species of *Iridaceae* (Tzvelev, 1979; Goldblatt, Manning, 2021). Wragg and Johnson (2009) confirmed the presence of self-pollination in one of the members of the genus *Gladiolus* from South Africa, *Gladiolus inandensis* Baker. Besides, the authors draw attention to the fact that much shorter pollen tubes and a small number of fruits are formed in this species after self-pollination.

It is also known that some North American *Iris* species have the ability to self-pollinate: *Iris douglasiana* Herb. (Uno, 1979), *I. lacustris* Nutt. (Planisek, 1983), *I. versicolor* L. (Kron et al., 1993; Zink, Wheelwright, 1997), and *I. cristata* Aiton (Hannan, Orick, 2000). Most Mediterranean species of the genus *Iris* are characterized by self-incompatibility (Tucić et al., 1989; Arafeh et al., 2002; Sapir et al., 2006; Imbert et al., 2014; Pellegrino, 2015). Among them, *Iris pumila* L., a Mediterranean species present in the Ukrainian flora, is also known to be self-incompatible (Tucić et al., 1989). However, for most of the irises present in the flora of Ukraine, the ability and mechanisms of self-pollination remain unknown.

The flora of Ukraine contains ca. 35 species and subspecies of the family *Iridaceae* (Mosyakin, Fedoronchuk, 1999), among them there are five species of *Gladiolus* and 14 species and two subspecies of

Iris. To study the pollination processes, one member from each of these two genera was selected: vulnerable species, according to the *Red Data Book of Ukraine* (Red…, 2009), *Gladiolus imbricatus* L. and *Iris sibirica* L.

The range of *Gladiolus imbricatus* is quite wide; it covers Central and Eastern Europe, the Balkans, the Mediterranean region, Turkey, the Caucasus, and Western Siberia (POWO, 2022; Meusel et al., 1965). Its typical habitats are wet well-drained meadows on rich soils. The species is protected and listed, mostly as Vulnerable, in Red books and Red lists in several European countries: Belarus (Semerenko, Morozova, 2005), the Czech Republic (Pladias…, 2021), Estonia and Latvia (Kose et al., 2019; Red…, 1995), Moldova (Postolache, 2015), France, Hungary, and Switzerland (Kostrakiewicz-Gierałt et al., 2018).

Iris sibirica is native to Europe and parts of Asia; it occurs on wet meadows in France, in the north of Italy, in Switzerland, Austria, the Czech Republic, Slovakia, Germany, Hungary, Poland, Romania, Bulgaria, the countries of former Yugoslavia, in the north of Turkey, in Belarus, Estonia, Latvia, Lithuania, Moldova, Ukraine, the European part of the Russian Federation, Armenia, Azerbaijan, northwestern Kazakhstan, and the southwest of Western Siberia (Doronkin, 1987; Tzvelev, 1979; Webb, 1980).

The conservation status of *I. sibirica* differs in various parts of its range. In Switzerland and Croatia, the species is considered in the IUCN category Vulnerable (VU) (Moser et al., 2002; Nikoli, Topi, 2005). In countries neighboring Ukraine, in particular, in Poland and Slovakia, the species is also considered to be Vulnerable (VU) (Mitka et al., 2008; Turis et al., 2014), in Belarus − Potentially Vulnerable (category IV) (Morozova, 2005), in Hungary − Endangered (EN) (Takács et al., 2015), in Lithuania and Latvia − Vulnerable (VU) (Red…, 1995; Patalauskaitė, 2021). *Iris sibirica* is also listed in the *IUCN Red List* with the category Near Threatened (NT) within its whole geographic range (Khela, 2013).

For species of the genus *Gladiolus*, the possibility of self-pollination on the last day of flowering is known. However, there is no such data for taxa of the genus *Iris* (Tzvelev, 1979). According to other published data (Goldblatt et al., 2001; Goldblatt, Manning, 2006), the species of both genera (*Gladiolus* and *Iris*), are characterized by physiological incompatibility; therefore, the effectiveness of indiogenous pollination (autogamy and geitonogamy) requires a special study to determine its significance in the reproductive processes.

From previously obtained data it is known that the main pollinator in both species is the honey bee *Apis mellifera* Linnaeus (Odintsova, Skrypec, 2014; Skrypec, 2020).

It also turned out that both species have certain morphological adaptations to self-pollination: the stamens and receptacles became closer to each other on the last day of flowering in *Gladiolus imbricatus* (Skrypec, Odintsova, 2014), and stigmas curl down and sometimes contact the anthers with the beginning of flower wilting in *I. sibirica* (Odintsova, Skrypec, 2014), just as it was observed by Kron with co-authors in *I. versicolor* (Kron et al., 1993).

The objective of further research was to determine experimentally the ability of autogenous and xenogenous pollen of these species to germinate in the receptable stigma at different times during the flowering period. This will help to clarify the question of the occurrence and effectiveness of different types of pollination in the species under study.

Material and Methods

The study of the germination of pollen grains on stigma was carried out according to the method proposed for *Amborella trichopoda* Baill. (Williams, 2009), modified for *G. imbricatus* and *I. sibirica* at the Botanical Garden of Ivan Franko National University of Lviv. The experiment was performed based on previously obtained data, which revealed the period and mechanisms of flowering. In particular, it was revealed that the flowering of *G. imbricatus* lasts four days, and that of *I. sibirica*, only two days (Odintsova, Skrypec, 2014, Skrypec, Odintsova, 2014). The research was conducted on 20 flowers from 20 individuals in sunny weather. The flowers were marked at the budding stage for both species in model populations: *G. imbricatus* − from village Kostryno, Zakarpattia (Transcapathian) Region, Uzhansky National Nature Park, *I. sibirica* − from village Naditychi, Lviv Region, Botanical Reservation of National Importance "Valley of Irises". Before opening, the flowers were isolated with a plastic mesh cover. Anthers in each experimental flower were excised. When the flower opened, it was hand pollinated with autogenous (own pollen) and xenogenous (cross pollen) on the first and last day of flowering. Transfer of pollen to the receptive stigma (in the evening of the first day of flowering) was carried out with a needle from the anthers of the studied flower in autogamy, and from the flowers of another individual – in xenogeny. After pollination of the flowers, the stigmas were cut off at different time intervals determined experimentally: after 5, 15, and 30 minutes, 1 hour, 3, 6, 12, and 24 hours, and fixed for 24 hours in acetic alcohol (3 : 1), then stored in 70% ethanol. The prepared stigmas were stained with 0.1% methylene blue and examined under a light microscope.

To study natural pollination, we took two types of flowers: the first – not isolated emasculated flowers, and the second – isolated flowers with anthers. After 6 hours their stigmas were fixed, stained and examined under a light microscope just as in the case with hand pollination. The length of the pollen tubes was measured using a Bresser PC-eyepiece VGA 640x480. Statistical data processing was performed using Microsoft Excel 2010.

Results

When pollinating flowers with autogenous pollen on the first day of flowering, we did not find germinated pollen grains on the stigmas during the entire study period (from five minutes to 24 hours) in both species (Figure 1A, D, Table 1).

In pollinated with xenogenous pollen on the first day of flowering we observed the initial germination of pollen and the appearance of single short pollen tubes 30 minutes after pollination in *G. imbricatus* (Table 2, Figure 1B). In *I. sibirica*, the germination of xenogenous pollen was observed only three hours after pollination (Table 2, Figure 1E).

A similar study was conducted on the last day of both species' flowering. *G. imbricatus* flowers were pollinated with autogenous pollen on the third day of flowering (in the afternoon) and a large number of germinated pollen grains with long pollen tubes were observed after 6 hours (Fig. 1C).

Iris sibirica flowers were pollinated by autogenous pollen (before the noon) on the second day (the last day) of flowering, and ungerminated pollen grains without germinated pollen tubes were observed 6 hours after the pollination (Fig. 1F).

In the second part of the experiment, the study of pollen germination after natural pollination in emasculated and intact flowers, in which geitonogamy was prevented in various ways, was carried out. On the first day of flowering in non-isolated emasculated flowers, pollen grains were observed on the stigmas in both species, indicating the receptive state of the stigmas.

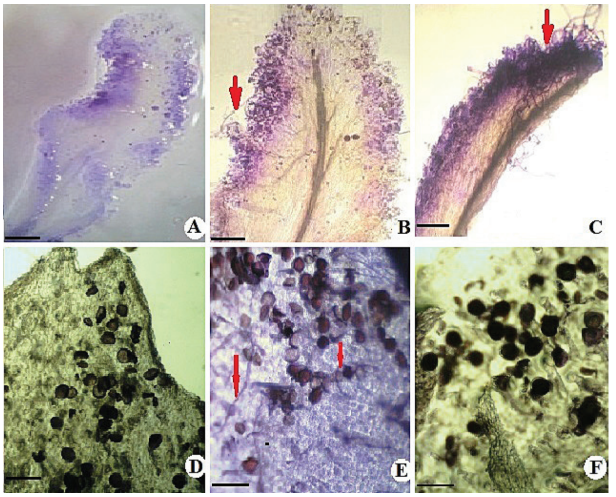

Fig. 1. Germination of pollen grains on the *Gladiolus imbricatus* (A, B, C) and *Iris sibirica* (D, E, F) stigma: autogenous pollen on the first day (A: *G. imbricatus*; D: *I. sibirica*), xenogenous pollen on the first day (B: *G. imbricatus*; E: *I. sibirica*), autogenous pollen on the last day of flowering (C: *G. imbricatus*; F: *I. sibirica*) (pollen tubes are marked with red arrows). Ruler of 100 microns

On the last day of flowering, a large amount of pollen with long pollen tubes was found on the stigmas. Therefore, it can be recognized that during the flowering period the flowers of the studied species are intensively visited by insects, which provide natural xenogenic pollination by entomophily.

On the first day of flowering no pollen grains were found on the stigmas of *G. imbricatus* isolated flowers with intact anthers, which mean the absence of self-pollination. However, on the last day of flowering, germinated pollen grains with long pollen tubes were detected at the *G. imbricatus* stigmas, confirming the species' ability to self-pollinate within the flower (autogamy) by anthers' and stigmas' contacts at the end of flowering. It occurs when the column elongates and leans toward the anthers, causing the style to be placed between the anthers. The anther sacs open completely and the pollen grains fall on the receiving surface of the stigma.

Pollens on the stigma of an isolated flower of *I. sibirica* were not detected on the first or last day of flowering, which means the absence of a mechanism of natural self-pollination (Table 1). After 24 h in artificial pollination the pollen tubes on the receiver of *G. imbricatus* are on average 480 μm long, i.e. slightly less than the length of the pollen tubes of *I. sibirica*, which reaches 568 μm.

Table 1. **Germination of pollen grains on the stigmas of *Gladiolus imbricatus* and *Iris sibirica***

Pollination conditions	*G. imbricatus*	*I. sibirica*
Hand pollination		
Pollination by autogenous pollen on the first day of flowering	−	−
Pollination by xenogenous pollen on the first day of flowering	+	+
Pollination by autogenous pollen on the last day of flowering	+	−
Natural pollination		
Autogenous pollen (isolated flowers with anthers), the first day of flowering	−	−
Xenogenous pollen (not isolated emasculated flowers), the first day / last day of flowering	+/+	+/+
Autogenous pollen (isolated flowers with anthers), the last day of flowering	+	−

(+) − the presence of germinated pollen grains on the stigma; (−) − no germinated pollen grains on the stigma.

Table 2. **The length of pollen tubes on the stigma after hand pollination of *Gladiolus imbricatus* and *Iris sibirica***

Interval from the beginning of pollination	Length of pollen tubes, μ	
	G. imbricatus	*I. sibirica*
	Average value	Average value
30 minutes	18 ±0,01	−
1 hour	44±0,02	−
3 hours	88±0,1	14±0,01
6 hours	176±0,01	100±0,04
12 hours	360±0,01	352±0,2
24 hours	480±0,01	568±0,05

Discussion

The mechanism of *G. imbricatus* flowering was described in detail in an earlier publication (Skrypec, Odintsova, 2014). It was noted that at the beginning of *G. imbricatus* flowering the herkogamy (spatial separation of stamens and stigma) is observed, but at the end of flowering it disappears and there is a convergence of anthers and stigmas (Skrypec, Odintsova, 2014; Scrypec et al., 2020). This indicates that self-pollination is inherent in *G. imbricatus* at the end of the flowering period. As a result of an experiment on pollen germination at the stigma, we found that pollination with autogenous pollen on the last day of flowering leads to the growth of pollen tubes in hand and natural pollination, which confirms the ability of *G. imbricatus* to self-pollinate within the flower (with autogenous pollen).

The flower of *I. sibirica* consists of three separate zygomorphic two-lipped units, meranthia (singular: meranthium). According to Burova (1970), *I. sibirica* in bad weather is capable of self-pollination within a meranthium, but in our studies, contact self-pollination did not occur even in rainy weather, because the anthers and the stigma have never been in contact. Troitsky (1948) also argued that *I. sibirica* flowers still have an adaptation to self-pollination. To confirm or deny the existence of this phenomenon, we performed an experiment and observed that autogenous pollens on the stigma of an isolated *I. sibirica* flower were not detected on the first or last day of flowering, which means that there is no mechanism of autonomous pollen transfer within a meranthium. Ungerminated pollen were also found on the stigma after hand autogenous pollination, which indicates sporophytic self-incompatibility. In addition, *I. sibirica* has a clonal population structure, and this leads to an increase in the frequency of inbreeding, which may be one of the reasons for the decrease in the adaptability of this species. Our data on the self-incompatibility of *I. sibirica* are consistent with those of Szőllősi et al. (2011).

Conclusions

The experiment confirmed that the herkogamy in *G. imbricatus* disappears at the last phase of flowering, and self-pollination (contact autogamy) happens.

Sporophytic self-incompatibility, which prevents fertilization after successful pollen transfer within the flower, individual and clone, has been experimentally confirmed for *I. sibirica*.

When hand pollinated with xenogenous pollen on the first day of flowering, pollen tubes germinate in 30 minutes in *G. imbricatus*, and after three hours in *I. sibirica*.

Since the members of the genera *Gladiolus* and *Iris*, including *G. imbricatus* and *I. sibirica,* are highly ornamental and are widely used in floriculture (Goldblatt, Manning, 1998; Komarnicki, 2016), the data presented on the specifics of pollination in both species can be important for using in selecting new breeds or improvement of known cultivated varieties, and for development of measures for protection of these useful very ornamental and endangered species of the Ukrainian flora.

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Скрипець Х., Тасєнкевич Л. 2022. **Особливості процесу запилення *Gladiolus imbricatus* та *Iris sibirica* (*Iridaceae*)**. *Український ботанічний журнал*, 79(6): 381–387 [In English].

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Реферат. У роботі наведено результати дослідження самозапилення двох видів флори України – *Gladiolus imbricatus* та *Iris sibirica* (*Iridaceae*). Щоб підтвердити або спростувати наявність самозапилення у *G. imbricatus* та *I. sibirica*, було проведено експеримент із пророщування пилку на приймочці. Встановлено, що у *G. imbricatus* запилення автогенним пилком в останній день цвітіння призводить до проростання пилкових трубочок як при ручному, так і природному запиленні. Проте пилку на приймочці ізольованої квітки *I. sibirica* не виявлено ні в перший, ні в останній день цвітіння, що означає відсутність механізму автономного перенесення пилку в межах мерантію. Непророслий пилок також був виявлений на приймочці після ручного автогенного запилення. Експериментально підтверджено, що за відсутності запилювачів наприкінці фази цвітіння у *G. imbricatus*, як і у деяких інших представників роду, можливе самозапилення та самозапліднення, що сприяє підтриманню життєвості популяції та виду. Стосовно *I. sibirica* було виявлено, що притаманна для цього виду автогамна самонесумісність перешкоджає інбридингу, підтримуючи гетерозиготність у популяціях рослин, що дозволяє рослинам краще адаптуватися до різних умов середовища.

Ключові слова: вразливі види, самозапилення, самонесумісність, пилкові зерна, пилкові трубки