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INVITED ORIGINAL RESEARCH PAPER

Breeding system variability, pollination biology, and reproductive success of rare *Polemonium caeruleum* L. in NE Poland

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Abstract
Polemonium caeruleum (Polemoniaceae) represents a very interesting system of compatibility transition. Studies of its biological and ecological properties in the context of the breeding system of various populations may help to understand the evolutionary mechanism of this process. We investigated some aspects of the breeding system, diversity and foraging behavior of the visitors, and relationship between population properties and fruit set in three populations from NE Poland. We found distinct compatibility systems in two studied populations and showed that if a population is self-compatible (SC), selfing is mediated by insects via geitonogamous pollen transfer. Despite the population properties (compatibility, visitor diversity and activity, population size, density, or floral display), *P. caeruleum* is not pollen limited and pollinators are highly important as a key factor determining the high reproductive success. Visitor assemblages (including key pollinators, bumblebees, and honey bees) and their foraging behavior on inflorescences vary between the populations, which may influence differences in the breeding system. The self-incompatible population was visited by a more diverse group of insects from Hymenoptera, Diptera, Lepidoptera, Heteroptera, and Coeloptera, which may favor effective cross-pollen transfer, whereas the SC population was pollinated mainly by *Apis mellifera*, which may promote mixed-mating. Studies on a wider range of *P. caeruleum* populations are needed to determine selective factors responsible for compatibility transition.

Keywords
compatibility system; fruit set; hand-pollination; seed set; visitation rate

Introduction

Recent studies have shown that the majority of angiosperms suffer from pollen limitation [1–3] and most of them are self-compatible (SC), which enables selfing and protects against pollinator deficiency [4–6]. Selfing may act autonomously, when flowers are structurally adapted to pollen transfer on their own stigma, or when pollinators as pollen vectors transfer pollen within the same flower or inflorescence [7,8]. On the other hand, because selfing progeny usually suffers strongly from inbreeding depression, plants may protect themselves against excessive share of selfing in the overall breeding system. These adaptations are connected with the spatial and temporal separation of male and female structures within the flower and inflorescence [9] or with modification of pollinators' behavior due to, e.g., floral display or deception [10–13]. Complete protection from selfing is guaranteed only by the self-incompatible system

(SI). In effect, self-compatible plants are distinguished by higher reproductive success and lower quality of offspring than self-incompatible species [5,11].

As autonomous selfing results only from physiological, anatomical, and morphological flower adaptations, facilitated selfing is also strongly dependent on pollinators' foraging behavior. Specific groups of pollinators exhibit different activity within and among the shoots of particular plant species. This, in different ways, may promote only crossing, only selfing, or both (mixed-mating). As the appropriate pollinators' assemblages are strictly connected with the availability of suitable habitats [14,15], their service for plants resulting in reproductive success is modified by plant population properties. Pollinator visitation rates, time spent on the plant, number of flowers and individuals visited during a single bout may vary depending on the size of the plant population, density, and spatial pattern of flowering shoots [11,16–18].

Among plants, this is a very rare phenomenon where various populations of the same species exhibit SC or SI [5]. This interesting system is observed in the genus *Polemonium*, belonging to Polemoniaceae. For example, in self-incompatible *Polemonium foliosissimum* [19] self-compatible populations have been suggested [20]. Recent studies also indicate SC–SI transition in *Polemonium caeruleum* populations [21,22], which are differentiated in size, density, population structure, and can occupy both natural and anthropogenic habitats. Flowers of this species are protected against autonomous selfing by the temporal separation of male and female phases due to protandry [20,21]. Dichogamous protection is not complete, however, as a few hours of overlap between both sexual phases were detected [22]. Additionally, *P. caeruleum* inflorescence is composed of many simultaneously open flowers, being at the same time under the male- or female-stage [22]. This facilitates mixed-mating in SC populations, especially since key pollinators are social bees whose foraging behavior on the inflorescence promotes crossing, geitonogamy, and facilitated autogamy [20,22,23]. Understanding the relationship between the demographic properties of *P. caeruleum* populations, pollinator abundance, and reproductive success in the context of SC–SI transition of these populations is currently the subject of intensive investigations. In the present study, we examined three populations of *P. caeruleum* located in NE Poland, in which we attempted to determine: (***i***) their compatibility system, (***ii***) visitor diversity and activity within inflorescences, (***iii***) the relationship between population properties and fruit set.

Material and methods

Study species

Polemonium caeruleum L. (Polemoniaceae) is a herbaceous perennial plant, with amphi-Atlantic distribution, found throughout Central and Northern Europe and in the Alps [24]. It prefers moist habitats, e.g., damp meadows, which are often under agricultural activities. The blue campanulate flowers are produced in a corymbose inflorescence, which develops gradually from the beginning of June to the middle of July. Flowers are protandrous and the anthers open first, then after a few days the 3-lobed stigma open, but these two stages slightly overlap [21,22]. Flowers produce nectar rich in sugar, which is secreted and stored by the ring-shaped nectary located at the base of the ovary [25,26]. Pollinators are mainly bumblebees and honeybees, although the list of potential pollinators of *P. caeruleum* might be more abundant [20–22,25]. Pollinators are very important in the reproduction of this species as it reproduces exclusively by seeds [21]. *Polemonium caeruleum* is a rare species, and has been entered in the red data lists of plants in some European countries [27,28]. In Poland, after the last regulation it is under strict protection (Dz. U. 2014, item 1409).

Study populations

We investigated three *P. caeruleum* populations which are situated in northeastern Poland and differ with respect to habitat. Two of them, Oparzelisko (OP) and Kopciowe

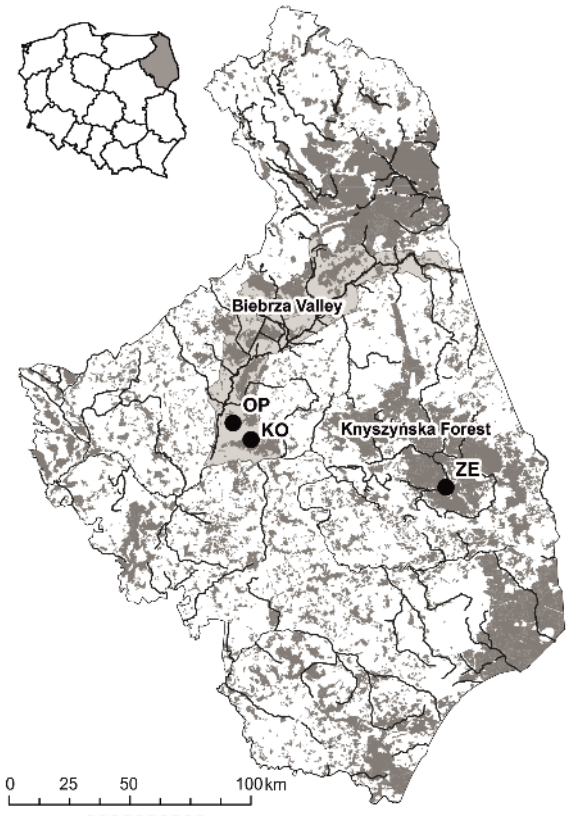

Fig. 1 Distribution of three investigated populations of *Polemonium caeruleum* in northeastern Poland.

(KO), occurred in a small clearing among deciduous forests on the mineral islands distributed throughout the wetlands of the Biebrza valley. The third population, Żednia (ZE), is located on a wet open meadow in the complex of the Knyszyńska Forest (Fig. 1, Tab. 1).

Pollination experiments

In 2013, we conducted hand pollinations to describe the potential of the breeding system of *P. caeruleum*. We randomly marked 70 flower buds in each population and bagged them to one of the assigned following treatments: (***i***) flower buds untreated and bagged in a nylon mesh bag to determine the probability of spontaneous autogamy or agamospermy, (***ii***) induced geitonogamy – emasculated and bagged flowers were pollinated by hand using pollen from other flowers on the same plant to evaluate the level of self-compatibility (SC), (***iii***) supplemental outcross – open flowers were additionally cross-pollinated with pollen collected from another plant, about 10 m away from the recipient plant to investigate pollen limitation, (***iv***) controlled pollination – flowers emasculated and open-pollinated to demonstrate pollinator importance. Fruit sets obtained from particular treatments were collected in July. In the laboratory, we counted the number of seeds in each capsule. For particular treatments, we calculated the percentage fruit set and mean seed set per fruit.

Tab. 1 The properties of three investigated *Polemonium caerulemu* populations.

Population	Code	Type of plant community	Area (m^2)	N_F	$N_{F/C}$ (*SD*)	K_D (*SD*)	H_F (*SD*)	F_N (*SD*)	F_R (%) (*SD*)
Oparzelisko	OP	Small clearing among deciduous forest with *Rhamnus cathartica* thickets (<1 m) with domination of *Galium mollugo*, *Convalaria majalis*, and *Dactylis glomerata* in undergrowth	~700	~1000	3.6 (±2.2)	4.3 (±4.5)	94.9 (±19.0)	71.0 (±46.0)	83.2 (±15.7)
Kopciowe	KO	Small clearing among deciduous forest with *Rhamnus cathartica* thickets (<1 m) with domination of *Thelypteris palustris*, *Geum urbanum*, and *Filipendula ulmaria* in undergrowth	~150	~350	4.0 (±2.2)	3.1 (±4.6)	90.6 (±17.6)	40.1 (±22.2)	86.6 (±19.1)
Żednia	ZE	Open *Molinia* meadow with domination of *Urtica dioica*, *Lythrum salicaria*, and *Phleum pretense*	~1200	~1000	-	-	-	-	-

N_F – number of flowering shoots in population; $N_{F/C}$ – mean number of flowering shoots in clumps; K_D – kernel density estimator for flowering shoots; H_F – average height of flowering shoots; F_N – average number of flowers per shoot; F_R – frequency of flowers that developed into fruits (natural fruiting); "-" – lack of data.

Insect visitor observations

Observations of insect activities were conducted in two populations, KO and ZE, during the peak of flowering in 2016. It was conducted periodically, 1–2 times every 2 weeks on sunny days. For each observation, we randomly chose flowering plants with from one to a few shoots. Insect activities were then recorded for 15 min in 30 min intervals (max six recordings per day). The recordings were then analyzed in the laboratory for the number and duration of insect visits on the inflorescence and the number of switches performed by a single insect among flowers within a particular inflorescence. Visitors were then taxonomically grouped. For each group we calculated average visitation frequency (V) as the number of visits per flower per time unit (h), average visit duration per inflorescence per second (T_{inf}), and average number of flowers visited during a single bout (N_f).

Population structure, floral display, and reproductive success

In 2013, in all populations we assessed the number of flowering shoots (N_F). Additionally, in the KO and the ZE populations we randomly chose and established permanent plots of about 50 m^2, on which all *P. caeruleum* clumps composed of flowering shoots and single flowering shoots were marked. All *P. caeruleum* flowering occurrences mapped in the field were digitized to a vector file under the PUWG 1992 projection. Then, the density of shoots was calculated with a kernel density tool (Spatial Analyst), ArcGIS 10.0 (ESRI 2011) [29]. Kernel density estimators (K_D) for each population as well as for each flowering unit (clump of flowering shoots or single flowering shoots) were extracted from the obtained raster file. Also, in ArcGIS, for every clump or single shoot, we measured the distance to the other closest flowering unit and the mean distance to all flowering units in the population. All these measures were used to describe the population's spatial structure and to assess the floral display in the populations. Secondly, we used the marked flowering shoots to calculate the individual floral display, measured by the height of shoots (H_F) and the number of flowers per inflorescence (F_N). We considered the reproductive success in study populations by assessing the fruiting ratio (F_R).

Subsequently, the analyses of variance (ANOVA) and *t* test were performed to consider differences in floral display (measured by H_F and F_N) and reproductive success (measured by F_R) among populations. Then, to analyze the relationship between floral display (H_F, F_N, $N_{F/C}$), flowering shoot density (K_D; minimal and mean distance between flowering shoots), and fruiting ratio, we used the Spearman or Pearson correlations (according to data distribution). All analyses were made using Statistica 10 [30].

Results

Pollination experiments

The fruit set obtained from covered and untreated flowers was noted only in population KO (17.6%), and average seed production per fruit was 7.8 ±6.8 (Fig. 2). We did not receive any results from induced geitonogamy in population OP due to plants being damaged by herbivores. In the remaining two populations, geitonogamous fruits were recorded only in the ZE population at the level of 38.5% and 4.8 ±3.9 average seed number per capsule (Fig. 2). High levels of fruiting from both supplemental outcross and controlled pollination were recorded in each population. The fruit set from supplemental pollination varied from 76.5% in ZE to 84.2% in KO. The highest number of seeds was noted in the supplemental pollination in OP (9.1 ±9.5), whereas in the remaining two populations it was at a similar level (7.4 ±5.3 in KO and 7.2 ±3.1 in ZE; Fig. 2). The highest fruit sets after controlled pollination, reaching 100%, were recorded in KO and ZE, and the lowest value of 63.2% was obtained in OP. The average seed number set after controlled pollination was highest in the

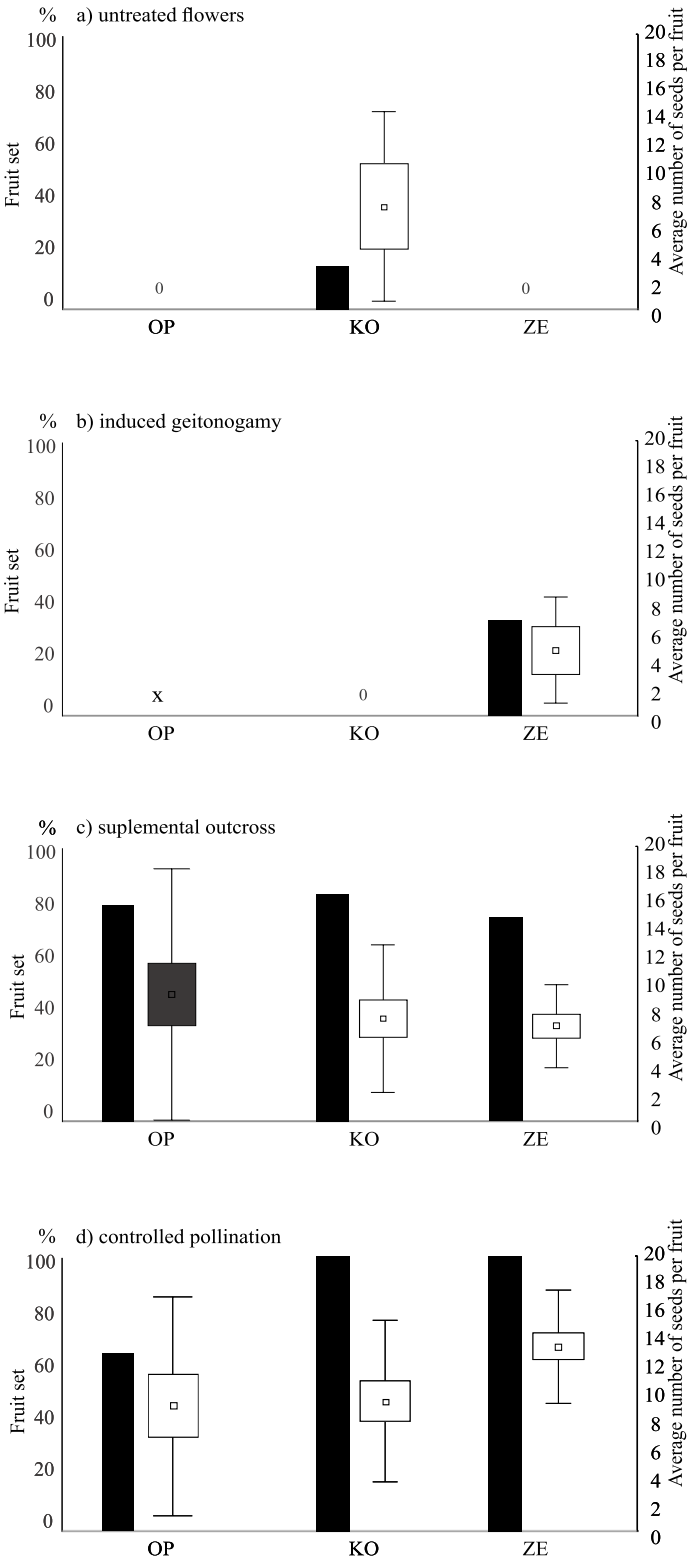

Fig. 2 Fruit set (bar graphs) and average seed set (±*SD*) (box graphs) in *Polemonium caeruleum* plants from three populations, subjected to four experimental pollination treatments (**a–d**).

ZE population (13.7 ±3.9), whereas in KO and OP it was at a similar level, i.e., 9.8 ±5.9 and 9.4 ±7.7, respectively (Fig. 2). In the particular populations, we detected no significant differences in fruit set between supplemental outcross and controlled pollination (Fisher's exact probability test, $p > 0.05$) and no significant differences in seed number obtained from both treatments in the OP and KO populations. Only in the ZE population, the mean seed number in controlled pollination was twice as high as that of supplementation (Kruskal–Wallis ANOVA, $H_{1,\ N=31} = 14.1$, $p < 0.001$).

Insect visitor observations

Substantial differences in insect visitation, namely in the number of insect taxonomic groups and their performance, were noted between the two study populations (Tab. 2, Fig. 3). In the KO population, 81.8% of open flowers were visited by insects, whereas in the ZE population it was significantly lower (59.7% of open flowers; Fisher's exact probability test, $\chi^2 = 3.88$, $p < 0.05$). The per-flower visitation rate (V) varied from 0.0 ±0.04 to 0.8 ±1.4 in KO and from 0.0 ±0.1 to 1.7 ±2.0 in the ZE population. In the KO population, honeybees and bumblebees had the same proportion: 12.1% of all recorded visits (Tab. 2, Fig. 3). However, honeybees in this population spent 35.9 ±35.1 s per inflorescence, and during this time visited 3.9 ±2.0 flowers. Bumblebee visits were much shorter, lasting 7.7 ±7.5 s, during which they visited 2.1 ±1.7 flowers (Tab. 2). The main group of insects visiting *P. caeruleum* in the KO population comprised other Hymenopteras, which accounted for 43.1% and contained mainly unmarked small sawflies. Additionally, we included in this group representatives of Ichneumonidae and Megachilidae families, presumably from the *Stelis* and *Megachile* genera. Moreover, we noticed in the KO population visits of butterflies, flies as well as beetles (Tab. 2, Fig. 3). In the ZE population, the most frequent insect visitors were honeybees, which accounted for 92.3% of all visits, and visited the highest number of flowers during a single bout (2.8 ±1.9). The remaining cases were single visits of insects from Diptera and Heteroptera, which although they were much longer, involved a smaller number of flowers (Tab. 2).

Population structure, floral display, and reproductive success

The three investigated populations of *P. caeruleum* differed in size. The ZE and OP populations consisted of ca. 1000 flowering shoots; the KO population ca. 350 flowering shoots (Tab. 1). All the populations were characterized by an aggregative spatial structure of flowering shoots. In two investigated populations (KO and OP), the

Tab. 2 Quantitative components of insect activities from seven groups visiting flowers of *Polemonium caeruleum* in two study populations (based on video recording).

	KO			ZE		
	V (*SD*)	T_{inf} (*SD*)	N_f (*SD*)	V (*SD*)	T_{inf} (*SD*)	N_f (*SD*)
Apis mellifera	0.5 (0.9)	35.9 (35.1)	3.9 (2.0)	1.7 (2.0)	19.8 (24.2)	2.8 (1.9)
Bombus	0.2 (0.4)	7.7 (7.5)	2.1 (1.7)	0.0	0.0	0.0
Other Hymoenoptera	0.8 (1.4)	155.1 (255.6)	1.9 (1.8)	0.0	0.0	0.0
Diptera	0.1 (0.4)	63.0 (76.4)	5.0 (4.2)	0.1 (0.1)	186.3 (194.4)	1.7 (0.6)
Lepidoptera	0.2 (0.3)	15.6 (13.9)	1.2 (0.4)	0.0	0.0	0.0
Heteroptera	0.0 (0.04)	900.0#	1.0#	0.0 (0.1)	900.0#	2.0#
Coleoptera	0.5 (0.9)	582.1 (391.0)	1.7 (1.2)	0.0	0.0	0.0

V – average visitation frequency (No. of visits/flower h^{-1}); T_{inf} – average visit duration per inflorescence expressed in seconds; N_f – average number of flowers visited during a single bout; # – single observation.

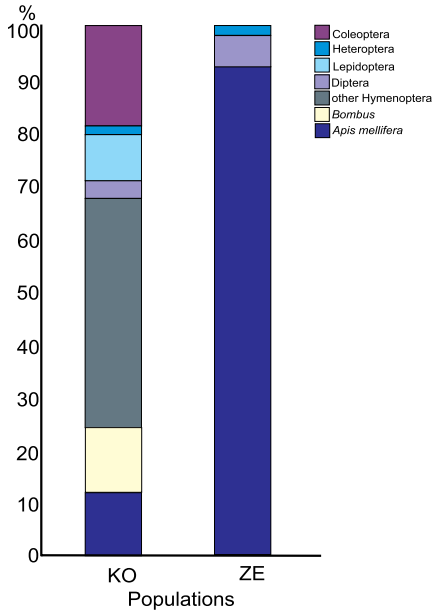

Fig. 3 Frequency of particular taxonomic insect groups in two investigated populations of *Polemonium caeruleum*.

densities of flowering shoots were comparable (K_D = 4.3 ±4.5 and 3.1 ±4.6, respectively) (Tab. 1, Fig. 4). We found no significant differences in the mean height of flowering shoots among these two studied populations (H_F: $F = 3.44$, $df = 1$, $p > 0.05$), although they significantly differed in the mean number of flowers per inflorescence, which was 71.0 ±46.0 for OP and 40.1 ±22.2 for KO, ($F = 47.7$, $df = 1$, $p < 0.001$) (Tab. 1). The reproductive success was high and reached similar levels in both populations (t test = 1.34, $df = 1$, $p > 0.05$), 83.2% in OP and 86.6% in the KO population (Tab. 1). We found no significant correlations between fruiting ratio and floral display components. Only in the KO population was there a positive and significant relationship between fruiting ratio and number of flowering shoots in clumps (F_R vs. $N_{F/C}$: $R = 0.27$, $p < 0.01$).

Discussion

The results of our study indicate differences in compatibility systems in two populations of *P. caeruleum*. The total lack of fruits after induced geitonogamy in KO imply self-incompatibility of individuals in this population. This system was also recorded in one of the Polish population of this species, where no pollen tubes or only weak signs of germinating pollen tubes were observed on the stigmas pollinated with self-pollen [22]. Self-pollen germinated on the stigma and formed pollen tubes that penetrated the ovules of other self-incompatible member of Polemoniaceae – *Ipomopsis aggregata*, but the ovules were subsequently aborted [31,32]. Fruits and seeds recorded after induced geitonogamy in another population (ZE) indicate that in this population the self-compatible system was realized. However, the frequency of geitonogamous fruits and mean number of seeds were not very high in comparison to many other self-compatible plants, which exhibit very high levels of fruiting (up to 100%) as a result of induced selfing [33–35]. Both the number of geitonogamous fruits and seeds were also significantly lower than those from controlled pollination recorded in the ZE population. In self-compatible *P. vanbruntiae*, the fruit set after induced geitonogamy was at the medium level (53%), but with an equivalent number of seeds when compared to purely outcrossed and open-pollinated flowers [36]. Our results imply pre-zygotic selection and incomplete self-compatibility in the ZE population. This feature is identified when self-pollination generates fruits with a significant reduction in seed set [37], which was recorded, e.g., after artificial autogamy in orchid, *Platanthera bifolia* [38]. The labile character of the self-compatibility system

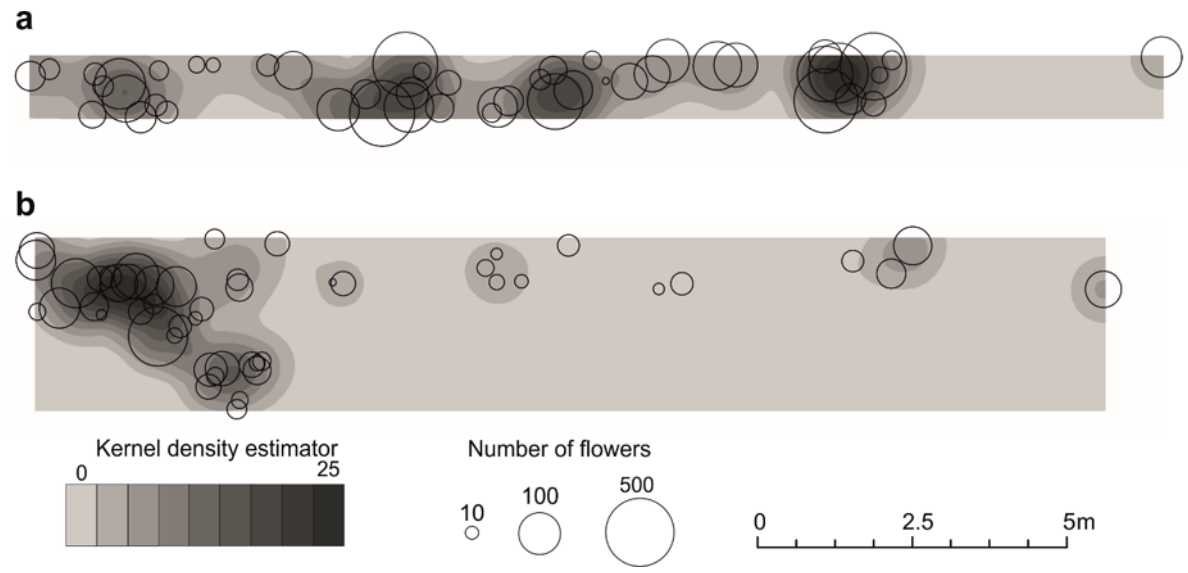

Fig. 4 Spatial structure of *Polemonium caeruleum* OP (**a**) and KO (**b**) populations; gradients show densities of flowering individuals estimated by kernel density estimator KD; circle sizes corresponds with the number of flowers per clump.

at the level of the Polemoniaceae family [20,23], *Polemonium* genus [19,36], and even distinct populations of the same species ([21,22] and present study) does not exclude a transitional phase of incomplete compatibility. Additionally, ovule wasting due to abortion after selfing, as recorded in *Ipomopsis aggregata* [31,32], could be responsible for lower fecundity in such a partially self-compatible stage.

If population KO is purely self-incompatible, the fruit set recorded from untreated, bagged flowers may originate from agamospermy. Asexual reproduction has not been observed in this species, but we cannot exclude such a possibility. On the other hand, the lack of fruit set from untreated, bagged flowers in the two other populations does not exclude agamospermy in OP (as we do not have information about self-compatibility in this population) or both agamospermy and autonomous autogamy in ZE. Despite the temporal separation of male and female phases, spontaneous autogamy in *P. caeruleum* is possible due to a few hours overlap between both sexual phases [22]. This process also took place in protandrous *P. vanbruntiae*, but the autonomously-selfed flowers set a significantly lower number of fruits and seeds compared to induced geitonogamy, and induced outcross and open pollination [36]. Spatial separation between the stigma (higher situated) and anthers (lower situated) in herkogamous flowers of *Polemonium* limits the structural availability and quantity of pollen grains reaching the stigma. Therefore, autonomous autogamy in this species is mostly accidental, with low seed production.

Comparison of fruit or seed set from natural reproductive success, supplemental outcrossing, and controlled pollination demonstrated the lack of pollen limitation and high importance of pollinators in the studied populations. No pollen limitation was also noted in self-compatible *Polemonium vanbruntiae* [36]. On the other hand, Zych et al. [22], studying a self-incompatible population of *P. caeruleum* over 2 years, observed pollen limitation only in 1 year. This was probably caused by differences in weather conditions between years that influenced insect activity. On the other hand, plant studies also documented that seed set from insect-mediated pollination is often better than hand-manipulated pollination [39]. In our study, if the KO population is self-incompatible, only pollen from distinct individuals can fertilize ovules. In turn, in the self-compatible ZE population progeny may originate from cross- and self-pollination. As a result, we observed the negative influence of selfing on seed production after controlled pollination, because this treatment does not exclude pollen transfer from the same plant. It is highly probable that in the KO population, in comparison to the ZE population, self-pollen limited seed set due to selfed ovule abortion and the reduction of cross-pollen export, as we discuss above. Insect pollination supplemented with hand-cross pollination did not show such a tendency between the SI and SC populations.

The participation of both cross- and geitonogamous pollen transfer results directly from pollinators' foraging behavior. Both studied populations were varied in terms of visitor assemblage and their activity within the inflorescence. The most diverse group of visitors was recorded in the KO population, but visits of the most important key pollinators for *P. caeruleum*, *Bombus* spp. [20,22,40], and *Apis* spp. [22,25,41] were infrequent (ca. 25% of all visits). The important group of visitors comprised other Hymenoptera. Visits of various hymenopterans on *P. caeruleum* were often observed [20–22,40], and it is highly probable that they include some effective pollinators if they are medium-large [20,40] and have short tongues, as flowers seem to represent "generalist-bee syndrome" [22]. Zych et al. [22] suggested that *P. caeruleum* may also be serviced by hoverflies and butterflies, which we also observed in the KO population. Beetles, which included almost 20% of all visits in the KO population, were also recorded as visitors by Grant and Grant [20]. An entirely different pollination biology of *P. caeruleum* was found for the ZE population, which was serviced almost exclusively by *A. mellifera*. Similarly to the Kleczkowo population studied by Zych et al. [22], the key pollinator *Bombus* spp. in population KO switched two or three times among flowers, but penetrated flowers for almost three times longer. In turn, the second key pollinator, *A. mellifera*, was less active in Kleczkowo than in our populations. Additionally, it behaved in a distinct way, when visitation frequency was very high. Frequent visits of *A. mellifera* in the ZE population were two times shorter than in the KO population, and on average these insects visited one flower less than in KO. This confirms that pollinator behavior may vary in different populations of the same plant species. The analyzed parameters of foraging behavior in the populations studied suggest that all observed insect taxa and taxonomic groups possess the potential for geitonogamous pollen transfer, similarly to visitors from the Kleczkowo population [22]. On the other hand, a higher diversity of visitors implies diverse scenarios of foraging behavior and, in our opinion, it is a key factor determining the same reproductive success in both studied populations, KO and ZE. The self-compatible ZE population pollinated by *A. mellifera* reveals high fruiting as bee behavior commonly promotes mixed-mating, which raises reproductive success [42,43]. If the KO population is self-incompatible, geitonogamous pollen transfer causes ovules and cross-pollen discounting, which decreases reproductive success in many SI species [11,32,44,45]. Diverse pollinator assemblages, behavior, and higher frequency of visited flowers prevent such a scenario and promote effective cross-pollen transfer [34,45].

Pollinator abundance and their foraging behavior depend on the size and spatial pattern of the plant population [46–48]. It is well documented that plant population size (especially the participation of flowering plants) and density affect the number of visits per plant and visitation rate [49–52]. First of all, flower density may affect pollen limitation [53]. Burd [54] reported that 62% of 158 plants were pollen limited at least in some places. In consequence, this is reflected in pollination success, which is often lower in smaller populations, because they are usually less attractive for pollinators [1,55,56]. This relation is especially underlined in self-incompatible species [11]. Our analyses do not confirm data about the relationships between population size or density and the level of fruiting in *P. caeruleum* populations. The only positive correlation between the number of flowering shoots in clumps and fruiting was noted in the KO (SI) population. Despite the fact that individuals in the studied populations varied in size (from single- to multi-shoot individuals) and floral display, and formed aggregations of different sizes, their pollination success was similar. This differentiation was probably neutralized by the spatial structure of the populations. Both populations occupied relatively small compact areas, with individuals growing close one to another. In such a situation, each individual had the same chance to be visited by pollinators. We also did not find any influence of plant height on their reproductive success. Such relations were observed by Galen and Stanton [57], who found that larger plants of SI *Polemonium viscosum* were more attractive for pollinators. On the other hand, larger plants of the self-incompatible *Ipomopsis aggregata* received more geitonogamous pollen [32]. The connection between pollination, reproduction success and different measures of individual plant floral display was shown for many species, both SI and SC [18,33]. The lack of the effect of population properties might be due to the small range of population sizes and densities (only two populations were studied); for instance Groom [58], studying *Clarkia concinna*, found that when population size

exceeded 50 individuals no clear relationship was observed. To verify these results, however, studies on a wider range of populations are needed.

Conclusions

- Within the studied *P. caeruleum* populations, a distinct compatibility system was observed, which confirms the transitional character of SC–SI system recorded in this species.
- If a population is self-compatible, selfing may be facilitated only by pollinators due to geitonogamous pollen transfer.
- Independently of population properties (compatibility, visitor diversity and activity, population size, density, and floral display), *P. caeruleum* is not pollen limited and pollinators are a key factor determining the high reproductive success.
- Visitor assemblages and their activity on *P. caeruleum* vary between plant populations. Similarly, the presence and foraging behavior of key pollinators, bumblebees and honey bees, are not constant.
- Visitation frequency, visit duration, and number of flowers visited during a single bout are differentiated between SI and SC populations, which influences the breeding system.

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Zmienność systemu rozrodu, biologia zapylania i sukces reprodukcyjny *Polemonium caeruleum* L. w Polsce płn.-wsch.

Streszczenie

U wielosiłu błękitnego, *Polemonium caeruleum* obserwuje się zróżnicowanie systemu samozgodności w różnych populacjach. Badania dotyczące właściwości populacji tego gatunku w kontekście jego potencjału systemu rozrodu są niezbędne w zrozumieniu ewolucyjnego mechanizmu tego procesu. W trzech populacjach *P. caeruleum* zlokalizowanych w płn.-wsch. Polsce analizowano system rozrodu, różnorodność i aktywność owadów wizytujących kwiaty wielosiła oraz relacje pomiędzy właściwościami populacji a sukcesem reprodukcyjnym. W populacjach stwierdzono odmienny system samozgodności. W populacji samozgodnej, samozapłodnienie może nastąpić jedynie przy udziale wektorów zewnętrznych, na drodze geitonogamii. Niezależnie od właściwości populacji (samozgodności lub samoniezgodności, różnorodności i aktywności owadów wizytujących, wielkości populacji, zagęszczenia oraz wielkości wystawy kwiatowej) *P. caeruleum* nie jest limitowany dostępnością zapylaczy. Zapylacze stanowią kluczowy czynnik kształtujący wysoki sukces reprodukcyjny we wszystkich badanych populacjach. Zespoły owadów wizytujących kwiaty wielosiłu (włączając w to również kluczowych zapylaczy jakimi są trzmiele i pszczoły) oraz ich aktywność na kwiatostanie różnią się pomiędzy populacjami, co wpływa na odmienny wzorzec realizowanego systemu rozrodu. Stwierdzono, że populacja samoniezgodna była wizytowana przez różnorodne owady należące do Hymenoptera, Diptera, Lepidoptera, Heteroptera i Coeloptera, których zachowanie mogło efektywnie realizować zapłodnienie krzyżowe. Z kolei populacja samozgodna była obsługiwana głównie przez *Apis mellifera*, której behawior mógł promować mieszany system rozrodu. Przedstawione w pracy wyniki mają charakter badań wstępnych. W celu ustalenia, które czynniki selekcyjne są odpowiedzialne za zmienność systemu samozgodności w różnych populacjach *P. caeruleum* konieczne są dalsze badania w większej liczbie populacji.