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THE LIFE-HISTORY TRAITS AND SEEDLING RECRUITMENT OF *Dianthus superbus* L. IN DIFFERENT STAGES OF MEADOW OVERGROWING

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A b s t r a c t

A study of the life-history traits and seedling recruitment in small and isolated populations of a rare clonal species, *Dianthus superbus* L., was carried out in the years 2011–2012 in Kraków-Kostrze (Southern Poland). Observations were conducted in unmanaged *Molinietum caeruleae* meadows situated along the successional gradient. The patch representing the initial stage of succession (P1) was dominated by small species creating delicate erect or procumbent stems, the patch representing the temporary stage of succession (P2) was prevailed by large-tussock grasses and tall-growing macroforbs, while the patch representing the terminal stage of succession (P3) was partly overgrown by bushes and trees. The number of generative shoots, flowers, fruits and seeds of *Dianthus superbus* L. diminished gradually from P3 *via* P2 to P1. The increase in abundance of generative shoots and flower number in the vicinity of tall plants contributes to increased visibility of inflorescences and may enhance the chances for nocturnal pollinator visits. A significant production of fruits and seeds in competitive neighborhood may augment the chances for successful dispersal and colonization of new, perhaps more favorable habitats. The recruitment of seedlings occurred only in artificially created gaps in plant canopy and litter. The appearance of seedlings and their survivorship were better in P1 than in P2 and P3. Such a phenomenon might be due to the locally rising water level and the diminishing amount of light reaching to the soil area along the successional gradient.

Concluding, it should be asserted that a low production of generative shoots, flowers, fruits and seeds by the population of *Dianthus superbus* L. established in the patch dominated by small meadow species is compensated by the highest seedling recruitment and their survival. On the other hand, a substantial production of generative structures is not sufficient to ensure the persistence of populations in meadows in advanced stages of secondary succession.

Key words: *Dianthus superbus,* generative shoot; flowers; fruits; secondary succession; seeds; seedling recruitment; seedling survivorship

INTRODUCTION

During the 20th century, traditional agricultural management in semi-natural communities was either heavily intensified or abandoned in Europe. Unmanaged lands were subjected to secondary succession and gradual encroachment of tall-growing macroforbs, shrubs and trees. Such phenomenon, directly leading to the deterioration and fragmentation of habitats, was repeatedly observed in calcareous grasslands [1], heathlands [2,3] and meadows [4, 5, 6]. As a result of advanced fragmentation of habitats, many species currently occur as small and isolated populations, suffering from loss of genetic diversity and high risk of extinction. The management of rare plant populations is facilitated by knowledge of the variability of life-history traits shaping the reproductive success, i.e. number of generative shoots, flower and fruit production, seed set, as well as knowledge of recruitment and survival of seedlings. Hitherto, such investigations have been carried out in populations of several taxa, such as *Carex davalliana* L. [7], *Dactylorhiza majalis* (Rchb.) P.F. Hunt & Summerh [8], *Genista anglica* L. [9], *G. pilosa* L. [9], *Gentiana pneumonanthe* L. [10, 11], *Orchis mascula* l. [12], *O. purpurea* Huds. [13], *Senecio coincyi* Rouy [14], and *Succisa pratensis* Moench. [7]. Despite of the growing interest in the above-mentioned issue, the reproductive success of several species still remains poorly understood. Considering the insufficient state of knowledge, investigations were undertaken in small populations of *Dianthus superbus* L. located in *Molinietum caeruleae* meadows in different stages of overgrowing. The main goals were focused on the evaluation of the influence of site conditions on: (1) the variability of life-history traits such as production of generative shoots, flowers, fruits and seeds; (2) the number and survivorship of seedlings in continuous plant cover and in artificially made gaps.

MATERIALS AND METHODS

Study species

Large pink *Dianthus superbus* L. is a loosely tufted perennial, clonal forb which consists of numerous vegetative and generative shoots. The generative shoots are topped with many flowers visited exclusively by migratory crepuscular and nocturnal hawkmoths [15]. The fruits, greenish four-valved capsules, contain self--sowing seeds. The large pink is listed as a species of the Euro-Siberian subelement, widely but patchily distributed in western, central and eastern Europe as well as in northern Asia [16]. In Poland the greatest number of localities occur in the Vistula valley, whereas the lowest density of stands is recorded in the Baltic coastal area and western Pomerania [17]. *Dianthus superbus* L. is a rare and strictly protected plant in Poland [18] and is included to The Red List of Vascular Plants [19].

Study area

The study was carried out in the Kostrze district located on the western edge of Krakow, south of the Vistula River (southern Poland) (Fig. 1). The patches of *Molinietum caeruleae* occurring in this locality are relicts of vast meadows, which previously existed along the Vistula River [20]. The abandonment of traditional land use for at least a dozen years promoted the development of *Phragmites* swamps and willow brushwoods leading to fragmentation of meadows [21, 22].

Description of the study site

The investigations were carried out simultaneously in three abandoned patches of *Molinietum caeruleae* representing the successional gradient of meadow overgrowing (Table 1). Patch P1 was established in a meadow being in the initial stage of succession. It was dominated by small-stature taxa intercepting a very low amount of irradiance, contributing to strong insolation and a fast decrease in groundwater level in early spring. Patch P2 was set in a meadow being in the temporary stage of succession. It was predominated by grasses forming large tussocks and tall-growing macroforbs. The closely packed shoots and leaves shaded the whole patch, while the hummocks-and-hollow micro-topography triggered the prolonged water. Patch P3 was established in a meadow being in the terminal stage of succession. It was overgrown by shrub willows and surrounded by groups of trees. The elevation of water level in the local depressions provided high soil water content till late spring or even early summer. Moreover, the compact canopy of willow leaves strongly decreased the amount of light reaching ground level.

Vegetation study

In all patches the evaluation of habitat factors such as light intensity at ground level, vegetation height, vascular plant cover and moss cover, was performed from the 3rd to 15th of July 2011. The mean light intensity at ground level was calculated on the basis of 10 measurements performed with a digital light meter Voltcraft MS-1300 (accuracy +/- 5% + 10 digits; measuring range 0.01–50 000 lx). Five measurements were performed on sunny days and five on cloudy ones. The average vegetation height was evaluated on the basis of measurements of 50 randomly chosen shoots of different species. Each shoot was measured from the ground level to the tip using a folding tape measure. The cover of vascular plants and the cover of mosses were visually estimated within an aluminum frame (30cm x 30cm) in 50 randomly chosen places.

Study of *Dianthus superbus* L. traits

The research was carried out in the period 2011–2012. In 2011 all aggregations of shoots of *Dianthus superbus* L. that occurred in the studied patches were marked with small plastic pegs. Individuals consisted of one shoot only were not observed in the study area. Subsequently, the number of generative shoots per aggregation as well as the number of flowers and fruits per generative shoot were counted in the years 2011 and 2012 separately. Seed production was evaluated in 10 capsules randomly chosen in each patch in 2012. The permit for capsule collection was issued by the Regional Director for Environmental Protection in Kraków. After counting, all seeds were scattered near the shoot aggregations.

Moreover, 10 permanent experimental plots (0.5 x 0.8 m) were randomly arranged in each patch in April 2011 to assess the spontaneous recruitment of seedlings. The experimental plots were established at least 3.0 metres from the patch border to avoid the edge effect. Each plot was divided into two square--shaped adjacent subplots measuring 900 cm^2. In one subplot, the established vegetation and litter were left untouched, while in the second subplot moss, plant canopy and decayed organic matter were clipped and removed. Such treatment is considered to be optimal for seedling establishment on the basis of the results of observations carried out in wet meadows [23, 24]. The establishment of generative offsprings was monitored once a week in May, June, July and August, and twice a month in April, September and October. Each seedling was tagged and the survived individuals were counted in 2012.

The nonparametric Kruskal-Wallis test and post--hoc test were applied to check the significance of the differences between patches P1, P2 and P3 in the number of: generative shoots per shoot aggregation, flowers per generative shoot, fruits per generative shoot, and seeds per capsule. Also, the aforementioned tests were used to check the significance of the differences

in the number of seedlings per gap as well as the number and percent of individuals that survived in openings till next year.

Post-hoc comparisons were made if the value of the test was significant. All statistical analyses were performed using *STATISTICA* 10 software.

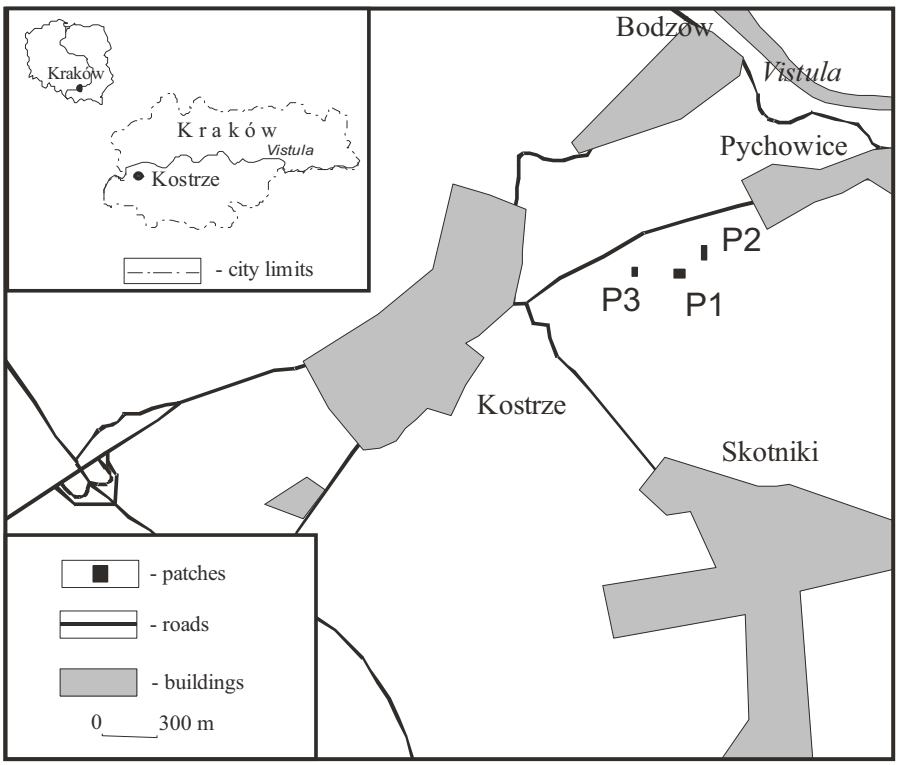

Fig. 1. The location of *Dianthus superbus* L. populations in the study patches representing the initial (P1), temporary (P2) and terminal (P3) stages of succession.

Table 1
Characteristics of the study patches

Patch name	P1	P2	P3
Successional stage	initial	temporary	Terminal
Coordinates	N 50° 01' 50.4''	N 50° 01' 52.5''	N 50° 01' 50.9''
	E 19° 52' 03.2''	E 19° 52' 03.0''	E 19° 52' 02.9''
Patch area (m^2)	1 400	1 300	1 450
Mean light intensity at ground level (lx)	43 000	32 000	20 000
Mean vegetation height (cm)	64	78	136
Mean cover of herb layer (%)	97	98	99
Mean moss cover (%)	2	2	1
Species number	76	61	48
Dominants	*Lathyrus pratensis* L.	*Molinia caerulea* (L.) Moench	*Salix repens*
(species with cover exceeding 20%)	*Lotus corniculatus* L.	*Deschampsia cespitosa* (L.) P.Beauv	*ssp. rosmarinifolia* (L.) Hartm.
	Lychnis flos-cucculi L.		*S. cinerea* L.
	Gladiolus imbricatus L.		*S. aurita* L.
Subdominants	*Briza media* L.	*Filipendula ulmaria* (L.) Maxim.	*Populus tremula* L.
(species with cover of 5-20%)	*Stelaria graminea* L.	*Serratula tinctoria* L.	*Betula pendula* Roth
		Phragmites australis (Cav.) Trin. ex Steud.	

Table 2
Mean values characterizing the life-history traits of *Dianthus superbus* in the study patches representing the initial (P1), temporary (P2) and terminal (P3) stages of succession. Different letters indicate statistically significant differences obtained in post-hoc comparison (Kruskal-Wallis test).

Life-history trait	Year	P1	P2	P3	Test value, *P*
Generative shoots per shoot aggregation	2011	1.80^{ab} N= 13	3.13^{a} N= 15	5.30^{b} N= 10	7.74, *P≤ 0.05*
	2012	2.00^{ab} N= 13	3.53^{a} N= 15	6.70^{b} N= 10	9.13, *P≤ 0.05*
Flowers per generative shoot	2011	7.95^{a} N= 22	11.25^{a} N= 47	16.33^{b} N= 53	26.52, *P < 0.001*
	2012	6.33^{a} N= 21	11.73^{b} N= 53	15.16^{c} N= 67	35.52, *P < 0.001*
Fruits per generative shoot	2011	5.54^{a} N= 22	9.12^{b} N= 47	11.75^{b} N= 53	21.48, *P < 0.001*
	2012	4.76^{a} N= 21	8.67^{b} N= 53	10.47^{b} N= 67	27.61, *P < 0.001*
Seeds per capsule	2012	40.83^{a} N= 30	52.33^{ab} N= 30	61.66^{b} N= 30	13.22, *P < 0.01*

Table 3
Recruitment and survivorship of *Dianthus superbus* seedlings in 10 artificially made openings in the study patches representing the initial (P1), temporary (P2) and terminal (P3) stages of succession. Different letters indicate statistically significant differences obtained in post-hoc comparison (Kruskal-Wallis test).

	Year	P1	P2	P3	Test value, *P*
Seedling number	2011	14.50^{ab}	9.60^{a}	6.70^{b}	15.57, *P <0.01*
Number of individuals that survived till next year	2012	8.60^{a}	3.30^{a}	2.80^{b}	16.74, *P <0.01*
Percent of individuals that survived till next year	2012	58.80^{a}	65.95^{a}	41.10^{b}	11.73, *P <0.01*

RESULTS

In the surveyed patches, the number of shoot aggregations of *Dianthus superbus* L. was rather low and reached 13 in P1, 15 in P2, and 10 in P3. The greatest number of generative shoots per aggregation was found in P3 where it amounted from 5.30 to 6.70 on average, a much lower number was recorded in patch P2, from 3.13 to 3.53, and in P1, from 1.80 to 2.00 (Table 2). The greatest number of flowers per generative shoot was observed again in patch P3, where it was from 15.16 to 16.33. A lower production of flowers was found in patches P2 and P1 where it reached from 11.25 to 11.73 and from 6.33 to 7.95, respectively. Also the number of fruits per generative shoot increased with the augmentation of shading level. It ranged from 4.76 to 5.54 in P1, from 8.67 to 9.12 in P2, and from 10.47 to 11.75 in P3. Similarly, the production of seeds substantially increased along the successional gradient.

In all populations, seedlings were recorded only in gaps artificially made in plant canopy and litter. The greatest emergence of generative offsprings was observed in P1, whereas much lower recruitment rates were noted in patches P2 and P3. Similarly, the survivorship of generative offsprings was significantly higher in P1 than in P2 and P3 (Table 3).

DISCUSSION

The increased abundance of generative shoots and flower number in *Dianthus superbus* L. populations occurring in the vicinity of tall plants contributes to increased visibility of inflorescences and may enhance the chances for nocturnal pollinator visits. A positive correlation between flower display and activity of crepuscular pollinators, ensuring pollen receipt and donation, was observed by Somanatham and Borges [25]. The increase in capsule and seed production in the populations of *Dianthus superbus* L. along the successional gradient is in accordance with the observations carried out in the populations of other species inhabiting abandoned *Molinietum caeruleae*. An increase in fruit number with the rising height of standing vegetation was found in the populations of *Trollius europaeus* L. [26] and *Gentiana pneumonanthe* L. [27],

whereas an increase in seed output was recorded in the populations of *Iris sibirica* L. [28]. According to the models developed by Loechle [29] as well as by Gardner and Mangel [30], a significant production of fruits and seeds in competitive neighborhood may augment the chances for successful dispersal and colonization of new, perhaps more favorable habitats.

The results obtained during the present study, showing that recruitment of seedlings may occur only in gaps in plant cover and litter, support observations carried out in populations of other taxa, such as *Dactylorhiza incarnata* (L.) Soó [31], *Gentiana pneumonanthe* L. [32], *Gladiolus imbricatus* L. [33], *Iris sibirica* L. [28], *Succisa pratensis* Moench. [34], and *Viola palustris* L. [35]. The gradual decline in emergence of *Dianthus superbus* L. offsprings along the successional gradient is in agreement with observations of gap colonization by individuals of *Trollius europaeus* L. and *Iris sibirica* L. in unmanaged wet meadows [36]. The decrease in the number of seedlings and juveniles might be due to unfavorable habitat conditions. The rising water level in hollows between grass tussocks or in local depressions appearing between creeping shoots of willows may inhibit seed germination. According to Blaney and Kotanen [37] as well as Schafer and Kotanen [38], an increase in soil moisture in wet habitats accelerates the development of pathogenic fungi which damage the diaspores of many species. At the same time, it should be added that seeds of *Dianthus superbus* L. are very susceptible to pathogen attack [39] and loss of germination ability [40]. The decreasing light availability at ground level seems to be another factor strongly limiting the establishment and survivability of seedlings of *Dianthus superbus* L. in successive patches. According to Isselstein *et al*. [41], Kotowski *et al*. [42] as well as Kotowski and van Diggelen [43], the diminishing amount of light reaching the soil area in fen meadows may suppress the growth of plantlets or even trigger their mortality.

In conclusion, it should be stated that a low production of generative shoots, flowers, fruits and seeds by the population of *Dianthus superbus* L. established in the patch dominated by small meadow species is compensated by the highest recruitment of seedlings and their survival. On the other hand, a substantial production of generative structures is not sufficient to ensure the persistence of populations in meadows in advanced stages of secondary succession.

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Cechy historii życiowych i rekrutacja siewek *Dianthus superbus* L. w płatach łąk o różnym stopniu zarośnięcia

Streszczenie

Badania cech historii życiowych oraz rekrutacji siewek w małych, izolowanych populacjach rzadkiego, klonalnego gatunku *Dianthus superbus* L. były prowadzone w latach 2011–2012 w Krakowie-Kostrzu (Południowa Polska). Obserwacje wykonano na nieużytkowanych łąkach *Molinietum caeruleae* o różnym stopniu zarośnięcia w procesie sukcesji wtórnej. Płat reprezentujący początkowe stadium sukcesji (P1) był zdominowany przez niskie gatunki tworzące delikatne, płożące pędy, w płacie reprezentującym pośrednie stadium sukcesji (P2) przeważały wysokępowe trawy oraz wysokie ziołorośla, natomiast płat reprezentujący końcowe stadium sukcesji (P3) był częściowo zarośnięty przez krzewy i drzewa. Liczba pędów generatywnych, kwiatów, owoców i nasion *Dianthus superbus* L. stopniowo malała począwszy od powierzchni P3, przez P2, do P1. Wzrost liczby pędów generatywnych w sąsiedztwie wysokich roślin może przyczynić się do lepszej widoczności kwiatostanów i zwiększyć szanse na wizytę nocnych zapylaczy. Znaczna produkcja owoców i nasion w sąsiedztwie gatunków o dużych zdolnościach konkurencyjnych może podnieść szanse na udane rozsiewanie nasion i kolonizację nowych, być może korzystniejszych siedlisk.

Przeprowadzone obserwacje wykazały, że rekrutacja siewek zachodziła jedynie w sztucznie utworzonych lukach w pokrywie roślinnej i ściółce. Pojaw nowych osobników i ich przeżywalność były znacznie większe w płacie P1 niż na powierzchniach P2 i P3, co może być spowodowane lokalnie stagnującą wodą oraz zmniejszającą się dostępnością światła w kolejnych stadiach sukcesji.

Podsumowując, można stwierdzić że niewielka produkcja pędów generatywnych, kwiatów, owoców i nasion w populacji *Diantus superbus* L. występującej w płacie zdominowanym przez niskie gatunki łąkowe jest równoważona przez najwyższą rekrutację i przeżywalność siewek. Z drugiej strony, znaczna produkcja pędów generatywnych, kwiatów, owoców i nasion nie wystarczy aby zapewnić utrzymanie populacji na płatach łąk będących w zaawansowanych stadiach sukcesji wtórnej.

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