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Spatio-temporal variability of *Gladiolus imbricatus* L. populations in different plant communities near Kraków

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Abstract. The investigations, aimed to assess the abundance, stage structure and distribution of shoots, as well as the chosen traits of generative shoots (number of leaves and length of the longest one, height of shoot, length of inflorescence and the dorsal tepal of the lowermost flower, number of seed capsules) of *Gladiolus imbricatus* L. were conducted in the years 2015–2017. The observations were carried out from Kraków-Pychowice to Tyniec in abandoned moor-grass meadow (Patch I), shrub willows (Patch II), macroforb community (Patch III) and community dominated by tall-growing grasses (Patch IV). The population abundance augmented gradually in subsequent study sites. Additionally, the temporal fluctuations of shoot number were recorded in all the Patches. The similar in consecutive years' stage structure differs among the study sites. The occurrence of juvenile, vegetative and generative shoots in Patch I might suggest the successful seedling recruitment, while the lack of shoots in pregenerative stages in Patches II–IV might indicate the absence of safe sites for the appearance of new genets. The occurrence of clusters of shoots in Patches II–IV might be a consequence of clonal growth. The traits of generative shoots rather did not show the temporal variability, but they presented spatial variability and in most cases augmented from Patch I, via Patches II and III, to Patch IV.

The performed studies enabled ascertaining that the population occurring in Patch I presents the best condition despite the lowest abundance of shoots. Also the other, more abundant populations, inhabiting Patches II–IV might persist in the colonised sites thanks to the vegetative multiplication of ramets and maximisation of chances for successful pollination and effective seed dissemination.

Key words: *Gladiolus imbricatus* L. abundance, stage structure, spatial structure, clonal plant, rare species, ecobiology, population dynamics.

1. Introduction

The sword lily *Gladiolus imbricatus* L. is a clonal plant creating underground tubers performing the role of storage and regenerative organs of shoot origin (Klimešová & Klimeš, 2006). However, according to Moora et al. (2007) the vegetative spread is limited, and production of more than one daughter corm within one season is rare, while reproduction from seeds is common. The aforementioned authors distinguished the following developmental stages: seedlings (individuals with cotyledon), juveniles (individuals forming a nonflowering shoot with one leaf), vegetative (individuals creating a nonflowering shoot with at least two leaves) and generative (individuals creating a flowering shoot). The adult generative individuals form 30–80 cm tall, leaved stalks, bearing one-sided inflorescence containing usually from several to a dozen or so purple flowers, blooming from June to July. The flowers are pollinated by insects from the order *Hymenoptera*. The fruit is a slightly inflated capsule containing numerous wind-dispersed seeds.

The area of distribution of *Gladiolus imbricatus* L. covers Central and Eastern Europe, the Mediterranean, Caucasia and West Siberia (Hultén & Fries, 1986). In Poland, it abundantly occurs in the southern highlands and lower mountains, whereas in the other regions it is rather rare

(Zając & Zając, 2001). The populations of *Gladiolus imbricatus* L. occur in termophilous oak forests *Potentillo albae-Quercetum*, humid lowland meadows from the *Molinion* alliance, oats and barley fields, as well as phytocenoses dominated by *Calamagrostis epigejos* and *Carex brizoides*.

Gladiolus imbricatus L. is included into numerous national Red Lists of Vascular Plants (Lilleleht, 1998; Holub & Procházka, 2000; Moser et al., 2002; Andrušaitis, 2003; Király, 2007). It is also enlisted in the Polish Red List of Vascular Plants (Kaźmierczakowa et al., 2016) in the category 'near threatened', as well as in many regional 'Red Lists or Books' (e.g. Jakubowska-Gabara & Kucharski, 1999; Głowacki et al., 2003; Markowski & Buliński, 2004; Jackowiak et al., 2007; Bróż, Przemyski, 2009; Kołodziejek, 2011; Babczyńska-Sendek et al., 2012; Cwener et al., 2016). Moreover, according to Rozporządzenie (2014) it belongs to strictly protected species.

The hitherto investigations concerning the sword lily individuals and populations have focused on the natural hybridisation between *Gladiolus imbricatus* and *G. palustris* (Szczepaniak et al., 2016), *in vitro* technologies for micropropagation, multiplication, corm development, somatic embryogenesis and medium-term storage culture (Rakosy-Tican et al., 2012), the influence of management on condition of populations (Moora et al., 2007), the effect of gaps in continuous plant cover and litter on seedling recruitment (Jõgar & Moora, 2008; Kostrakiewicz-Gierałt, 2014a) and the abundance and structure of populations in *Molinion caeruleae* meadows (Kubikova & Zeidler, 2011; Kostrakiewicz-Gierałt, 2014b).

Despite the gradual growth in the number of studies carried out in populations of *Gladiolus imbricatus* in the last decades, the current state of knowledge is still insufficient and further investigations are still required. Therefore the variability of sword lily populations in different phytocenoses was investigated. The detailed aims concentrated on the assessment of: (i) the abundance of shoots, (ii) the age structure and distribution of shoots, and (iii) the chosen traits of generative shoots (i.e. the number of leaves and length of the longest of them, height of stems and inflorescences, number and length of flowers, as well as number of capsules).

2. Study area

The investigations were carried out in the southern part of Poland from Kraków-Pychowice to Tyniec, south of the Vistula River. The research area is at ca. 210 m a.s.l, on a low flood terrace of the Vistula, 3–6 m high. The water table is 0–2 m below the ground surface. Formerly, in the aforementioned area, patches of *Molinion caeruleae* prevailed (Zarzycki, 1958), but long-time lack of management promoted the development of macroforb communities, *Phragmites* swamps and willow brushwood (Dubiel, 1991, 1996). Other plant communities also occur in the vicinity, such as deciduous forests, xerothermic calcareous grasslands and ruderal communities.

The study area consisted of four study Patches differentiated by species composition and habitat conditions: (1) Patch I measuring ca. 800 m^2 represented moor-grass meadow characterised by the presence of rosette-form species with erect or procumbent stems and delicate underground organs, e.g. *Centaurea jacea, Lychnis flos-cuculi* and *Succisa pratensis*; (2) Patch II covering an area ca. 900 m^2 represented willow thicket dominated by *Salix rosmarinifolia*; (3) Patch III reaching ca. 600 m^2 was established in a macroforb community prevailed by *Filipendula ulmaria, Lythrum salicaria* and *Valeriana officinalis*; and (4) Patch IV achieving approximately 600 m^2 represented by phytocenose of tall-growing grasses such as *Molinia caerulea* and *Deschampsia caespitosa*.

3. Material and methods

3.1 Field study

In all of the above-mentioned patches, the survey of habitat conditions was performed on 15 July 2015. The cover of cryptogams, herbaceous plant, as well as shrubs and trees were visually estimated. In order to obtain the random samples in each plot, 20 throws with an iron ring, 30 cm in diameter, were made. Each time, one stem occurring in the centre of the ring was measured using a folding tape measure. Simultaneously, soil humidity in the centre of the ring was measured using a BIOWIN soil moisture sensor (range 1–10). The gradual increase of height of plant cover and soil moisture in consecutive patches are given in Table 1.

In 2015, in each of the aforementioned patches, all the shoots of *Gladiolus imbricatus* were inventoried. Subsequently, within each patch the one representative, permanent study plot (10 m x 10 m) was set and fenced. Then, all the shoots growing within the study plots were counted and tagged with plastic pegs for further observations, carried out in the years 2013–2015. Each year the shoots were inventoried and assigned to a developmental stage according to Moora et al. (2007). Also, the distribution of shoots in the study plots was surveyed. Moreover, the following parameters were measured for all the labeled, generative shoots: (1) the number and leaves and the length of the longest leaf blade, (2) the height of the generative shoot from ground level to the tip, (3) the length of inflorescence from the lowermost to the uppermost flower, (4) the length of the dorsal tepal of the lowest flower, and (5) the number of capsules.

Table 1. The characteristics of study patches

	Patch I	**Patch II**	**Patch III**	**Patch IV**
Area (m^2)	800	900	600	600
Habitat	Moor-grass meadow	Willow brushwood	Macroforb community	Tall-grass community
Dominants (species with cover exceeding 20 %)	*Centaurea jacea, Succisa pratensis, Lychnis flos-cuculi*	*Salix rosmarinifolia*	*Filipendula ulmaria, Valeriana officinalis, Lythrum salicaria*	*Molinia caerulea, Deschampsia caespitosa*
Bryophyte cover (%)	5	10	8	6
Herbaceous plant cover (%)	85	80	92	94
Shrub cover (%)	0	10	0	0
Mean (range) height of standing vegetation (cm)	44.6 (13–92)	45.2 (21–78)	68.9 (29–124)	79.2 (38–145)
Mean (range) soil humidity (range: 1–10)	3.8 (2–5)	4.5 (3–7)	5.6 (4–7)	6.1 (5–7)

The length of leaves and height of the generative shoots were performed using a folding tape measure, while measurements of length of inflorescences, flowers and capsules were performed with a digital caliper. The investigations of shoot height, as well as traits of leaves, inflorescences and flowers, were conducted during the last week of July. The number of capsules was counted during the last week of August (the beginning of the seed release) to check the eventual number of capsules without seeds.

3.2 Statistical analysis

Chi-square statistics were used to test if there were significant temporal and spatial differences in the percentage of shoots representing diverse developmental stages. Subsequently, normal distribution of the untransformed data of the traits of generative shoots (number and length of leaves, height of shoots, length of inflorescences, length of the tepal of the lowermost flowers and number of capsules) in an individual sample (from a particular patch and year) was tested using the Kolmogorov-Smirnov test, while variance homogeneity was tested using the Levene test at the significance level of $p < 0.05$. As the values of individual characteristics in some groups were not consistent with normal distribution, and the variance was not homogeneous, the non-parametric Kruskal-Wallis H test was used to check the significance of the differences of the aforementioned traits over consecutive years, as well as among successive Patches. All statistical analyses were performed using STATISTICA 10 software.

4. Results

The total abundance of *Gladiolus imbricatus* shoots achieved the lowest value in Patch I and the greatest value in Patch IV. A similar tendency was found in the permanent plots, where also the slight temporal changes of shoot numbers occurred (Table 2). The occurrence of juvenile, vegetative and generative shoots was found in Patch I, whereas only generative shoots appeared in the other Patches. Test χ^2 confirmed the significant spatial differences and lack of temporal variability (Fig. 1). Within the study plot established in Patch I, the singular shoots of *Gladiolus imbricatus* were distributed randomly, while in the remaining study sites clusters of shoots were also observed (Fig. 2).

The traits of the generative stems rather did not present temporal variability, but they showed significant spatial variability. The number of leaves per shoot achieved the highest values in Patch IV, while the length of the longest leaf blade reached much greater values in Patches III and IV than in Patches I and II (Table 3). The height of shoot rose gradually in subsequent study sites, while the inflorescence length achieved the lowest values in Patch I and

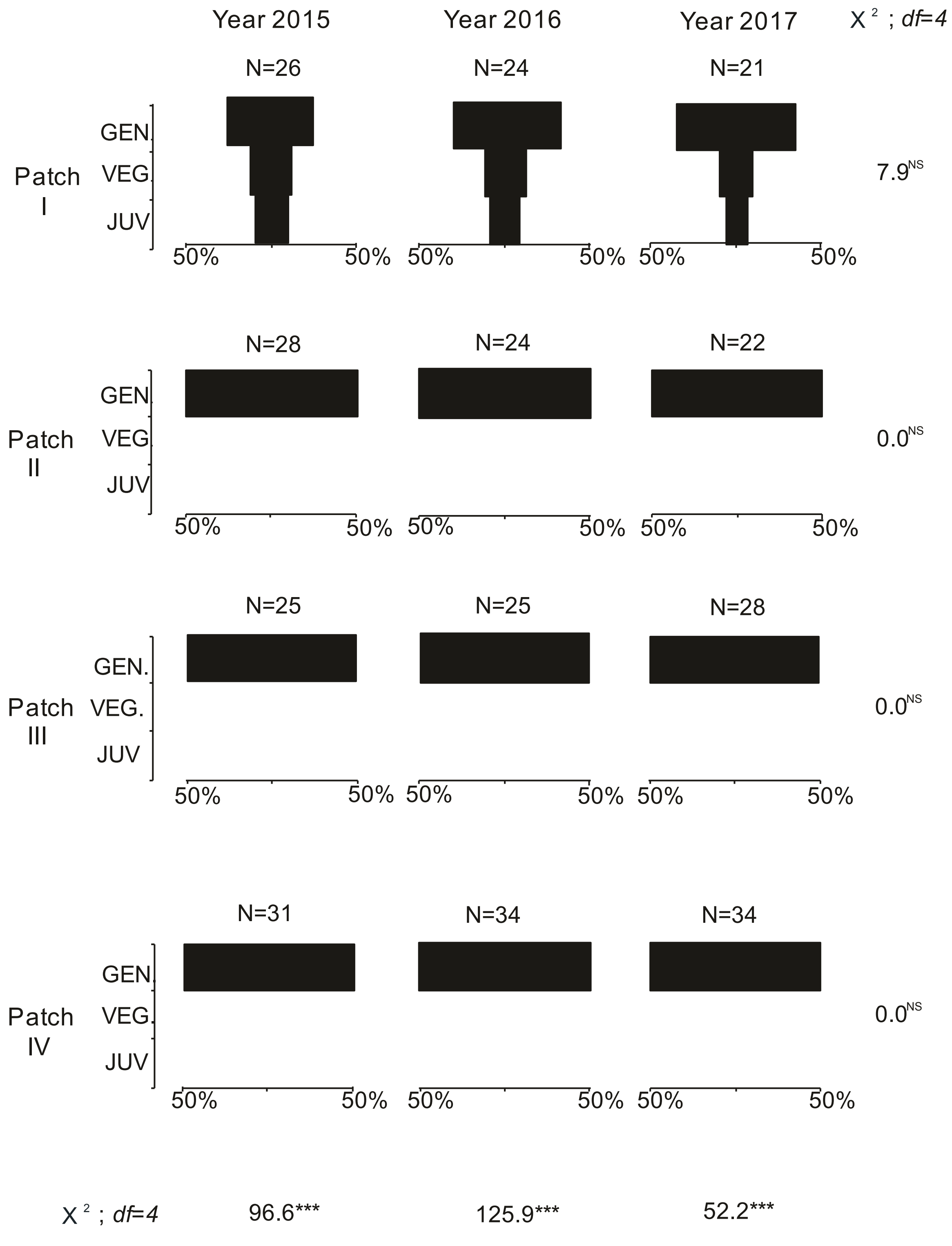

Figure 1. The structure of developmental stages of shoots of *Gladiolus imbricatus* L. in study plots established within studied moor-grass meadow (Patch I), willow brushwood (Patch II), macroforb community (Patch III) and tall-grass community (Patch IV) in the years 2015–2017. The symbols mean the level of statistical significance (χ^2 test): ^{NS}-not significant; *-P<0.05; **- P<0.01; ***-P<0.001. Abbreviations; JUV- juvenile shoots, VEG- vegetative shoots, GEN- generative shoots.

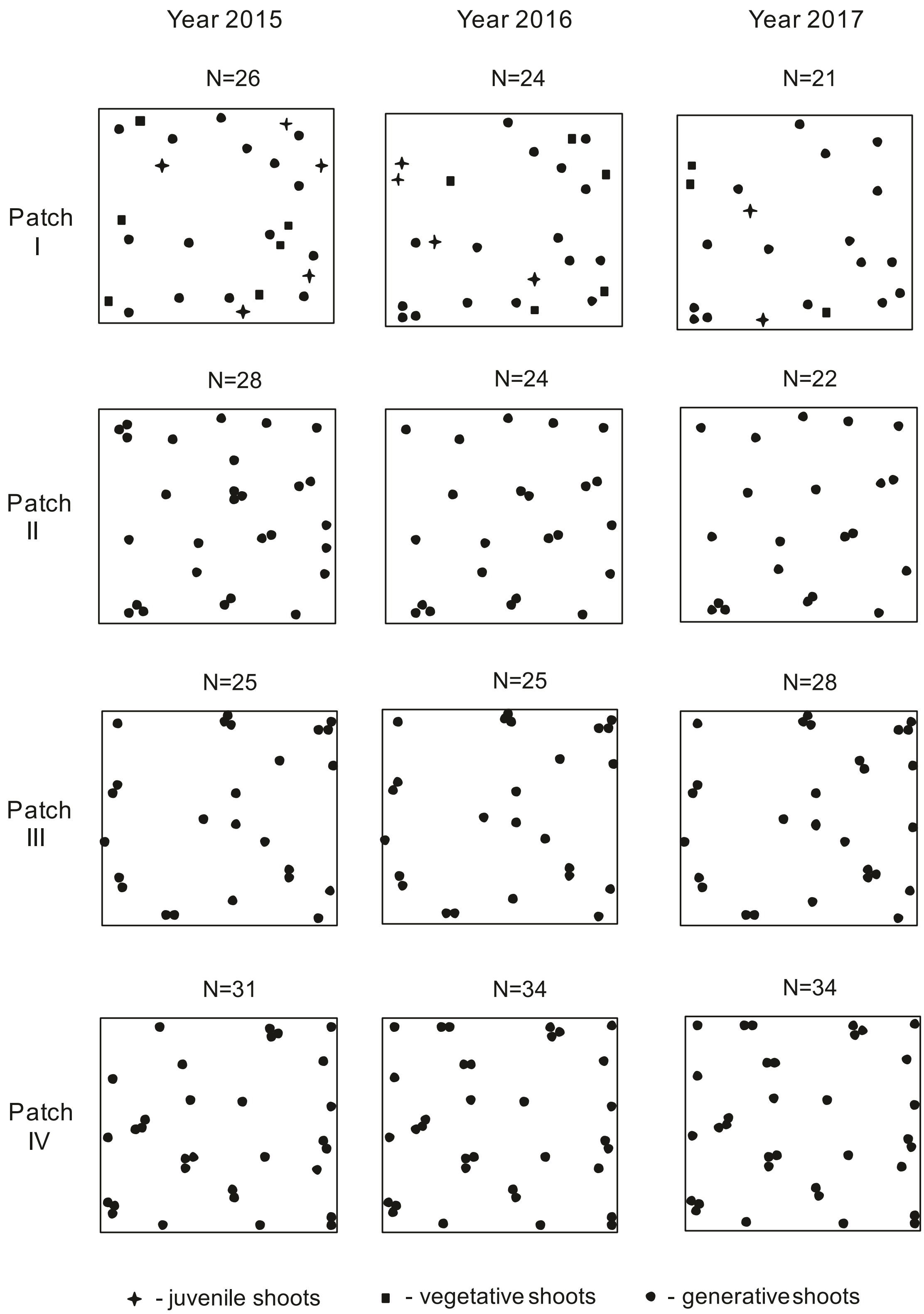

Figure 2. The spatial distribution of juvenile, vegetative and generative shoots of *Gladiolus imbricatus* L. in study plots established within studied moor-grass meadow (Patch I), willow brushwood (Patch II), macroforb community (Patch III) and tall-grass community (Patch IV) in the years 2015–2017. Abbreviations: N-number of shoots.

the highest ones in Patch IV. The length of the dorsal tepal of the lowermost flower reached the highest values in Patch IV (Table 4). In all the study sites all the capsules contained seeds. The number of fruits augmented gradually in subsequent study sites (Table 5).

5. Discussion

The performed observations showing that total number of shoots of *Gladiolus imbricatus,* rising in subsequent study sites and reaching from 157 to 197, is rather low. The much more abundant populations, reaching from about 600 to 250,000 individuals, were observed in meadows (Rombel-Bryzek, 2007; Mirek et al., 2014; Kołos, 2015; Ziaja & Wójcik 2016), while the less abundant were found in forest communities (Piórek & Krechowski, 2009; Gorzelak, 2012), as well as in phytocoenoses dominated by *Calamagrostis epigejos* (Falkowski, 2002) or *Carex brizoides* (Falkowski, 2002).

The temporal changes of the number of *Gladiolus imbricatus* shoots observed in all the study sites are an effect of dominance of factors contributing to a decrease or increase of the number of individuals. The decrease of shoot number might be an effect of individual mortality or physical damage of the aboveground parts of indi-

Table 2. The abundance of shoots of *Gladiolus imbricatus* L. in studied moor-grass meadow (patch I), willow brushwood (patch II), macroforb community (patch III) and tall-grass community (patch IV) in the years 2015–2017

		Patch I	Patch II	Patch III	Patch IV
Total number of shoots per Patch		157	143	169	197
Number of shoots per study plot in the year	2015	26	28	25	31
	2016	24	24	25	34
	2017	21	22	28	34

Table 3. Number of leaves and the length (cm) of the leaf blade of the longest one in generative shoots of *Gladiolus imbricatus* L. occurring in study plots established within studied moor-grass meadow (Patch I), willow brushwood (Patch II), macroforb community (Patch III) and tall-grass community (Patch IV) in the years 2015–2017. The symbols mean the level of statistical significance: ^{ns}-not significant; *-P<0.05; **- P<0.01; ***-P<0.001

	Year	Patch I	Patch II	Patch III	Patch IV	The value of the Kruskal-Wallis H test
Mean number (range) of leaves in the year	2015	2.7 (2–4)	2.8 (2–4)	2.9 (2–4)	3.2 (2–4)	2.2^{ns}
	2016	3.0 (2–4)	2.9 (2–4)	2.8 (2–4)	3.3 (2–4)	17.8***
	2017	2.9 (2–4)	3.5 (3–4)	3.5 (2–4)	3.6 (2–4)	12.8**
The value of the Kruskal-Wallis test		1.3^{ns}	7.6*	5.9^{ns}	7.4*	
Mean length (range) of the longest leaf blade in the year	2015	38.5 (30–51)	41.3 (25–48)	47.1 (29–67)	47.4 (29–68)	25.0***
	2016	40.8 (28–51)	36.7 (25–52)	47.8 (30–68)	48.6 (27–72)	23.0***
	2017	41.3 (35–51)	39.0 (26–52)	51.0 (32–71)	49.7 (30–72)	28.4***
The value of the Kruskal-Wallis test		2.0^{ns}	1.5^{ns}	1.3^{ns}	1.7^{ns}	

Table 4. Height of generative shoots (cm), length of inflorescences (cm) and the dorsal tepal of the lowermost flower of *Gladiolus imbricatus* L. occurring in study plots established within studied moor-grass meadow (Patch I), willow brushwood (Patch II), macroforb community (Patch III) and tall-grass community (Patch IV) in the years 2015–2017. The symbols mean the level of statistical significance: ^{ns}-not significant; *-P<0.05; **- P<0.01; ***-P<0.001

	Year	Patch I	Patch II	Patch III	Patch IV	The value of the Kruskal-Wallis H test
Mean height (range) of generative shoots in the year	2015	66.6 (55–80)	77.7 (58–96)	83.9 (58–103)	89.1 (64–120)	25.8***
	2016	68.3 (55–87)	79.4 (61–98)	87.8 (60–111)	94.0 (69–128)	31.5***
	2017	73.2 (58–89)	81.8 (65–102)	92.6 (63–118)	96.1 (69–134)	28.9***
The value of the Kruskal-Wallis test		3.9^{ns}	2.9^{ns}	2.2^{ns}	5.2^{ns}	
Mean length (range) of the inflorescence in the year	2015	6.0 (4.5–8.6)	8.3 (5.9–13.2)	7.0 (1.9–12.5)	9.4 (6.0–13.6)	27.1***
	2016	6.1 (4.8–8.5)	7.2 (5.9–15.5)	7.2 (1.9–12.5)	10.0 (5.4–17.0)	28.3***
	2017	6.3 (4.5–9.0)	7.2 (5.9–15.5)	8.3 (2.5–19.0)	10.2 (6.0–17.0)	26.2***
The value of the Kruskal-Wallis test		1.1^{ns}	1.5^{ns}	2.4^{ns}	1.6^{ns}	
Mean length (range) of dorsal tepal in the year	2015	2.2 (1.6–2.7)	2.5 (2.0–3.1)	2.5 (1.4–2.9)	2.6 (2.0–3.0)	18.7***
	2016	2.3 (1.7–2.9)	2.6 (2.3–3.1)	2.4 (1.6–2.9)	2.7 (2.0–3.8)	14.9**
	2017	2.4 (1.9–2.9)	2.2 (2.3–3.2)	2.4 (1.5–2.9)	2.7 (2.0–3.8)	11.9**
The value of the Kruskal-Wallis test		5.2^{ns}	1.8^{ns}	1.4^{ns}	2.6^{ns}	

viduals. The mortality of sword lily individuals might be caused by the natural processes of senescence, the diseases triggered by pathogens such as fungi, bacteria and viruses, as well as rodent activity (Cantor & Tolety, 2011), while the damage to shoots might be an effect of grazing (Kose & Moora, 2005). On the other hand, the increase of shoot number might be the result of recruitment of new individuals in generative or in vegetative ways. Additionally, it is worth mentioning that the fluctuations in the number of *Gladiolus imbricatus* shoots might be an effect of vegetative dormancy of mature individuals, which spend at least one year entirely below ground without the appearance of any aboveground organs. Such a phenomenon, occurring in response to resource depletion or environmental stress, enables avoidance of unfavorable habitat conditions. Such a phenomenon in individuals of *Gladiolus imbricatus* was already observed by Kubikova and Zeidler (2011 and literature cited here), who noticed that ca. 50% of individuals from the examined sword lily populations remained in dormancy for two years. It is worth mentioning that although the dormancy was observed among numerous herbaceous perennial plants, it was best documented in orchids (Reintal et al., 2010; Tałałąj, 2015 and literature cited here).

The occurrence of shoots in pregenerative stages only in Patch I suggest the successful seedling recruitment and

Table 5. Number (range) of seed capsules in generative shoots of *Gladiolus imbricatus* L. in study plots established within studied moor-grass meadow (Patch I), willow brushwood (Patch II), macroforb community (Patch III) and tall-grass community (Patch IV) in the years 2015–2017. The symbols mean the level of statistical significance: ns-not significant; *-P<0.05; **- P<0.01; ***-P<0.001

	Year	Patch I	Patch II	Patch III	Patch IV	The value of the Kruskal-Wallis H test
Mean number (range) of seed capsules in the year	2015	4.3 (4–6)	5.6 (3–10)	5.9 (4–11)	6.7 (3–10)	27.8***
	2016	5.1 (3–7)	5.0 (2–9)	6.3 (3–12)	6.8 (3–11)	15.4**
	2017	4.3 (3–7)	5.2 (2–9)	5.7 (3–12)	6.1 (3–10)	12.5**
The value of the Kruskal-Wallis test		6.1^{ns}	2.1^{ns}	2.4^{ns}	2.6^{ns}	

their subsequent growth and development. According to Clothier (2003), germination of *Gladiolus imbricatus* occurs during cool, moist spring conditions, following periods of warm then cold stratification. The previous investigations showed that the spontaneous seedling recruitment occurs in gaps in the continuous plant canopy and litter layer (Kostrakiewicz-Gierałt, 2014a), originating as a result of human or animal activities. Additionally, the sowing experiments proved that seed germination might also occur in mowing patches (Jõgar & Moora, 2008). The advantageous role of openings in the continuous plant cover and litter for the presence of individuals in early ontogenic stages was also observed in other bulbous geophyte inhabiting moist meadows of the *Molinietalia* order – *Colchicum autumnale* (Mróz, 2006).

The occurrence of clusters of generative shoots in Patches II, III and IV presumably indicate the successful clonal growth contributing to the multiplication of ramets and the production of descendants with the potential to become independent of the mother organism. The previous observations showed the clonal growth in *Gladiolus* cultivars (Rameau & Gouyon, 1991) and its great enhancement after the clipping of leaves and inflorescences (Memon et al., 2009) or the adding of fertiliser (Ali et al., 2014; Saeed et al., 2014; Khattab et al., 2016). Successful clonal growth was also observed in other tuberous taxa such as *Dicentra canadensis* (Lin et al., 2016) and *Crocus sativus* (Negb et al., 1989).

The much greater number of leaves in Patch IV and the greatest length of leaves in Patches III and IV might increase the effectiveness of light capture during photosynthesis in the neighbourhood of plants with considerable dimensions. The lack of temporal variability and significant spatial variability of *Gladiolus imbricatus* leaf blade dimensions was already observed by Kostrakiewicz-Gierałt (2014b). The aforementioned author found that the rise of the dimensions of leaf blades of *Gladiolus imbricatus* was observed in populations inhibiting *Molinion* meadows in the course of succession. The observed increase of leaf blade dimensions might be result of augmentation of soil humidity. Similar scenario was noticed in *Gladiolus grandiflorus* (Pereira et al., 2016a). On the other hand, the findings of Kubikova and Zeidler (2011) did not show either temporal or spatial variability.

The lack of temporal and considerable spatial variability of dimensions of generative shoots, inflorescences and flowers support previous outcomes (Kostrakiewicz-Gierałt, 2014b). The significant augmentation of dimensions of generative shoots might be result of growing ground moisture. The positive relationship among soil humidity and number and dimensions of shoots, flowers and inflorescences was observed in *Gladiolus grandiflorus* (Porto et al. 2014; Pereira et al. 2016a, 2016b). The reducing flowering of *Gladiolus* individuals in effect of decrease of soil moisture was also observed by Shillo and Halevy (1976). The occurrence of the highest generative shoots of *Gladiolus imbricatus*, as well as the longest inflorescences and flowers in the vicinity of tall-growing neighbours might improve the flower visibility for pollinators from the order *Hymenoptera*, which are attracted particularly by blue, pink, purple and mauve colours (Kevan & Baker, 1983; Menzel & Shmida, 1993; Miller et al., 2011). The number of seed capsules growing in subsequent study sites seems to confirm the successful pollination.

At the same time, it should be pointed out that the increase in the dimensions of generative shoots of *Gladiolus imbricatus* in the vicinity of tall-growing species enables the location of seed capsules in higher layers of the plant cover. The position of the fruits seems to be one of the decisive factors in the enhancement of wind disseminated propagules in new sites. Such a phenomenon was previously observed in several anemochorous species such as *Serratula tinctoria* (Bischoff, 2002; Bischoff et al., 2009).

6. Conclusions

In light of the performed investigations it can be concluded that the population occurring in Patch I (abandoned moorgrass meadow) presents the best condition despite the lowest abundance of shoots. The occurrence of juvenile, vegetative and generative shoots in Patch I might suggest the successful seedling recruitment. Moreover, the other more abundant populations (Patches II–IV) might persist in the colonized sites thanks to the vegetative multiplication of ramets and maximisation of chances for successful pollination and effective seed dispersal.

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