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Regular research paper

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THE INFLUENCE OF SHADOW CREATED BY ADJACENT PLANTS ON PHENOTYPIC PLASTICITY OF ENDANGERED SPECIES *TROLLIUS EUROPAEUS* L (RANUNCULACAE)

ABSTRACT: The assessment of phenotypic plasticity expressed as the response to abiotic and biotic site factors is important for successful conservation of endangered and threatened species. In Poland one of the strictly protected plant requiring an active conservation is globeflower *Trollius europaeus* L. It is the perennial forb, consisted of numerous dark green, deeply cut basal leaves and generative shoots with flowers composed of several multi-ovulate carpels. The investigations of morphological traits of *Trollius europaeus* i.e. number and height of generative shoots and basal leaves as well as the production of flowers, multi-follicles and follicles at stem- and cluster levels, were carried out between 2005 and 2008 on two patches of *Molinietum caeruleae* localized in Kraków vicinity (Southern Poland) and having different height of litter and herb layer. The study plot labelled NS- “not shaded” (2 000 m²) was prevailed by perennials with delicate procumbent or erect stems, small-tussock grass or short rosette-forb species. The height of the tallest plant has not exceeded 98 cm, while the litter layer measured from 10 cm to 28 cm. The study plot named SH- “shaded” (6 000 m²) was characterised by presence of tall perennials as well as grass and sedges forming large compact tussocks. The tallest plants attained 186 cm, whereas the layer of litter reached from 18 cm to 42 cm.

In NS plot -32 clusters were observed, whereas in SH plot 39 clusters occurred. In both populations, clusters were situated in close vicin-

ity, forming large aggregations. The number of aboveground units per cluster in both populations were similar. The longer petioles (higher petiole average length), caused by maximization of light capture were noted in SH, than in NS plot. In SH plot higher sexual shoots were also noted as well as greater number of flowers per shoot. Such phenomenon presumably makes the plant more attractive for pollinators and thus pollen receipt and donation. The similar number of flowers and multi-follicles per cluster were observed in both populations, while the greater number of follicles was observed in NS, than in SH plot.

Due to morphological plasticity established clusters of *T. europaeus* might presumably endure among the vegetation cover or adapt to new environmental conditions. It might be considered that making the gaps in vegetation cover and litter can be an effective way for active protection of *Trollius europaeus* populations.

KEY WORDS: basal leaf, cluster, generative shoot, plasticity, *Trollius europaeus*

1. INTRODUCTION

The study of phenotypic plasticity, being the fundamental property of organisms to produce different phenotypes in different environments, has progressed significantly over the past few decades and has become a central

issue of ecological and evolutionary research (Schlichting and Smith 2002, Pigliucci 2005, Pigliucci *et al.* 2006, Valladares *et al.* 2007). A wealth of data reviewed by Schlichting (1986, 2002) and Miner *et al.* (2005) have demonstrated the effect of abiotic factors considering light, temperature, water and nutrients availability as well as biotic factors including the role of competitors, predators and pollinators on plant plasticity. Initial studies of plant plasticity have focused on plant size, morphology or physiology. More recent investigations have concentrated on aspects of plasticity that relate directly to the functional and reproductive success of plants in their environments. Several authors have observed plasticity of developmental and reproductive timing, breeding system and offspring developmental patterns (Sultan 2000). The main directions in future studies of plant phenotypic plasticity have been proposed by Sultan (2004). She argued that investigations of plastic response to naturally and human-mediated environmental variation in narrowly distributed and threatened species is necessary for understanding current distributions of organisms and is ecologically and evolutionary important. Based on plasticity it may be possible to predict whether a population will be successful in environment. The knowledge of plasticity has the potential to provide useful biological information for the conservation and management strategies for rare species. Indeed, a growing number of studies have focused on plasticity of endangered species (Kéry *et al.* 2000, Aleric and Kirkman 2005, Berg *et al.* 2005, Becker *et al.* 2006, Hensen and Wesche 2006, Jongejans *et al.* 2006, Noel *et al.* 2007).

Despite of voluminous literature, the current state of knowledge of plasticity of threatened species is still insufficient. In Poland one of the rare and strictly protected plant with a requirement for active conservation is globe-flower *Trollius europaeus* L. (Rozporządzenie 2004). This species is evaluated as endangered in Mecklenburg (Ingelög *et al.* 1993) and Brandenburg (Benkert and Klemm 1993) and classified as vulnerable in Schleswig-Holstein (Ingelög *et al.* 1993), Ireland (Curtis and McGough 1988) and Belarus (Sachanka *et al.* 1993).

T. europaeus is listed as a species of the Euro-Siberian subelement, widely but patchily distributed in northern and central Europe (Hultén and Fries 1986). The populations are found in damp ground in shady areas of oak woods (*Potentillo albae-Quercetum*) and macroforb community (*Filipendulo-Gerani-etum*), but the most often they are recorded in moist meadows of the alliance *Molinion: Cirsio-Polygonetum bistortae*, *Polygono bistortae-Trollietum europaei* and *Molinietum caeruleae* (Matuszkiewicz 2001). The globe-flower is perennial forb, consisted of numerous dark green, deeply cut basal leaves and generative shoots. The plant usually produces flowers composed of several multi-ovulate carpels. The self-incompatible flowers are pollinated by bumblebee queens as well as *Chiastocheta* flies, which lays eggs on the developing fruits. The larvae destroy some seeds but many more are left intact, so that the overall interaction is mutually beneficial. Mature follicles open, liberating seeds that germinate next season (Pellmyr 1989, Despres *et al.* 2002).

The present studies was undertaken to quantify the morphological plasticity of chosen features in *T. europaeus* populations in different grassland habitats within a relatively small area. The specific objectives were:

1. to examine how the shadow conditions created by the plant living in close vicinity affect the numbers of above ground units in *T. europaeus* clusters;
2. to investigate how neighbourhood of other plants influences on the height of basal leaves petioles and sexual shoots;
3. to study the production of flowers, multi-follicles and follicles in stem- and cluster-levels in populations from different shadow conditions.

2. STUDY AREA

The studies were carried out in western edge of Krakow area (South Poland) (Fig.1). The research area is located at ca 210 m a.s.l., on a low flood terrace of the Vistula, 3.0–6.0 m high. The water table is 0–2 m below the ground surface. The soils in the Vistula River valley consist of black earth and light clay. The area is covered by *Molinietum caeruleae* patches, which are the relicts of vast mead-

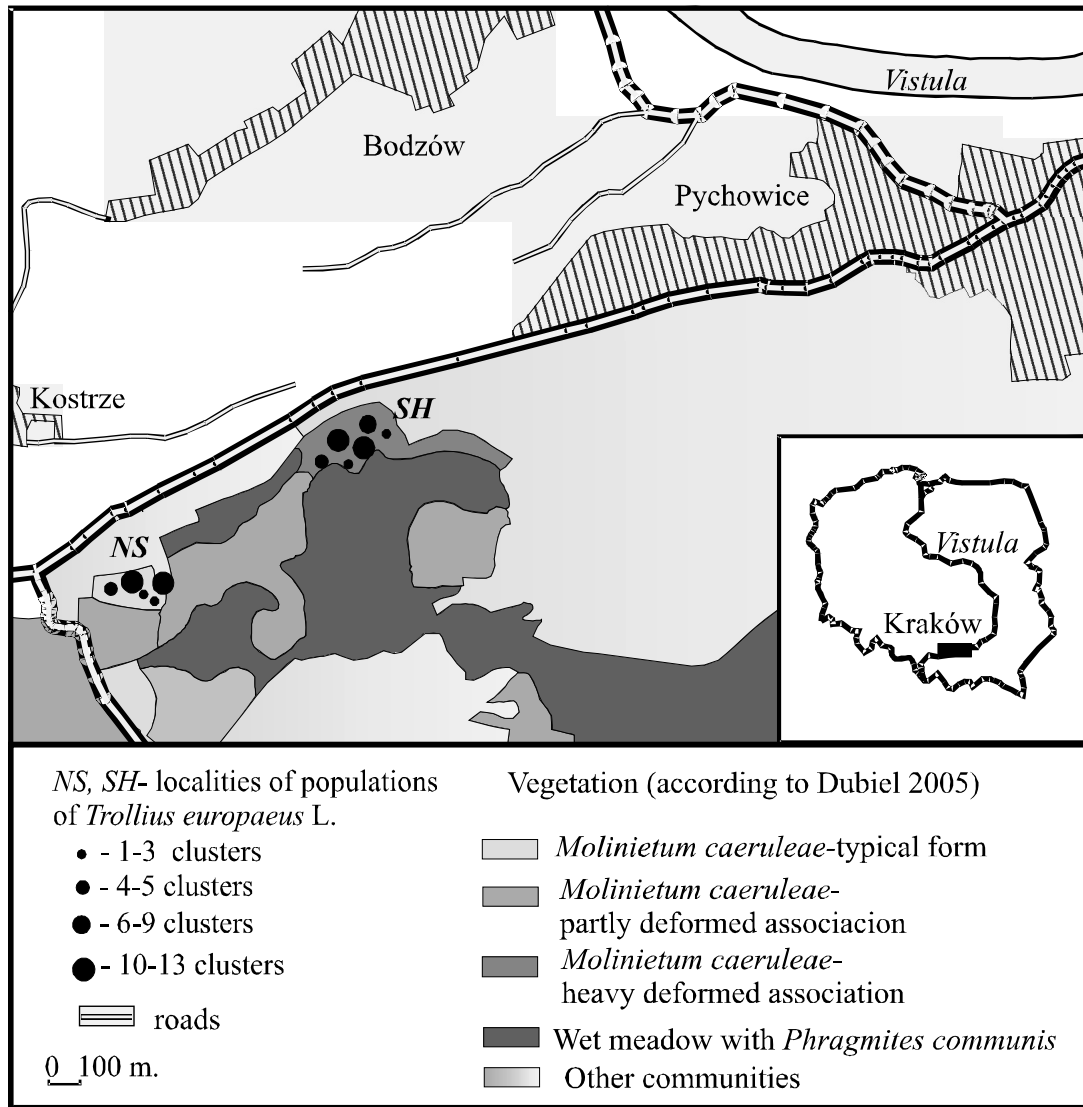


Fig. 1. The locality of studied *Trollius europaeus* L. populations in Krakow (South Poland): SH- shaded plot, NS- not-shaded plot.

ows once occurring in the region (Zarzycki 1958), nowadays very rare in the Upper Vistula River Valley (Dubiel 1989). Several authors (Denisiuk 1987, Denisiuk *et al.* 1995, Zając and Zając 1998, Dubiel and SzwaGrzyk 2008) classified the blue moor grass meadows occurring in the study area to the most valuable in Kraków because of the presence of several rare, endangered and vulnerable plant species. Additionally, it should be stressed that The World Conservation Union (IUCN) includes the wet and humid meadows among the most threatened habitats of Europe (Denisiuk 1991). The *Mo-*

linion alliance can be found in Annex I to the Habitat Directive (Council Directive 92, Council Directive 97) and it is included in the net NATURA 2000 (Interpretation 2003).

The studies were conducted in two patches, which had not been managed for at least a dozen years (Dubiel 1991, 1996). The both patches differ with respect to vegetation structure *i.e.* the floristic composition and layer of litter. The study area (50°01'01"N; 19°52'03.2"E), named NS- "not shaded" measured 2 000 m² and was prevailed by species creating delicate, erect or procumbent stems (*i.e.* *Lathyrus pratensis* L., *Lotus corniculatus*

L.), small-tussock grass (*i.e.* *Briza media* L., *Holcus lanatus* L.) or short rosette-forb species (*i.e.* *Lychnis flos-cucculi* L., *Succisa pratensis* Mnch.). The height of the tallest plant not exceeded 98 cm, while the litter layer achieved from 10 cm to 28 cm. The study area named labeled SH- "shaded" (50°01'55"N; 19°52'02.3"E), measured 6 000 m² was characterised by presence of tall plant. In observed plot prevailed tall perennials (*i.e.* *Phragmites australis* Trin.), grass and sedges forming large compact tussocks with high stems (*i.e.* *Molinia caerulea* (L.) Moench, *Carex gracilis* Curt.), and willows (*i.e.* *Salix rosmarinifolia* L. and *S. cinerea* L.). The tallest plants attained 186 cm, whereas the layer of litter reached from 18 cm to 42 cm.

3. MATERIAL AND METHODS

A cluster of basal leaves (butt end leaves) with sexual stems was adopted as the basic demographic unit. The cluster might contain an individual or several genets. The field work was performed during the period 2005–2008. During the whole study period, at both plots, the abundance of clusters stayed constant. In NS plot 32 clusters occurred forming 5 aggregations, while in SH plot 39 clusters were found forming 6 aggregations (Fig. 1). All clusters were ringed and marked with small

numbered plastic pegs. Also each sexual shoot was tagged. The same number of clusters was counted each year. Every year following parameters were counted and measured: number and percentage of butt end leaves and generative shoots per clusters, height of petioles of basal leaves, length of sexual shoots, number of flowers, multi-follicles and follicles per stems and clusters. The normal distribution of collected data were tested using the Kolmogorow-Smirnow test, while the homogeneity of variances were checked using the Brown-Forsythe test. The data were not transformed to meet the normal distribution and improve homogeneity of variances. When the variances were unequal the statistical analysis was performed with non-parametric U-Mann-Whitney test, when they were equal - the t-Student test was applied.

4. RESULTS

During whole study period the number of aboveground units per cluster in SH and NS plots were similar (Table 1). In both populations the clusters were consisted of 11.0 basal leaves and 2.0 sexual stems on average.

The length of petioles of basal leaves and sexual stems in consecutive years were rather constant but differed significantly between plots. The diameter of basal leaf petioles in

Table 1. The average number (SD) of basal leaves and generative shoots of *Trollius europaeus* L. per cluster in not-shaded NS and shaded SH plots in the period 2005–2008. Asterisks mean differences statistically significant between populations (the U Mann-Whitney test). * $P \leq 0.05$

Plot	Year	Number of clusters	Total number of above ground units		Number of basal leaves per cluster		Number of generative shoots per cluster	
			Mean	SD	Mean	SD	Mean	SD
NS	2005	32	11.1	6.6	9.7	6.2	2.1	1.7
	2006	32	12.7	7.2	10.9	6.0	2.5	1.2
	2007	32	15.0	9.6	11.9	9.0	3.3*	2.0
	2008	32	16.2	11.4	13.7	9.3	3.6	3.1
SH	2005	39	11.4	7.6	10.1	7.1	1.5	1.2
	2006	39	13.7	9.0	11.2	8.5	1.8	1.1
	2007	39	15.5	9.2	11.7	7.6	1.8	1.3
	2008	39	18.3	11.5	16.5	10.7	2.3	1.7

Table 2. The mean (SD) number of flowers, multi-follicles and follicles per generative shoot in *Trollius europaeus* L. populations in not-shaded NS and SH shaded plots in the period 2005–2008. Asterisks mean differences statistically significant between populations (the U Mann-Whitney test). * $P \leq 0.05$; ** $P < 0.01$; *** $P < 0.001$

Plot	Year	Total number of generative shoots in population	Number of flowers per generative shoot		Number of multi-follicles per generative shoot		Number of follicles per generative shoot	
			Mean	SD	Mean	SD	Mean	SD
NS	2005	83	1.0***	0.4	1.0**	0.4	40.4**	14.2
	2006	76	1.0***	0.4	1.0**	0.5	41.3**	15.4
	2007	99	1.3***	0.5	1.3*	0.5	41.0**	15.3
	2008	117	1.2***	0.4	1.2*	0.4	39.0***	14.9
SH	2005	76	1.8	1.0	1.8	0.5	49.7	22.2
	2006	66	1.9	1.0	1.9	0.7	51.1	24.0
	2007	70	1.8	0.9	1.8	0.6	47.6	21.7
	2008	89	1.6	0.9	1.6	0.7	48.2	25.7

SH plot was about two-fold greater than in NS plot (Fig. 2). Also the generative shoots were much higher in SH plot (Fig. 3).

The observations showed that in consecutive years the number of flowers, multi-follicles and follicles per generative shoot were greater in SH plot than in NS plot (Table 2). The number of flowers as well as multi-follicles per cluster in both populations were similar, whereas the number of follicles was much higher in NS than in SH plot (Table 3).

5. DISCUSSION

Basic plant ecology suggests that plant-plant interactions in space are common in nature and the individuals interact with their neighbours over restricted distances. Positive neighbour effects strengthen the protection from herbivores or excessive solar radiation. Negative influences are more important because all plants require the same resources. Therefore, plant response to neighbourhood is an adaptation to avoid, retard or at least reduce competitive suppression (Ballaré 1999, Stoll and Weiner 2000). Such adaptation, expressing in variability of plant size, stem and leaves diameter as well as flowers and fruits production in different vicinity has been ob-

served in several annuals (Diethart 1990, Bell and Galloway 2007), herbaceous perennials (Vermeulen *et al.* 2007), shrubs (Tyler and D'Antonio 1995) as well as trees (Brisson 2001, Tucić *et al.* 2005).

Performed studies suggest that, shadow created by adjacent plants do not effect on number of aboveground units of *T. europaeus* clusters. Other studies found that dimensions of globeflower individuals increase with augmentation of soil saturation ratio with basic cations and sorption capacity (Antkowiak 1999) and diminish with altitudinal gradient (Hemborg and Karlson 1998). The influence of availability of soil nutrients and other plants vicinity on plant size was observed in closely related species *T. ranunculoides* Hemsl. (Zhao *et al.* 2007). The individuals achieved great dimensions in shaded bottom layer of shrub community because of high values of phosphorus and nitrogen as well as organic matter and moisture in the soil. Much smaller individuals were noted in grassland in effect of great density of neighbouring plants and limitation of soil nutrients.

Presented results imply that the greater length of petiole of basal leaves in population in shaded plot (SH) was caused by necessity to maximize the light interception. Another

Table 3. The average number (SD) of flowers, multi-follicles and follicles per cluster in *Trollius europaeus* L. populations localized in NS and SH plots in the period 2005–2008. Asterisks mean differences statistically significant between populations (the Student-test). * $P \leq 0.05$; ** $P < 0.01$; *** $P < 0.001$

Plot	Year	Number of clusters	Number of flowers per cluster		Number of multi-follicles per cluster		Number of follicles per cluster	
			Mean	SD	Mean	SD	Mean	SD
NS	2005	32	4.1	2.7	4.1	2.7	106.2**	92.2
	2006	32	4.2	2.8	4.2	2.8	104.9*	90.3
	2007	32	4.3	3.8	4.3	3.8	131.4***	124.1
	2008	32	4.7	4.1	4.7	4.1	156.1***	138.2
SH	2005	39	3.9	2.2	3.9	2.2	94.3	75.3
	2006	39	3.5	2.6	3.5	2.6	95.5	54.9
	2007	39	3.4	2.3	3.4	2.3	89.4	53.6
	2008	39	3.8	2.6	3.8	2.6	110.0	84.6

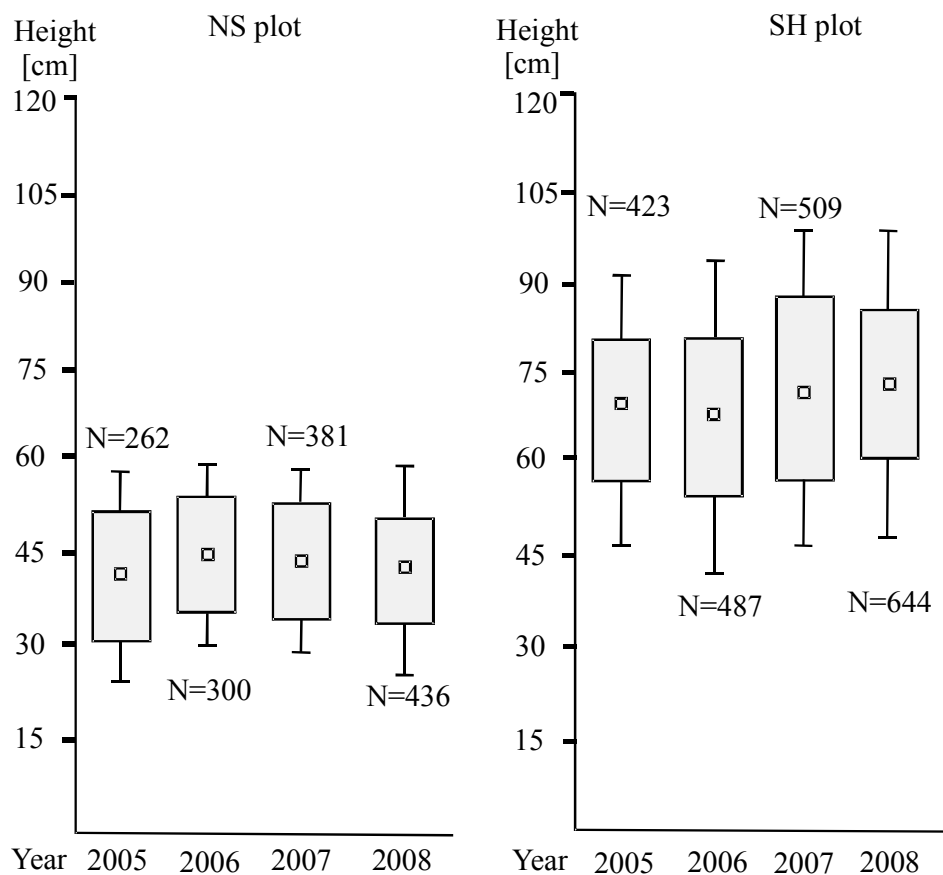


Fig. 2. The height (cm) of basal leaves of *Trollius europaeus* L. in NS (not-shaded) and SH (shaded) plots in the years 2005–2008. Box and whisker plots give the mean (square), SE (box) and SD (whiskers). There are significant differences among NS and SH plots in each year by the U Mann-Whitney test at the 0.001 level.

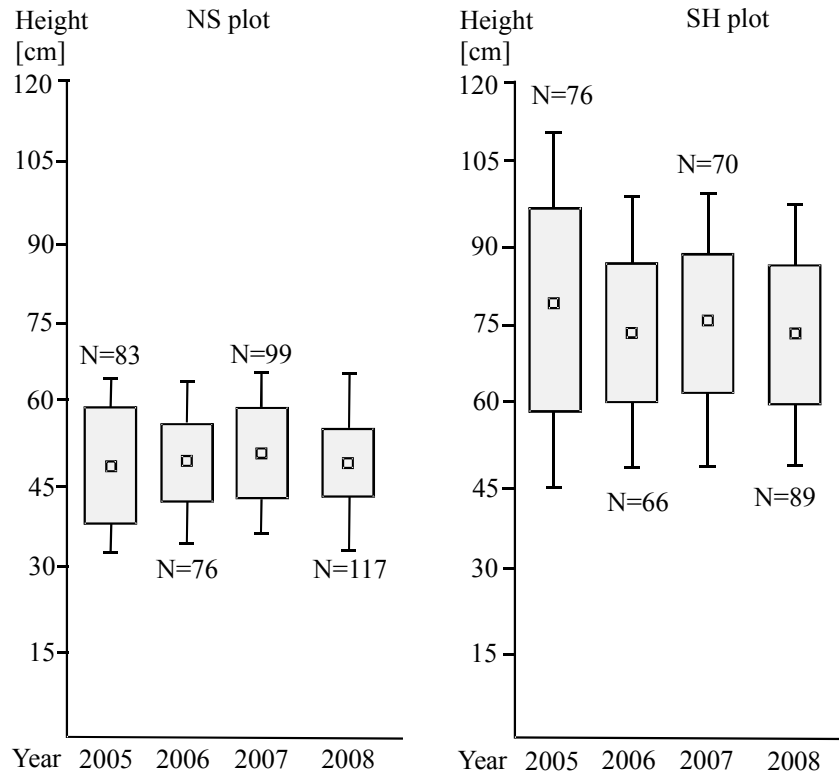


Fig. 3. The height (cm) of sexual shoots of *Trollius europaeus* L. in NS (not-shaded) and SH (shaded) plots in the years 2005–2008. Box and whisker plots give the mean (square), SE (box) and SD (whiskers). There are significant differences among NS and SH plots in each year by the U Mann-Whitney test at the 0.001 level.

observations carried out by Hitchmough (2003) confirmed that seedlings of globeflower in unmown swards were etiolated in comparison with seedlings in the mown swards. The strong vertical growth, achieved through long internodes and petioles in response to shading were observed in several herbaceous plant (Baumann *et al.* 2001, Jensen and Meyer 2001) as well as tree species (King 1990). The generative stems of *T. europaeus* are taller in shaded environment as well. Current observations confirmed previous investigations made by Antkowiak (2002), showing that elongation of sexual shoots in *T. europaeus* is linked with increase of number of flowers. Such phenomenon contributes to augmentation of visit frequency of pollinators and thus pollen receipt and donation. Many authors confirmed that large inflorescences are more conspicuous and more attractive to pollinators (Pyke 1981, Williams *et al.* 2001, Biernaskie and Cartar 2004, Williams 2007). On the other hand the in-

vestment in height incurs costs in construction and maintenance of stem (Falster and Westoby 2003). In light of these findings, it might be assumed that low length of petioles of basal leaves and sexual stems in not-shaded plot (NS) was caused by their greater accessibility for pollinators and availability of solar radiation. Apart from this, low height of generative shoots and petioles of basal leaves decrease risk of breakage. The similar pattern of plasticity of morphological and generative traits showed *Scabiosa columbaria* L. and *Plantago media* L. growing in calcareous grassland. The diameter of rosettes, shoot height and the number of flower-heads and diaspores per inflorescence increased significantly with increasing vegetation cover and litter (Mückschel and Otte 2003). Performed observations showed great plasticity in number of fruits per *T. europaeus* cluster as well. According to Aguilar *et al.* (2006), the lower production follicles in shaded plot might be the result of unfavourable habitat

conditions. The reduction of fecundity under low availability of solar radiation was observed in several species (McCall and Primack 1987, Vila and Terradas 1991, Pfitsch and Pearcy 1992, Naito and Nobukazu 1995, Honnay *et al.* 2005).

Lepik *et al.* (2005) stressed, that plasticity favor plant coexistence in numerous communities of herbaceous vegetation. In light of these findings, the morphological variability in *T. europaeus* is a key to success for the individual plant in environments, because it enables presumably endure in the adjacent vegetation and adjust to new habitat conditions. The persistence of established clusters is especially important because in both studied populations the number of clusters stayed constant from year to year. Several authors (Milberg 1994, Danvind and Nilsson 1997, Hitchmough 2003) added, that although seeds of globe flower are dispersed by rain or seasonally high flood water and possess the abilities to germinate in light and darkness, in natural stands the seedlings are growing only in artificially made gaps. Combining results of performed observations and published data it should be stress that artificial gaps might be an effective way for populations restoration and active protection this species.

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