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THE EFFECT OF VEGETATION CHARACTER ON ABUNDANCE AND STRUCTURE OF SUBPOPULATIONS OF RARE HERB SPECIES GENTIANA PNEUMONANTHE L.

ABSTRACT: During the 20th century in Central and Eastern Europe, traditional agricultural management was either heavily intensified or abandoned due to socio-economic reasons. The land abandonment led to subsequent secondary succession reverted many wet meadows into Phragmites swamps, Salix or Alnus thickets, as well as woodlands. Therefore, the understanding of changes in abundance and structure of populations in the process of succession has become very important especially for rare and endangered species. In Poland one of strictly protected plant is Gentiana pneumonanthe L. It is a nonclonal, long-lived, iteroparous plant consisted of numerous vegetative and generative stems, bearing 1–25 flowers per year. The investigations of abundance and structure of subpopulations of Gentiana pneumonanthe were conducted in the years 2009–2011 in abandoned Molinietum caeruleae meadows dominated by low-stature species (Patch I), prevailed by tall grasses (Patch II), willows (Patch III), as well as partly overgrown by shrubs and trees (Patch IV). The average height of vegetation cover achieved from 65.3 cm (Patch I), via 85.8 cm (Patch II) and 94.0 cm (Patch III), to 142.7 cm (Patch IV).

The gradually decline of abundance of Gentiana pneumonathe subpopulations and increased trend toward their senilization along the gradient of vegetation height might be due to successional closure of plant cover, preventing seedling recruitment. The total number of stems per individual and length of vegetative stems decreased with augmentation of neighbouring plants dimensions, whereas the height of generative stems, as well as flower and fruit production presented inverted trend. The greatest dimensions of capsules found in patch dominated by small meadow species might be due to greater availability of solar radiation.

The conditions of studied subpopulations decrease gradually from patch dominated by small meadow species, via sites prevailed by grasses and willows, to place overgrown by shrubs and trees. Although obvious differences in abundance and structure of individuals, the prospects of all observed populations are poor, especially that patches are not subjected active protection.

KEY WORDS: flowers, fruits, Gentiana pneumonanthe, individual, shading, stem, subpopulation, vegetation

1. INTRODUCTION

During the 20th century in Central and Eastern Europe, traditional agricultural management was either heavily intensified or abandoned due to socio-economic reasons. The land abandonment led to subsequent secondary succession reverted many wet meadows into Phragmites swamps, Salix or Alnus thickets, as well as woodlands. The fragmentation
or loss of habitats directly contributed to a decrease of species diversity and a replacement of specialist species by more generalist ones (Joyce and Wayde 1998, Green 1990, Diemer et al. 2001, Muller 2002, Peintinger and Bergamini 2006, Burnside et al. 2007, Truus and Puusild 2009, Rosenthal 2010, Op den Kamp et al. 2012). Therefore, the understanding of changes in abundance of individuals, as well as structure of populations in the process of succession has become very important in ecology. However, in spite of increasing interest in this issue and steadily growing number of studies (Falińska 1986, 1997, Brzosko 1999, 2001, Billeter et al. 2003), the present state of knowledge still remains unsatisfactory. Especially there is lack of investigations of effect of cessation of management on number and structure of populations of rare and threatened species. Such studies provide data useful to presenting the present vitality of populations and predicting the future fate of individuals, necessary for effective protection of endangered taxa.

Taking into account insufficient state of knowledge the objective of presented study was to recognize the abundance and developmental structure of subpopulations, (2) the size of individuals in the studied subpopulations based on total number of stems, as well as height of generative and vegetative stems, (3) the flower and fruit production in subpopulations, (4) the dimensions of fruits produced in particular subpopulations.

2. STUDY AREA

The studies were carried out in Kostrze district located on the western edge of Kraków, south of the Vistula River (Fig. 1). The patches of Molinietum caeruleae occurring in these locality are remnants of vast meadows, which existed along the Vistula River from Czernichów to the Niepołomice Primeval Forest (Zarzycki 1958). The investigations were conducted in unmanaged Molinietum caeruleae patches abandoned at different times, at least 15 years before that study began (Dubiel 1996) and characterized by various species composition:

– Patch I (50°01’54.65”N, 19°52’07.55”E) measured ca 1 400 m² was dominated by species creating shallowly rooted rhizomes or stolons and delicate, erect or procumbent stems.

– Patch II (50°01’56.01”N, 19°52’08.83”E), covered an area of 1 300 m² was prevailed by grasses growing to 2.0 m and forming large tussocks or robust rhizomes.
The abundance and structure of subpopulations of *Gentiana pneumonanthe* L.

– Patch III (50°01′40.39″N, 19°51′33.52″E) measured about 1 450 m² was overgrown by *Salix repens* var. *rosmarinifolia* forming creeping, procumbent stems and low-growing branches.

– Patch IV (50°00′57.00″N, 19°50′39.67″E) covered ca 1 600 m² was partly overgrown by shrubs achieved 3–5 m and trees growing to 8–10 m with wide-spreading large roots.

The average vegetation height in described patches (calculated on the basis of 50 measurements of randomly chosen stems of different species) differed substantially. The detailed descriptions of character of vegetation in studied patches are given in Table 1.

3. MATERIALS AND METHODS

3.1. Study object

Marsh gentian *Gentiana pneumonanthe* L. is a nonclonal, long-lived, iteroparous plant that usually produces numerous vegetative stems and 1–10 generative stems, bearing 1–25 flowers per year. The capsules containing 300–700 seeds, weighing on average 0.05 mg, ripen during September and October. The small and light seeds, adapted to wind dispersal germinate in the following spring (Simmonds 1946). *Gentiana pneumonanthe* L. belongs to rare and strictly protected plants in Poland (Rozporządzenie Ministra Środowiska 2012), included to Red List of Vascular Plants (Zarzycki and Szeląg 2006). This species represents Euro-siberian subelement occurring in Europe from southern Scandinavia to northern Portugal and eastern Russia (Den Virtuellra Floran 1996). In Poland the majority of localities occur in Lower Silesia, the Lublin upland and Roztocze (Zajac and Zajac 2001). The populations of *Gentiana pneumonanthe* develop on wet, acid, lowland heaths and meadows.

3.2. Field study and statistical analysis

In the year 2009 the abundance and development structure of populations occurred

<table>
<thead>
<tr>
<th>Patch</th>
<th>Coordinates</th>
<th>Patch area (m²)</th>
<th>Number of species per patch</th>
<th>Dominants in plant canopy (species, with cover exceed 20%)</th>
<th>Subdominants in plant canopy (species, with cover achieved 5–20%)</th>
<th>Average vegetation height (cm)</th>
<th>Average vegetation cover (%)</th>
<th>Average cryptogamme cover (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>50°01′54.65″N, 19°52′07.55″E</td>
<td>1 400</td>
<td>53</td>
<td><em>Lotus corniculatus</em>, <em>Lychnis flos-cuculi</em>, <em>Briza media</em></td>
<td><em>Succisa pratensis</em>, <em>Betonica officinalis</em>, <em>Lysimachia vulgaris</em></td>
<td>65.3</td>
<td>100</td>
<td>0</td>
</tr>
<tr>
<td>II</td>
<td>50°01′56.01″N, 19°52′08.83″E</td>
<td>1 300</td>
<td>48</td>
<td><em>Molinia caerulea</em>, <em>Deschampsia caespitosa</em>, <em>Phragmites australis</em></td>
<td><em>Serratula tinctoria</em>, <em>Succisa pratensis</em></td>
<td>85.8</td>
<td>100</td>
<td>0</td>
</tr>
<tr>
<td>III</td>
<td>50°01′40.39″N, 19°51′33.52″E</td>
<td>1 450</td>
<td>39</td>
<td><em>Salix repens</em> ssp. <em>rosmarinifolia</em></td>
<td><em>S. aurita</em>, <em>S. cinerea</em>, <em>Galium boreale</em>, <em>G. verum</em></td>
<td>94.0</td>
<td>90</td>
<td>2</td>
</tr>
<tr>
<td>IV</td>
<td>50°00′57.00″N, 19°50′39.67″E</td>
<td>1 600</td>
<td>32</td>
<td><em>Crataegus sp.</em>, <em>Sambucus nigra</em>, <em>Populus tremula</em>, <em>Betula verrucosa</em></td>
<td><em>Phragmites australis</em>, <em>Chamaenerion angustifolium</em>, <em>Lythrum salicaria</em></td>
<td>142.7</td>
<td>95</td>
<td>5</td>
</tr>
</tbody>
</table>
in aforementioned patches were investigated. Then, in each population the permanent plots measured 30 m × 30 m were set and surrounded. All genets growing within them were marked with small, numbered plastic pegs and each sexual shoot was tagged. In the period 2009–2011 the following parameters were counted and measured: total number of stems per individual, height of vegetative and generative stems, number of flowers and fruits per generative stem and per individual, the length and width (in central part) of all capsules.

The chi-square statistics was applied to check whether there were significant differences among subpopulations in percentage of individuals:
- creating various total number of stems,
- achieving different height of vegetative and generative stems.

The H Kruskal-Wallis test was used to test whether there were significant differences among subpopulations in number of flowers and fruits, as well as in length and width of capsules.

4. RESULTS

The largest subpopulation of *Gentiana pneumonanthe* occurred in patch I, lower number of individuals were recorded in sites II and III, while the smallest subpopulation was noted in place IV. In all plots the seedlings and juvenile individuals were not found. The percentage of vegetative adults decreased, while share of generative adults augmented gradually from patch I, via II and III, to site IV (Fig. 2). The total number of stems per individual, height of vegetative and generative stems, as well as flower and fruit production and capsule dimensions in consecutive years were constant but differed substantially between patches. The greatest total number of stems per individual was observed in patch I and declined gradually in the other sites (Fig. 3). The highest vegetative stems occurred in patch I, while the lowest ones were noted in place IV (Fig. 4). The generative stems presented inversed tendency (Fig. 5). Much greater production of flowers (Fig. 6) and fruits (Fig. 7) were observed in patch IV, than in other plots. The substantially larger capsules occurred in patch I, than in places III and IV (Fig. 8).

5. DISCUSSION

The gradually decline of abundance of *Gentiana pneumonanthe* populations and increased trend toward their senilization along the gradient of vegetation height might be due to successional closure of plant cover. Similar tendency were previously observed in heathlands and grasslands (Oostermaijer *et al.* 1994, 1996, 1998). On the other hand, numerous authors (Křenová and Lepš 1996, Rose *et al.* 1998, Volis *et al.* 2005) claimed, that disturbances in continuous plant canopy and litter layer enables the recruitment of *Gentiana pneumonanthe* seedlings, leading to maintenance or increase of population vitality. Similar phenomenon were also recorded in populations of other several species occurring in unmanaged wet meadows such as *Viola palustris* L. (Jensen and Meyer 2001), *Succisa pratensis* Moench. (Soons *et al.* 2005), *Gladiolus imbricatus* L. (Moora *et al.* 2007), and *Dactylorhiza incarnata* (L.) Soo (Schrautzer *et al.* 2011).

In light of findings of Casper and Jackson (1997), the gradually decline of total number of stems per individual in populations of *Gentiana pneumonanthe* occurring along the gradient of vegetation height might be caused by space depletion by neighbouring plants, achieving great dimensions and creating robust underground organs. The negative influence of strong competitors occurring in abandoned wet meadows on size of individuals of clonal species were already observed. The macroforbs with robust, deeply rooted rhizomes and sedges forming large tussocks successfully fill up free space, limiting ramet multiplication and vegetative spread of genets *Filipendula ulmaria* (L.) Maxim. (Falińska 1995), *Iris pseudacorus* L. (Falińska 1986) and *I. sibirica* L. (Kostrakiewicz 2007).

Performed results, showing that the dimensions of vegetative stems of marsh gentian dropped significantly along the gradient of vegetation height are in contrary to wide array of observations reviewed by Poorter *et al.* (2011). Aforementioned authors argued, that under crowding conditions and in the vicinity of tall-growing plants, the height increment is advantageous because it allows to overtop neighbours and contributes to more effective light interception. The
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Fig. 2. The development structure of studied populations of *Gentiana pneumonanthe* L. in the year 2009. S – seedlings, JUV – juvenile individuals, VEG – vegetative adults, GEN – generative adults. The horizontal axes depict the percentage of genets in particular stages.

Fig. 3. The structure of size of *Gentiana pneumonanthe* L. individuals in the studied populations based on total number stems in the years 2009–2011. The horizontal axes depict the percentage of genets in particular size classes. There are significant differences between patches in each year by the χ test ($df = 6$) at the level 0.001.

Fig. 4. The structure of size of *Gentiana pneumonanthe* L. individuals in the studied populations based on the height of vegetative stems (cm) in the years 2009–2011. The horizontal axes depict the percentage of genets in particular size classes. There are significant differences between patches in each year by the χ test ($df = 6$) at the level 0.001.
observed in populations of *Gentiana pneumonanthe* rise of length of generative stems and increase of flower and fruit production along the gradient of vegetation height, stay in accordance with observations carried out in populations of nonclonal *Trollius europaeus* L. in unmanaged *Molinietum caeruleae* meadows. The sexual stems of globeflower achieved greater dimensions, and produced more flowers and fruits in shaded place, than in open site (Kostrakiewicz 2009). Additionally, it is worth noticing, that negative relation between size of capsules of *Gentiana pneumonanthe* and vegetation height might be connected with level of solar radiation. The decreasing dimensions of fruits at low light availability were previously found in annual species (Piskorz 2005), perennials (Jacquemyn et al. 2008, Schoeb et al. 2010, Stachurska-Swakoń and Kuź 2011), as well as shrubs (Delgado et al. 2011).

Concluding, it should be pointed out, that condition of studied subpopulations decreases gradually from plot dominated by small meadow species, via sites prevailed by grasses and willows, to place overgrown by shrubs and trees. Although obvious differences in

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**Fig. 5.** The structure of size of *Gentiana pneumonanthe* L. individuals in the studied populations based on the height of generative stems (cm) in the years 2009–2011. The horizontal axes depict the percentage of genets in particular size classes. There are significant differences between patches in each year by the χ test (df = 6) at the level 0.001.

**Fig. 6.** The number of flowers per stem and par genet in studied populations of *Gentiana pneumonanthe* L. in the years 2009–2011. Box and whisker plots give the mean (square), SE (box) and SD (whiskers). Asterisks mean significant differences in number of flowers between patches I and II (a), I and III (b), I and IV (c), II and III (d), II and IV (e), III and IV (f). *P ≤0.05, **P <0.01, ***P <0.001.
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The abundance and structure of individuals, the prospects of all observed subpopulations are poor, especially that patches are not subjected active protection.

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Fig. 7. The number of capsules per stem and par genet in studied populations of *Gentiana pneumonanthe* L. in the years 2009–2011. Box and whisker plots give the mean (square), SE (box) and SD (whiskers). Asterisks mean significant differences in number of capsules between patches I and II (a), I and III (b), I and IV (c), II and III (d), II and IV (e), III and IV (f). * P≤0.05, ** P <0.01, *** P <0.001.

Fig. 8. The length and width of capsules (cm) in studied populations of *Gentiana pneumonanthe* L. in the years 2009–2010. Box and whisker plots give the mean (square), SE (box) and SD (whiskers). Asterisks mean significant differences in length/width of capsules between patches I and II (a), I and III (b), I and IV (c), II and III (d), II and IV (e), III and IV (f). * P≤0.05, ** P <0.01, *** P <0.001.

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