Population traits of the rare plant species *Succisa pratensis* Moench. in meadow overgrowing

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Abstract: This paper examines the population traits of the rare plant species *Succisa pratensis* Moench. in the course of meadow overgrowing. The investigations were conducted in the years 2010-13, in *Molinia caeruleae* meadows situated in Kraków-Kostrze (southern Poland). The study sites represented the early (Patch I), medium (Patch II and III) and late (Patch IV) stages of succession. The abundance of subpopulations diminished from Patch I, via Patches II and IV, to Patch III. The increase in abundance in consecutive years was noticed in Patch I; an inverse tendency was found in Patches II and III, whereas lack of variability was recorded in Patch IV. The signs of senescence found in consecutive years in all subpopulations were mostly pronounced in Patches III and IV. The number of rosettes per ramet cluster did not show either temporal or spatial variability. The number of leaves per rosette diminished, while the dimensions of rosette leaves gradually increased in time and space due to diminishing light availability. The number and height of flowering stems, number of cauline leaves, as well as number of flower heads per flowering stem increased from Patch I to Patch III due to lateral shading, and then it diminished in Patch IV due to shading from above. The performed studies indicate that the subpopulation occurring in Patch I has the greatest chance for maintenance in the colonized sites, while the subpopulation occurring in Patch III is the most endangered by extinction.

Key words: genet; *Molinia caeruleae;* ramet cluster; secondary succession; subpopulation, *Succisa pratensis*

INTRODUCTION

Almost all organisms on earth live in environments that have been altered to some degree by humans. According to Sih et al. [1], habitat loss or fragmentation along with the spread of exotic species, pollutants and climate change, is one of the major types of human-induced environmental changes. Today, the vanishing habitats are represented *inter alia* by the humid meadows of *Molinietalia*, whose maintenance is enabled due to medium mowing management. The lack of land use contributing to secondary succession promoted the changes in abiotic conditions and the development of swamps and brushwood, which finally effected the disappearance of numerous plant species and a decrease in biodiversity. The encroachment of tall-growing native and alien perennials, as well as shrubs and trees, leading to habitat fragmentation and diminishing of the aforementioned communities' area, was noted across the whole of Europe since the 1970s [2-7]. As a result, the most endangered types of humid meadows were listed among other protected habitats in the Annex I Habitat Directive [8,9] and they were included in the net NATURA 2000 [10].

Over the last few decades, a growing interest in the changes of habitat conditions in the course of secondary succession in *Molinia* meadows has been observed. Such studies concentrated on transformations in species composition, in particular [11-15]. Much fewer authors additionally studied the changes of Ellenberg values [16], as well as groundwater level and soil parameters [17]. At the same time, an increase in the number of investigations of the impact of meadow overgrowing on the population traits of chosen species has been noted. However, the majority of investigations have been focused on threatened and protected species, such as *Dianthus superbus* [18-20], *Gentiana pneumonanthe* [21-23], *Gladiolus imbricatus* [24-26], *Iris sibirica* [27-31] and *Trollius europaeus* [32-36], while the observations of rare but not legally protected taxa have been rather neglected.

Considering the unsatisfactory current level of knowledge, the investigation of the habitat conditions and *Succisa pratensis* population traits in the case of blue moor-grass meadow overgrowing were performed. The specific aims were to examine the temporal and spatial variability of i) the biotic habitat

conditions (i.e. plant and cryptogams cover, height of vascular plants, species richness), ii) the abiotic habitat conditions (light availability at ground level, soil moisture), and iii) the abundance and structure of subpopulations of *Succisa pratensis*.

MATERIALS AND METHODS

Study species

Devil's-bit Scabious *Succisa pratensis* Moench (*Dipsacaceae*) occurs throughout the temperate zones of Eurasia [37]. Its populations might establish themselves in a wide spectrum of habitats: from woodland rides, through heathland, grassland and mires, to uplands on cliff ledges and ravines. At the same time, Herben et al. [38] pointed out that, as the effect of land abandonment and habitat fragmentation, the number of populations of the abovementioned species diminished significantly during the last century. Also, it is worth mentioning that *S. pratensis* is included in several national Red Lists and Books [39-41].

S. pratensis is a polycarpic, perennial herb with ca. 25-year genet longevity. The individuals form a short vertical rhizome bearing a rosette of leaves. The flowering stems usually carry up to six, but occasionally more, flower heads with up to 100 small, pale violet flowers. Most seeds land close to the mother plant, but long-distance dispersal by animals or wind is likely to occur. Clonal propagation occurs occasionally and it is realized by the production of adventitious buds in stolons. The side rosettes are attached for the first year to the maternal plant [42].

Considering the opportunity for vegetative growth, the individual and the ramet cluster were adopted as the basic demographic units in the presented investigation. An individual (genet) is a plant emerging from a single zygote. The terms 'individual' and 'genet' are used in association with the seedling and juvenile stage, since only at this stage can it be established with certainty that it has developed from a zygote. The term 'ramet cluster', understood as an integral group of the aboveground units (leaf rosettes or/and generative stems), is applied to plants representing later developmental stages (adult vegetative and adult generative).

Study area

The investigations were conducted in patches of abandoned *Molinia caeruleae* meadows situated in Kostrze, southern Poland. All patches were characterized by the presence of *Betonica officinalis, Dianthus superbus, Galium boreale, Gentiana pneumonanthe, Gladiolus imbricatus, Inula salicina, Iris sibirica*, as well as *Selinum carvifolia*.

Patch I (representing an early stage of succession), unmanaged for 10-12 years and measuring approximately 1600 m², was dominated by small-tussock grasses such as *Briza media* and rosette-forb species with erect or procumbent stems, i.e. *Lychnis flos-cuculi, Lotus corniculatus* and *Lathyrus pratensis*. Patch II (representing a medium stage of succession) had not been used for 15 years and covered an area of 1600 m²; shrub willow *Salix rosmarinifolia* prevailed. Patch III (representing a medium stage of succession), unmanaged for 20 years and measuring approximately 1300 m², was dominated by *Deschampsia caespitosa* and *Phragmites australis*. Patch IV (representing a late stage of succession) had not been used for at least 25 years and covered an area 1700 m²; tall-growing macroforbs such as *Serratula tinctoria, Sanguisorba officinalis, Filipendula ulmaria* and *Solidago serotina*, as well as bushes and trees (i.e. *Crataegus* sp*., Populus tremula, Betula pendula*) prevailed.

Habitat condition studies

On 6 July 2010, one permanent plot in all the Patches, characterized by the occurrence of individuals and/or ramet clusters of *Succisa pratensis* and measuring 15 m x 15 m, was established and fenced in. Within each plot, 20 measuring points were chosen, labeled by plastic pegs. Five of them were established systematically in the middle and in the corners of the permanent plots, while the remaining were chosen randomly. The marked points were centers of setting the iron rim, 30 cm in diameter, which was used for evaluation of the biotic habitat conditions (plant and cryptogam cover, species richness and height of the vascular plants). During the first week of July, 2010-2013, the percent of ground surface covered by the vascular plants, as well as cryptogam (moss and lichens) within the rim, was estimated visually

and the number of vascular plants species occurring within the rim was counted. Also, the height (from soil level to the top) of the lowest and highest stems (excluding *Succisa pratensis*) growing within the rim was measured using a folding tape. In the aforementioned points, the light intensity at soil level and the soil moisture were surveyed. The light intensity was examined during the first week of July between 10:00 and 12:00 a.m. in the years 2010-2013 with a Voltcraft MS-1300 digital light meter (accuracy ±5% + 10 digits; range 0.01-50000 lx). The soil moisture was surveyed each year, once a week from 1 June to 30 September. Altogether, 340 measurements were obtained in each Patch in the years 2010-2012, and 360 measurements in the year 2013. The soil humidity was measured using an OMEGA HSM50 handheld digital soil moisture sensor (accuracy ±5% + 5 digits; measuring range 0% to 50% moisture content of soil).

Subpopulation trait studies

The investigations of population traits were conducted in the years 2010-2013 in the abovementioned permanent plots, where all genets and ramet clusters of *Succisa pratensis* were labeled with plastic pegs. In order to investigate the spatiotemporal variability of abundance and age structure of *Succisa pratensis* subpopulations, each year all the individuals and ramet clusters were counted and assigned to developmental stages according to Adams [42]. These were: seedlings (with usually 4 leaves), juveniles (forming 5-6 rosette leaves), vegetative adults (consisting of 6-12 leaves) and generative adults (flowering mature plants with rosette and flowering stalks). Each year in the adult ramet clusters the following traits were noticed: i) the total number of leaf rosettes, ii) the greatest number of leaves in the rosette, iii) the length and width of the largest rosette leaf blade, iv) the number of generative stems, v) the height of the longest flowering stem (from the soil level to the top flower head), vi) the greatest number of pairs of cauline leaves, and vii) the greatest number of flower heads in the generative stem.

Measurement of the height of the generative stems was carried out using a folding tape measure, while the dimensions of the leaf blades were measured using a Lux Tools Comfort digital caliper (accuracy +/-0.01; measuring range 0.1-150 mm).

Statistical analysis

Normal distribution of the untransformed data of habitat conditions 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 a significance level of P<0.05. As the values of the individual characteristics in some groups were not consistent with normal distribution and the variance was not homogeneous, the Kruskal-Wallis test was applied to check whether there was temporal and spatial variability in terms of plant and cryptogams cover, number of taxa, height of vascular plants, light intensity at soil level and soil humidity.

The chi-square test was applied to establish whether significant differences existed among the sites and years in terms of the age structure of subpopulations, as well as the structure of the size of the ramet clusters based on the number of rosette leaves, length and width of the largest rosette leaf, maximal number of pairs of cauline leaves, number and maximal dimensions of generative stems, as well as the maximal number of flower heads. Statistical analyses were performed using STATISTICA 10 software (Statsoft Inc. 2010).

RESULTS

Habitat conditions

The plant cover did not change in time and space (Table 1). The cryptogam cover presented a similar trend (Table 2). Species richness (number of taxa) decreased in consecutive sites and did not differ significantly among the years (Table 3). The height of vascular plants showed solely the spatial variability and augmented in successive study sites (Table 4). The light availability decreased in successive years and in consecutive Patches (Table 5), whereas soil moisture showed an inverse tendency (Table 6).

Subpopulation trait studies

The abundance of subpopulations diminished from Patch I, via Patches II and IV, to Patch III. An increase in the total number of individuals and ramet clusters in consecutive years was noticed in Patch I, while an

Table 1. Mean (±SD) percentage cover of plants in patches of *Molinia caeruleae* dominated by small meadow species (Patch I), willow shrubs (Patch II), large tussock grasses (Patch III) and macroforbs (Patch IV) in the years 2010-2013.

		Patch				Kruskal-Wallis test
		I	II	III	IV	
Year	2010	97.5 (±1.6) N=20	97.3 (±3.1) N=20	98.0 (±1.2) N=20	98.2 (±1.5) N=20	2.56 ns
	2011	97.4 (±1.7) N=20	96.3 (±2.5) N=20	97.9 (±1.4) N=20	98.8 (±1.2) N=20	3.10 ns
	2012	97.3 (±1.3) N=20	97.0 (±3.1) N=20	97.9 (±1.0) N=20	98.2 (±1.0) N=20	6.49 ns
	2013	97.7 (±1.4) N=20	97.3 (±3.2) N=20	98.2 (±0.9) N=20	98.3 (±0.7) N=20	2.20 ns
Kruskal-Wallis test		1.54 ns	9.95 ns	0.79 ns	2.20 ns	

Level of statistical significance: * – P<0.05, ** – P<0.01, *** – P<0.001, ns – not significant

Table 2. Mean (±SD) percentage cover of cryptogams in patches of *Molinia caeruleae* dominated by small meadow species (Patch I), willow shrubs (Patch II), large tussock grasses (Patch III) and macroforbs (Patch IV) in the years 2010-2013.

		Patch				Kruskal-Wallis test
		I	II	III	IV	
Year	2010	2.0 (±1.2) N=20	1.9 (±1.1) N=20	1.4 (±1.0) N=20	1.3 (±0.8) N=20	6.46 ns
	2011	1.8 (±0.9) N=20	1.8 (±1.8) N=20	1.2 (±1.0) N=20	(±0.9) N=20	8.14 ns
	2012	1.5 (±1.2) N=20	(±0.9) N=20	(±0.8) N=20	(±0.9) N=20	2.90 ns
	2013	1.5 (±1.3) N=20	0.9 (±0.9) N=20	0.8 (±0.5) N=20	0.9 (±0.6) N=20	3.43 ns
Kruskal-Wallis test		3.17 ns	10.8*	3.15 ns	3.24 ns	

Level of statistical significance: * – P<0.05, ** – P<0.01, *** – P<0.001, ns – not significant

Table 3. Mean (±SD) number of species of vascular plants in patches of *Molinia caeruleae* dominated by small meadow species (Patch I), willow shrubs (Patch II), large tussock grasses (Patch III) and macroforbs (Patch IV) in the years 2010-2013.

		Patch				Kruskal-Wallis test
		I	II	III	IV	
Year	2010	12.7 (±3.4) N=20	9.7 (±2.3) N=20	8.8 (±1.2) N=20	7.9 (±1.8) N=20	24.3***
	2011	12.1 (±3.9) N=20	9.3 (±1.9) N=20	8.5 (±1.1) N=20	7.5 (±1.5) N=20	25.6***
	2012	11.8 (±2.5) N=20	8.9 (±1.8) N=20	8.0 (±1.2) N=20	7.2 (±1.6) N=20	35.6***
	2013	11.7 (±2.7) N=20	8.6 (±1.8) N=20	7.7 (±1.4) N=20	6.9 (±1.8) N=20	33.4***
Kruskal-Wallis test		0.9 ns	2.4 ns	9.7*	3.8 ns	

Level of statistical significance: * – P<0.05, ** – P<0.01, *** – P<0.001, ns – not significant

Table 4. Mean (±SD) height of vascular plants (cm) in patches of *Molinia caeruleae* dominated by small meadow species (Patch I), willow shrubs (Patch II), large tussock grasses (Patch III) and macroforbs (Patch IV) in the years 2010-2013.

		Patch				Kruskal-Wallis test
		I	II	III	IV	
Year	2010	55.1 (±23.4) N=40	78.9 (±8.8) N=40	135.2 (±13.6) N=40	149.3 (±18.1) N=40	126.87***
	2011	57.1 (±24.6) N=40	81.2 (±10.5) N=40	137.8 (±18.9) N=40	152.5 (±11.8) N=40	134.91***
	2012	59.2 (±20.3) N=40	85.1 (±12.6) N=40	148.10 (±9.3) N=40	154.0 (±13.2) N=40	120.23***
	2013	63.2 (±22.0) N=40	84.6 (±9.2) N=40	140.9 (±19.4) N=40	157.6 (±19.3) N=40	113.21***
Kruskal-Wallis test		3.03 ns	8.83*	2.79 ns	4.72 ns	

Level of statistical significance: * – P<0.05, ** – P<0.01, *** – P<0.001, ns – not significant

Table 5. Mean (±SD) light intensity at soil level x 1000 (lx) in patches of *Molinia caeruleae* dominated by small meadow species (Patch I), willow shrubs (Patch II), large tussock grasses (Patch III) and macroforbs (Patch IV) in the years 2010-2013.

		Patch				Kruskal-Wallis test
		I	II	III	IV	
Year	2010	44.5 (±2.3) N=20	37.9 (±2.8) N=20	24.8 (±3.4) N=20	20.8 (±2.3) N=20	70.02***
	2011	43.0 (±2.4) N=20	36.9 (±1.8) N=20	23.0 (±4.1) N=20	19.2 (±3.9) N=20	68.7***
	2012	40.6 (±3.6) N=20	35.2 (±2.9) N=20	19.2 (±3.8) N=20	17.0 (±2.8) N=20	55.3***
	2013	36.7 (±3.5) N=20	32.6 (±3.7) N=20	17.2 (±5.8) N=20	15.6 (±2.8) N=20	62.9***
Kruskal-Wallis test		31.2***	25.6***	39.7***	33.4***	

Level of statistical significance: * − $P<0.05$, ** − $P<0.01$, *** − $P<0.001$, ns − not significant

Table 6. Mean (±SD) percentage content of water in the soil in patches of *Molinia caeruleae* dominated by small meadow species (Patch I), willow shrubs (Patch II), large tussock grasses (Patch III) and macroforbs (Patch IV) in the years 2010-2013.

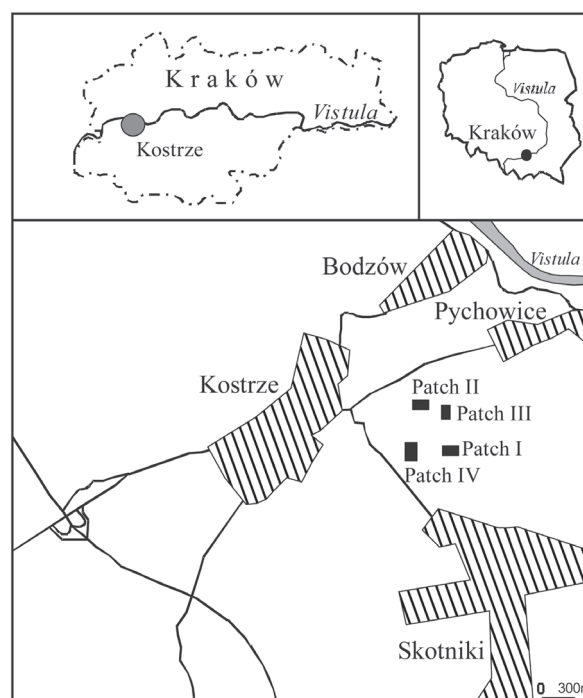|		Patch				Kruskal-Wallis test
		I	II	III	IV	
Year	2010	14.9 (±6.8) N=20	23.4 (±11.1) N=20	26.4 (±6.7) N=20	27.3 (±7.2) N=20	277.4***
	2011	16.5 (±4.8) N=20	27.9 (±10.1) N=20	28.0 (±8.9) N=20	30.0 (±7.9) N=20	400.0***
	2012	15.4 (±9.1) N=20	24.3 (±12.8) N=20	29.3 (±7.9) N=20	29.8 (±8.4) N=20	444.4***
	2013	16.4 (±10.5) N=20	27.6 (±8.9) N=20	29.6 (±8.9) N=20	32.1 (±9.2) N=20	483.0***
Kruskal-Wallis test		29.0***	27.4***	38.5***	52.7***	

Level of statistical significance: * − $P<0.05$, ** − $P<0.01$, *** − $P<0.001$, ns − not significant

Table 7. The abundance of individuals and ramet clusters of *Succisa pratensis* within permanent plots established in patches of *Molinia caeruleae* dominated by small meadow species (Patch I), willow shrubs (Patch II), large tussock grasses (Patch III) and macroforbs (Patch IV) in the years 2010-2013.

		Patch			
		I	II	III	IV
Year	2010	74	66	40	56
	2011	68	62	40	56
	2012	74	56	40	56
	2013	78	54	38	56

Fig. 1. Locality of studied *Molinia caeruleae* patches dominated by small meadow species (Patch I), willow shrubs (Patch II), large tussock grasses (Patch III) and macroforbs (Patch IV) in Kraków-Kostrze (southern Poland).
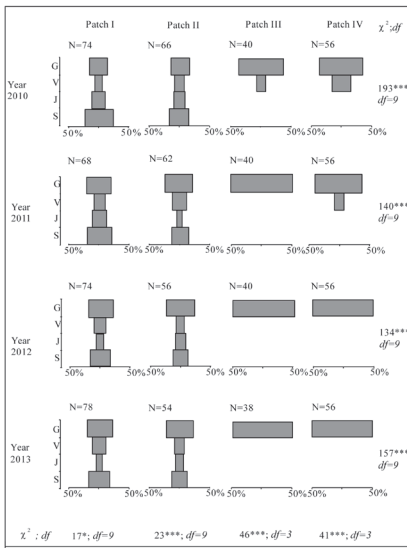
inverse tendency was found in Patch II. In Patch III, after a period of constant abundance, a decrease in the number of genets and ramet clusters was observed, whereas in Patch IV the abundance did not show this temporal variability (Table 7).

The age structure of the observed subpopulations of *Succisa pratensis* show considerable spatial variability, from expanded in Patch I, via stable in Patch II, to declining in Patches III and IV. All subpopulations showed increased signs of senescence in consecutive years, mostly pronounced in Patches III and IV (Fig. 1).

Fig. 2. The structure of developmental stages of subpopulations *Succisa pratensis* within permanent plots established in patches of *Molinia caeruleae* in the years 2010-2013. Vertical axis depicts developmental stages (S − seedlings, J − juveniles, V − vegetative adults, G − generative adults); horizontal axis depicts percentage of individuals/ramet clusters. Name of patches as in Fig. 1. Abbreviations: N − number of individuals and ramet clusters. The statistical significance levels (the χ^2 test) as in Tables.
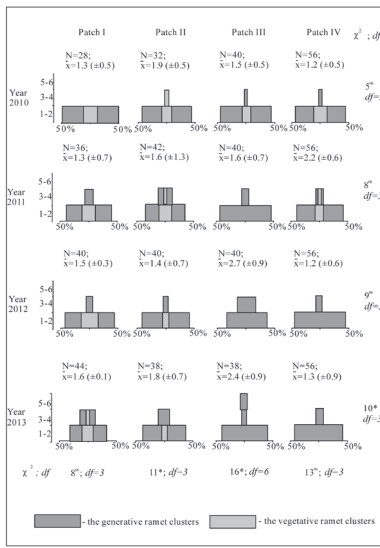

Fig. 3. The size structure of ramet clusters *Succisa pratensis* based on number of rosettes within permanent plots established in patches of *Molinia caeruleae* in the years 2010-2013. Vertical axis depicts number of rosettes; horizontal axis depicts percentage of ramet clusters. Abbreviations: N − number of ramet clusters, $\bar{x}$ − average number of ramet clusters. Names of Patches as in Fig. 1; statistical significance levels as in Fig. 2.
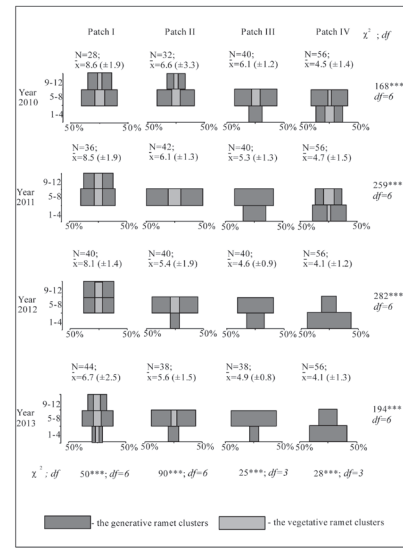

Fig. 4. The size structure of ramet clusters *Succisa pratensis* based on maximal number of leaves per rosettes within permanent plots established in patches of *Molinia caeruleae* in the years 2010-2013. Vertical axis depicts number of leaves per rosettes, horizontal axis depicts percentage of ramet clusters. Names of Patches as in Fig. 1, statistical significance levels as in Fig. 2,; abbreviations as in Fig. 3.
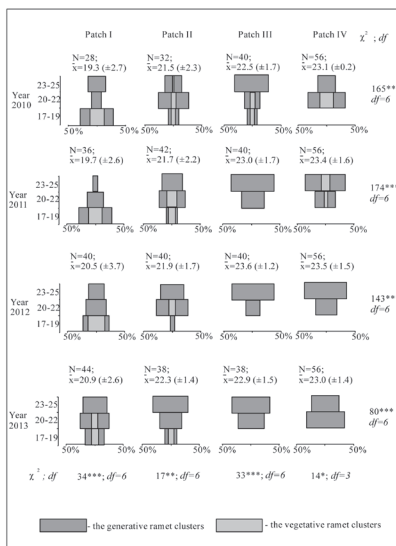

Fig. 5. The size structure of ramet clusters *Succisa pratensis* based on length of the longest rosette leaf within permanent plots established in patches of *Molinia caeruleae* in the years 2010-2013. Vertical axis depicts length of the longest rosette leaf; horizontal axis depicts percentage of ramet clusters. Names of Patches as in Fig. 1, statistical significance levels as in Fig. 2; abbreviations as in Fig. 3.
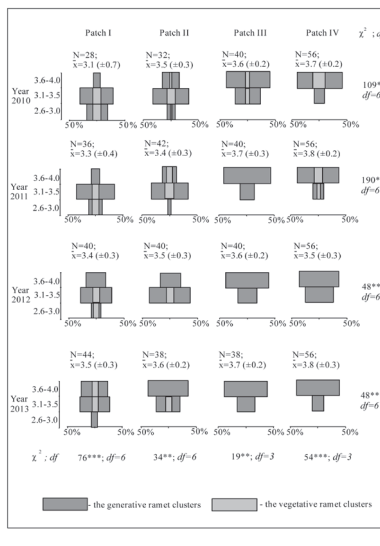

Fig. 6. The size structure of ramet clusters *Succisa pratensis* based on width of the longest rosette leaf within permanent plots established in patches of *Molinia caeruleae* in the years 2010-2013. Vertical axis depicts width of the longest rosette leaf; horizontal axis depicts percentage of ramet clusters. Names of Patches as in Fig. 1, statistical significance levels as in Fig. 2; abbreviations as in Fig. 3.
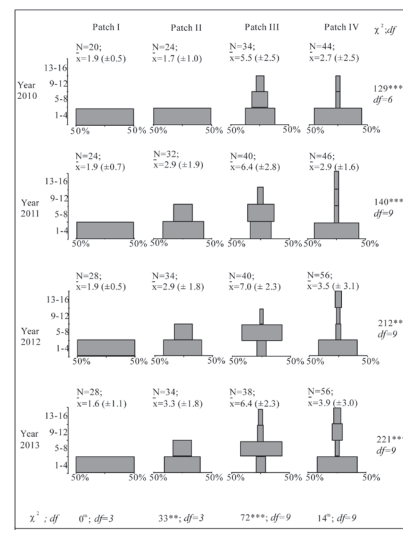

Fig. 7. The size structure of generative ramet clusters *Succisa pratensis* based on number of flowering stems within permanent plots established in patches of *Molinia caeruleae* in the years 2010-2013. Vertical axis depicts number of flowering stems; horizontal axis depicts percentage of ramet clusters. Names of Patches as in Fig. 1, statistical significance levels as in Fig. 2; abbreviations as in Fig. 3.
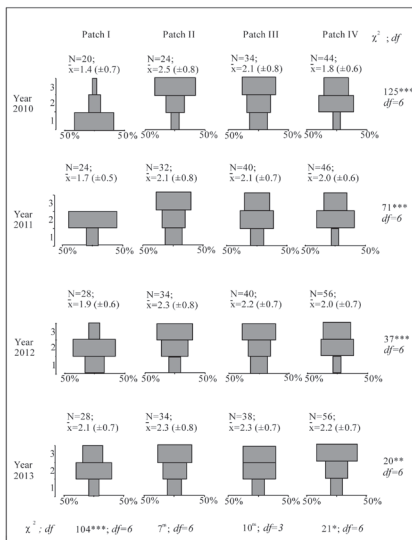
Fig. 8. The size structure of generative ramet clusters *Succisa pratensis* based on maximal number of pairs of cauline leaves within permanent plots established in patches of *Molinia caeruleae* in the years 2010-2013. Vertical axis depicts maximal number of pairs of cauline leaves, horizontal axis depicts percentage of ramet clusters. Names of Patches as in Fig. 1, statistical significance levels as in Fig. 2; abbreviations as in Fig. 3.

Fig. 9. The size structure of generative ramet clusters *Succisa pratensis* based on maximal height of flowering stems within permanent plots established in patches of *Molinia caeruleae* in the years 2010-2013. Vertical axis depicts maximal height of flowering stems; horizontal axis depicts percentage of ramet clusters. Names of Patches as in Fig. 1, statistical significance levels as in Fig. 2; abbreviations as in Fig. 3.
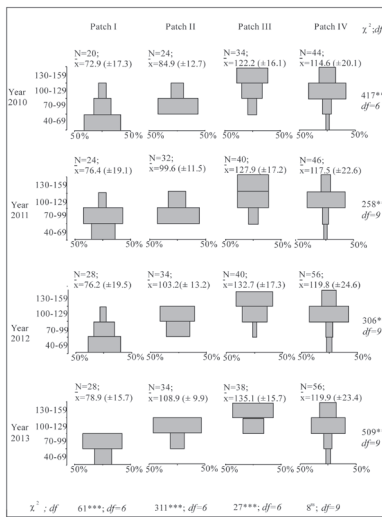
Fig. 10. The size structure of generative ramet clusters *Succisa pratensis* based on maximal number of flower heads within permanent plots established in patches of *Molinia caeruleae* in the years 2010-2013. Vertical axis depicts maximal number of flower heads, horizontal axis depicts percentage of ramet clusters. Names of Patches as in Fig. 1, statistical significance levels as in Fig. 2, abbreviations as in Fig. 3.
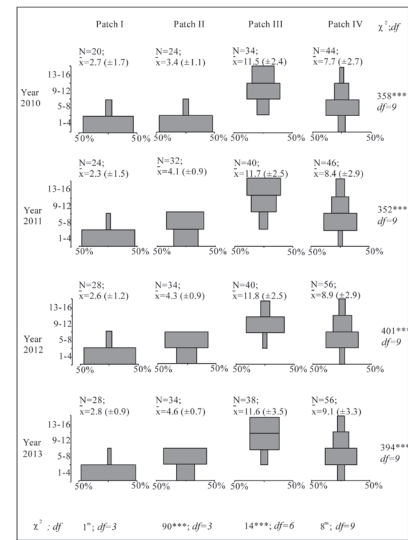
The number of rosettes per ramet cluster did not show either temporal or spatial variability (Fig. 2). The number of leaves per rosette diminished gradually in time and space (Fig. 3). The length (Fig. 4) and width (Fig. 5) of the largest rosette leaves gradually increased in consecutive years and in successive study sites. The number of flowering stems increased from Patch I to III, and then diminished in Patch IV. Such a trait did not present the temporal variability in Patch I, whereas in the other study sites it increased in consecutive years (Fig. 6). The maximal number of pairs of cauline leaves per ramet cluster (Fig. 7), height of generative stems (Fig. 8) and number of flower heads per flowering stem (Fig. 9) increased from Patch I to III, and then diminished in Patch IV. In all the study sites the aforementioned traits increased in consecutive years.

DISCUSSION

Habitat conditions

The constant cover of vascular plants and cryptogams observed in the presented study suggests the sporadic occurrence of gaps, which might play the role of "safe sites for seedling recruitment" *sensu* Harper et al. [43] and "regenerative niches" *sensu* Grubb [44].

The observed constant number of species in successive years in the performed study did not support previous studies conducted in abandoned *Molinia* meadows, showing a sharp increase of species richness in the initial stage of succession and a gradual decrease of species in its more advanced phases [12-45]. In turn, the progressive decline of number of species noticed along the successional gradient might be a result of the intensive horizontal spread of tall-growing plants occurring abundantly in Patches III and IV. Such a phenomenon contributes to the elimination of small meadow species, as was previously recorded in meadows in various stages of overgrowing [45-47]. Moreover, the obtained results prove that in consecutive Patches the number of taxa diminished, while the average height of plant augmentation seemed to correspond with the findings of Wheeler and Giller [48]. The authors provided evidence that in fens the number of species is negatively correlated with aboveground plant biomass. Additionally, it is worth mentioning that

many authors [46-50] have observed that there is much greater aboveground biomass in unused patches of calcareous fens than in managed or recently abandoned ones. Furthermore, the increase in the height of standing vegetation observed in the consecutive study sites is in accordance with the observations of Sienkiewicz-Paderewska et al. [51], who found that the mean height of plant cover in unmanaged meadows is significantly greater than in mowed patches. The observed lack of temporal variation in the height of standing vegetation in the performed study corresponds with the findings of van der Hoek and Sýkora [17], who found only a small increase of plant biomass in abandoned *Molinia* meadows over a ten-year period.

The obtained results also confirm the observations of other authors [47,50], who provided evidence that in fens with increasing height of standing vegetation, light availability at soil level diminishes. Simultaneously, the performed study proved that despite a lack of temporal variability of standing vegetation height, the light intensity decreased in consecutive years. Such a phenomenon might be connected with an increasing number of lateral branches of plants during their development, which might contribute to intensive light capture.

The observed increase in soil humidity in the consecutive patches and in the successive sites might be due to a growing accumulation of litter and concomitant water retention. The obtained results correspond with previous studies, providing evidence that the number of hygrophytes increases gradually after land abandonment [12,15]. Also, observations conducted in other communities [52,53] showed a significant increase in soil humidity in the course of secondary succession.

Subpopulation traits

The much greater abundance of genets and ramet clusters of *Succisa pratensis* noticed more in Patches I and II than in Patches III and IV might be due to seedling recruitment. The lack of seedlings in sites overgrown by large tussock grasses or macroforbs and trees is likely due to insufficient light conditions. According to Grime et al. [54], the seeds of *Succisa pratensis* germinate much better in light than in part shading or darkness. Also, other authors [55-58] have

provided evidence that the seeds of *Succisa pratensis* germinate much better in gaps occurring as a result of artificial plant removal than in continuous plant cover and litter layer. A similar phenomenon was also found in the closely related *Succisella inflexa* [59], as well as other wet meadow taxa such as *Serratula tinctoria* [60] and *Viola palustris* [61].

The temporal increase of abundance in Patch I caused by considerable seedling recruitment, as well as the survivability of juvenile genets and adult ramet clusters, might be linked with insignificant competition from neighboring species. The decrease of abundance of the subpopulation occurring in Patch II might be a consequence of the modest survivability of the genets due to the allelopathic activities of *Salix caprea* [62]. The diminishing abundance in Patch III is the effect of lack of seedling recruitment as well as the mortality of adult ramet clusters. The absence of seedling recruitment in Patch IV and the survivability of adults allows maintaining of constant abundance in subpopulation.

The described processes of recruitment and mortality of genets/ramet clusters influenced the spatial and temporal variability of age structure of subpopulations. A similar pattern of age structure variation was found in the subpopulations of *Trollius europaeus* growing across the successional gradient [63].

The presented findings correspond with previous observations proving the rather constant number of rosettes in time and space [64]. Controversially, Davis et al. [65], Crone and McDaniel [66], as well as Sotek [67] observed a reduction in the number of rosette leaves in the vicinity of strong competitors, whilst Jensen and Meyer [61] found an increase in their number in managed meadows. The observed temporal and spatial increase of the dimensions of the rosette leaves of *Succisa pratensis* due to an increase in crowding and shading was also found in other rosette-form species, such as *Arabidopsis thaliana* [68], *Taraxacum officinale* [69], *Saxifraga nivalis* and *S. moschata* [70] and *Valeriana jatamansi* [71]. The increase in leaf dimensions in plants growing in close proximity in dense habitats such as forests, grasslands, orchards and hedgerows might be interpreted as 'shade avoidance syndrome' [72].

The increase in the number and height of flowering stems, number of cauline leaves and flower head

number from Patch I, through Patch II, to Patch III might be due to lateral shading, whereas the decrease of these traits in Patch IV might be caused by shading from above. A similar phenomenon was observed in *Trollius europaeus* growing across the successional gradient [63]. At the same time, it should be added that the performed observations correspond with previous findings conducted in the subpopulations of *Succisa pratensis* occurring in sites characterized by a rising level of lateral shading [64]. Also, van der Meer et al. [73] recorded higher growth rates and greater production of flower heads in populations of *Succisa pratensis* occurring more in abandoned meadows than in managed ones, while Vergeer et al. [74] argued that the increase in the number and height of flowering stems and flower head number might be due to the growing eutrophication level.

CONCLUSIONS

To summarize, it might be concluded that despite the constant, incomplete cover of cryptogams and plants in successive sites and in consecutive years, the seedlings of *Succisa pratensis* were observed solely in Patches I and II. The age structure of the observed subpopulations differed significantly, from expanded in Patch I, through stable in Patch II, to declining in Patches III and IV. Additionally, all the subpopulations showed increased signs of senescence in consecutive years.

The progressive diminishing of species richness, the growing share of tall-growing taxa and the increased height of the standing vegetation in successive sites, as well as the gradual augmentation of shading in time and space contributed to the progressive increase in rosette leaf dimensions, improving light capture. Also, the increase in the number and height of flowering stems, number of cauline leaves and flower head number from Patch I, through Patch II, to Patch III might be due to lateral shading, whereas the decrease of these traits in Patch IV might be caused by shading from above.

In light of this study, it could be stated that the subpopulation occurring in Patch I has the greatest chances for maintenance in the colonized site, while the subpopulation occurring in Patch III is the most endangered by extinction. Additionally, it is worth mentioning that the observations of spatiotemporal variability of population traits of rare species inhabiting semi-natural habitats has a broad scientific meaning and a practical importance. Such studies might provide a basis for appropriate management and conservation strategies of whole plant communities particularly threatened due to land abandonment or anthropogenic pressure.

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