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THE EFFECTS OF SUCCESSIONAL STAGE AND SIZE OF GAPS ON RECRUITMENT OF CLONAL PLANTS IN OVERGROWING *Molinietum caeruleae* MEADOWS

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Abstract

In majority of plant communities with a closed canopy, the disturbances created by abiotic factors and biotic agents contribute to origin of an area free of existing vegetation and considered as safe sites for seedling recruitment. Although the gaps are characterized by several features, the size is proposed to be the most important characteristic. The investigations of recruitment of clonal taxa in different–sized gaps were conducted in the years 2011–2012 in *Molinietum caeruleae* meadows representing various successional stages and dominated by different species. Patch ES, representing early-successional stage, was dominated by small meadow species, Patch MS, representing mid-successional stage, was prevailed by tall-growing macroforbs, while Patch LS representing late-successional stage was overgrown by macroforbs and willows. In the successive sites the mean height of plant canopy, as well as the period of spring inundation increased gradually.

The total number of species and seedlings decreased from the Patch ES, through the Patch MS, to the Patch LS. Almost all plants presenting positive correlation between seedling number and gap area created hypogeogenous stems with substantial lateral growth and considerable number of short-lived daughter ramets allowing the fast colonization of neighbourhood. The majority of species showing negative relationship formed epigeogenous stems with slight lateral growth, as well as low number of long-lived ramets contributing to slow colonization of area.

In light of performed studies, it might be concluded, that making disturbance in continuous plant canopy and litter might be very effective way of conservation of *Molinietum caeruleae* meadows. The creation of different-sized gaps seems to be especially valuable due to the maintenance of heterogeneity of clonal species, which is particularly important in advanced successional stages.

Key words: colonization of openings; disturbance; gap; meadows, life-history traits.

INTRODUCTION

In majority of semi-natural plant communities with a closed canopy, the disturbances created by abiotic (such as windstorms, floods, fires, landslides), as well as biotic factors (i.e. death of plant individuals or their parts, animal and man activities) contribute to the origin of areas free of existing vegetation and considered as safe sites for seedling recruitment [1]. Although the gaps are characterized by several features such as size, shape, micro-topography, age, season of creation and origin [2,3], the size is proposed to be the most important characteristic [4]. Until now the colonization of gaps with various size was mostly investigated in relation to seed dimensions. Such observations were carried out in wide spectrum of habitats from semi-natural pastures [5], *via* grasslands [6] and meadows [7], to forests [8–10]. Moreover, Williams [11] studied the effect of gap size on recruitment of species with various growth form, while Kotanen [12] investigated the impact of opening area on seedling recruitment in relation to growth form and lifespan of species, as well as their mode of reproduction.

Despite of growing interest in the role of gap area on plant recruitment process the present state of knowledge is still unsatisfactory. Particularly, there is lack of investigations of natural recruitment of clonal plants with various life-history traits relevant to iterative growth and influencing the colonization abilities. The studies of regularities governing the recruitment of fast and slow colonizers are very valuable from academic point of view and also they might be crucial for nature conservation.

Taking into account the insufficient state of knowledge, the main aim of undertaken studies was to investigate the recruitment of clonal plants in overgrowing *Molinietum caeruleae* meadows The detailed goals focused on assessment of: (1) the number of species and seedlings in patches representing various successional stages, (2) the species diversity in the different-sized gaps in each patch, (3) the correlation between gap area and number of seedlings of particular species, (3) the relationship between opening size and occurrence of taxa adapted to the fast and slow clonal spread.

I hypothesized, that: (1) the species/ seedling abundance diminishes in course of succession, (2) the similar assemblages of taxa fill all gaps, (3) there is no correlations between gap area and seedling number, (4) the life-history traits relevant to clonality do not influence gap colonization.

Study area

The studies were carried out in *Molinietum caeruleae* meadows being one of the rapidly vanishing communities of Central Europe [13–17]. The study area, located in Kostrze (south-western part of Kraków), is a remnant of meadows extending in the past from the Niepołomice Primeval Forest to Czernichów [18–20]. In the study area three patches were established. The Patch ES, representing early-successional stage, was prevailed by small meadow taxa such as loosely tufted grasses and small rosette-forb species. The Patch MS, representing mid-successional stage, was overgrown by tall-growing macroforbs creating robust, fleshy underground organs. The Patch LS, representing late-successional stage, was dominated by macroforbs and shrub-willows (Fig. 1).

MATERIALS AND METHODS

The investigations of site conditions

In order to capture the ending of the inundation, the observations of the occurrence of stagnant water were carried out once a week from 1st March to 30th April in the years 2011 and 2012. The first day, in which the water table was not observed on the soil surface, was considered as the end of temporal flooding period. Each year the average height of vascular plants in each patch was evaluated on the basis of measurements of 20 randomly chosen stems of different species. The measurements were performed using a folding tape measure on 8th July 2011 and on 12th July 2012. The light intensity at the soil level was surveyed with a digital photometer Voltcraft MS-1300 (accuracy +/- 5% + 10 digits; measuring range 0.01–50 000 lx). Each year 50 measurements per patch was performed; the half of measurements was done in the sunny days (8th July 2011 and 12th July 2012) and the others in the clouded days (28th July 2011 and 26th July 2012). The detailed description of habitat conditions is given in Table 1.

Table 1
The characteristic of site conditions in the sites dominated by small meadow species (Patch I), prevailed by tall-growing perennials (Patch II), as well as overgrown by large-tussock species and shrub-willows (Patch III).

Patch	ES	MS	LS
The patch area (m^2)	4 400	5 600	9 000
Successional stage	Early	Medium	Late
The number of species in patch	46	41	35
The dominants (species, with cover exceeding 20%)	*Brizamedia, Lychnis flos-cuculi, Succisa pratensis*	*Lysimachia vulgaris, Filipendula ulmaria, Lythrum salicaria*	*Salix repens* ssp. rosmarinifolia *Filipendula ulmaria, Lythrum salicaria, Serratula tinctoria*
The subdominants (species, with cover level ranging 5-20%)	*Leucanthemum vulgare, Centaurea jacea*	*Serratula tinctoria, Polygonum bistorta*	*Salixcinerea, Carex gracilis Molinia caerulaea, Deschampsia caespitosa*
End of period of permanent water stagnation in the spring 2011	26Mar	14Apr	24Apr
End of period of permanent water stagnation in the spring 2012	29Mar	18Apr	28Apr
The mean vascular plant height (cm) in 2011	36.6 (±16.9)	79.9 (±22.6)	146.8 (±44.9)
The mean vascular plant height (cm) in 2012	41.9 (±12.3)	86.7 (±38.9)	157.6 (±51.2)
The mean light intensity at the soil level (lx) in 2011	48 000.0 (±12 000)	43 000.0 (±11 000)	37 000.0 (±15 000)
The mean light intensity at the soil level (lx) in 2012	47 000.0 (±18 000)	40 000.0 (±21 000)	35 000.0 (±16 000)

The gap creation

In each of aforementioned patches ten permanent experimental plots were randomly arranged on 29th April 2011. Each plot was consisted of four square-shaped, adjacent subplots measuring 0.16 m^2 (subplot 1), 0.09 m^2 (subplot 2), 0.04 m^2 (subplot 3), and 0.01 m^2 (subplot 4). In each subplot the aboveground plant biomass and litter layer were removed. Such treatment is considered as an optimal for seedling establishment in the Molinietum caeruleae meadows [20]. The plots were separated from each other by at least 3.0 m wide belts of intact vegetation to ensure sample independency. Moreover, all plots were situated ca 2.0 metres from the border of patch to avoid edge effect. The design of experiment is given in Fig. 1.

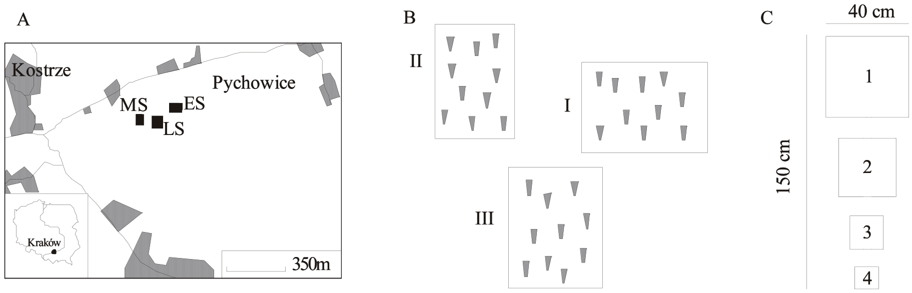

Fig. 1. The study area and experimental design.
Location of patchrepresenting early-successional stage (ES), mid-successional stage (MS), as well as late-successional stage (LS).
Location of experimental plots in particular patches
Location of subplots measured 0.16 m^2 (1), 0.09 m^2 (2), 0.04 m^2 (3), and 0.01 m^2(4) within experimental plots

The observations of seedling recruitment

The seedling recruitment was monitored once a week in May, June, July and August, and once every two weeks in September and October, in 2011 and 2012. The seedlings and saplings were removed and determined according to Csapodý [21] and Muller [22] with support of own comparative collection. The nomenclature of taxa follows Mirek et al. [23]. The genets of rare and protected plants were replanted and marked with plastic rings and sticks. The colonization of patches was characterized by mean cumulative number of species and seedlings calculated by adding species (seedlings) that appeared over the course of two years in all experimental plots. Simultaneously, the presence of particular species (with seedling numbers) in different-sized subplots was noted. In order to evaluate the correlations between opening area and seedling number the absolute cumulative numbers of seedlings of particular species noted in each subplot measuring 0.16 m^2, 0.09 m^2, 0.04 m^2 and 0.01 m^2 were divided by 0.16, 0.09, 0.04 and 0.01, respectively. Altogether, 40 values were computed for each species occurring in seedling pool of particular patch. Such relative, comparable values were used for evaluation of the correlation ranks. In order to estimate the influence of life history traits relevant to clonality on colonization of gaps, for each species appearing in seedling pool the values of selected features were assigned. These were: the necessary clonal growth organ (categories: horizontal above ground stems, epigeogenous stems, hypogeogenous stems, roots with adventitious buds, root-spitters), the lateral spread per year (categories: 0.01/ 0.01–0.25/ >0.25 m), the number of offspring per parent ramet per year (categories: <1/1/1–10/>10) and the lifespan of a shoot (categories: 1/2/>2 years). According to Klimešová et al. [24] the aforementioned traits seem to be "ecologically meaningful" in managed grasslands and meadows. The information about values of life-history traits was obtained from the database CLO-PLA 3 [25,26]. For taxa capable of developing more than one type of necessary clonal growth organ or presenting different values of other traits, the most commonly noted data was incorporated in the analysis.

The statistical analysis

The normal distribution of the untransformed data was tested using the Kolmogorov-Smirnov one-sample test at the significance level of $p<0.05$. Subsequently, the variance homogeneity was tested using the Brown-Forsythe test at the significance level of $p<0.05$.

As the distribution of characteristics in some groups of data was not consistent with the normal distribution and the variance was not homogeneous, the statistical analysis was based on the nonparametric tests. The H Kruskal-Wallis test was applied to examine if there were significant differences in the number of appearing taxa/seedlings between particular patches. After a significant value of test, the post-hoc comparisons were made. The statistical significance of relationship between opening size and relative numbers of seedlings of each taxa was tested with Spearman correlation coefficient for each patch separately. All analyses were computed using *STATISTICA* software (version 10).

RESULTS

Altogether, 34 species were found in the seedling pool of the Patch ES, 33 taxa occurred in the Patch MS and 28 species appeared in the Patch LS. The average number of species per plot in Patch ES achieved 32.0 (± 1.2), in Patch MS it reached 28.7 (± 1.9), while in Patch LS it amounted 24.7 (± 1.1). The species number differed significantly among patches (H= 23.29; *df*=2; P<0.001). The greatest statistical difference at the level P<*0*.001 was noted among Patches ES and LS, while among Patch ES and MS it reached P<0.05.

In total, 4977 seedlings were appeared in whole study area. In Patch ES the average number of seedlings per plot achieved 240.0 (± 32.4), in Patch MS it reached 159.8 (± 35.5), whereas in Patch LS it amounted 97.9 (± 22.5). The number of seedlings differed significantly among patches (H= 23.29; *df*=2; P<0.001). The greatest statistical difference at the level P<0.001 was found among Patches ES and LS, whereas among Patch ES and MS it amounted P<0.05.

Table 2

The occurrence (+) and absence (-) of particular species in subplots measured 0.16 m^2 (1), 0.09 m^2 (2), 0.04 m^2 (3), and 0.01 m^2 (4), in the sites dominated by small meadow species (Patch ES), prevailed by tall-growing perennials (Patch MS), as well as overgrown by large-tussock species and shrub-willows (Patch LS in the years 2011 and 2012

Species	Patch ES				Patch MS				Patch LS			
	1	2	3	4	1	2	3	4	1	2	3	4
Achillea millefolium L.	+	+	+	+	+	+	+	+	+	+	+	+
Betonica officinalis L. (Trevis)	+	+	+	+	+	+	+	+	+	+	+	+
Caltha palustris L.	+	+	+	+	+	+	+	+	-	-	-	-
Centaurea jacea L.	+	+	+	+	-	-	-	-	-	-	-	-
Cirsium arvense (L.) Scop.	+	+	+	+	+	+	+	+	+	+	+	+
Cirsium rivulare (Jacq.) All.	+	+	+	+	+	+	+	+	+	+	+	-
Cruciata glabra (L.) Erhend.	+	+	+	+	+	+	+	+	+	+	+	+
Dianthus superbus L.	+	+	+	+	-	+	-	-	-	+	-	-
Filipendula ulmaria (L.) Maxim.	+	+	+	+	+	+	+	+	+	+	+	+
Filipendula vulgaris Moench.	+	+	+	+	+	+	+	+	-	-	-	-
Galium boreale L.	+	+	+	+	+	+	+	+	+	+	+	+
Galium verum L.	+	+	+	+	+	+	+	+	+	+	+	+
Geranium palustre L.	+	+	+	+	+	+	+	+	+	+	+	+
Geranium pratense L.	+	+	+	+	+	+	+	+	-	-	-	-
Geum rivale L.	+	+	+	+	+	+	+	+	+	+	+	+
Inula salicina L.	+	+	+	+	+	+	+	+	+	+	+	+
Iris sibirica L.	+	-	-	+	+	+	-	-	-	+	-	+
Leucanthemum vulgare Lam.	+	+	+	+	+	+	-	-	+	+	+	+
Lotus corniculatus L.	+	+	+	-	+	+	-	-	+	+	+	+
Lychnis flos-cuculi L.	+	+	+	+	+	+	+	+	+	+	+	+
Lysimachia nummularia L.	+	+	+	+	+	+	+	+	+	+	+	+
Lysimachia vulgaris L.	+	+	+	+	+	+	+	+	+	+	+	+
Lythrum salicaria L.	+	+	+	+	+	+	+	+	+	+	+	+
Mentha longifolia (L.) L.	+	+	+	+	+	+	+	+	+	+	+	+
Polygonum bistorta L.	+	+	+	+	-	-	-	+	-	-	-	-
Potentilla erecta (L.) Raeusch.	+	+	+	+	+	+	+	+	+	+	+	+
Ranunculus acris L.	+	+	-	-	+	-	-	-	+	+	-	+
Rumex acetosa L.	+	+	+	+	+	+	+	+	-	-	-	-
Sanguisorba officinalis L.	+	+	+	+	+	+	+	+	+	+	+	+
Selinum carvifolia (L.) L.	+	+	+	+	+	+	+	+	+	+	+	+
Serratula tinctoria L.	+	+	+	+	+	+	+	+	+	+	+	+
Solidago canadensis L.	+	+	+	+	+	+	+	+	+	+	+	+
Succisa pratensis Moench.	+	+	+	+	+	+	+	+	+	+	+	+
Valeriana officinalis L.	+	+	+	+	+	+	+	+	+	+	+	+
Total	34	33	32	32	31	31	27	28	26	28	25	26

Performed observations showed that 22 taxa appeared in all-sized subplots in all patches, 10 species occurred in all-sized subplots in at least one study site, while two taxa recruited in the different-sized gaps depending of patch (Table 2). In total,14 species showed positive correlation between area of opening and offspring number, 17 taxa demonstrated negative relationship, while 3 taxa presented positive or negative correlation depending on the patch. The values of Spearman coefficient ranged from -0.78 to 0.78 (Table 3). The majority of taxa presenting strong positive correlation formed hypogeogenous stems with substantial lateral growth, considerable number of daughter ramets, as well as short lifespan of shoots. On the other hand, taxa with strong negative relationship formed epigeogenous stems with slight lateral growth, as well as low offspring number (Table 4).

Table 3
The coefficient of correlation between gap size and proportional number of seedlings of particular species in the sites dominated by small meadow species (Patch ES), prevailed by tall-growing perennials (Patch MS), as well as overgrown by large-tussock species and shrub-willows (Patch LS) in the years 2011 and 2012. The asterisks mean the significant values of Spearman coefficient at the level 0.05.

Species	Patch ES	Patch MS	Patch LS
Achillea millefolium L.	0.78*	0.43*	0.38*
Filipendula ulmaria (L.) Maxim.	0.56*	0.35*	0.40*
Leucanthemum vulgare Lam.	0.32*	0.59*	0.06
Lysimachia vulgaris L.	0.51*	0.34*	0.22
Cirsium arvense (L.) Scop.	0.14	0.39*	0.45*
Galium boreale L.	0.00	0.42*	0.31*
Lysimachia nummularia L.	0.34	0.03	0.38
Iris sibirica L.	0.30	0.46*	0.29
Lotus corniculatus L.	0.26	0.44*	0.14
Geum rivale L.	0.43*	0.16	0.09
Solidago canadensis L.	0.42*	0.26	0.22
Galium verum L.	0.41*	0.26	0.03
Cirsium rivulare (Jacq.) All.	0.28	0.13	0.27
Mentha longifolia (L.) L.	0.01	0.01	0.07
Dianthus superbus L.	-0.05	0.16	0.10
Ranunculus acris L.	0.04	-0.14	0.20
Valeriana officinalis L.	0.25	-0.18	0.21
Serratula tinctoria L.	-0.09	-0.01	-0.12
Centaurea jacea L.	-0.11	-	-
Polygonum bistorta L.	-0.14	-0.30	-
Succisa pratensis Moench.	-0.28	-0.25	-0.17
Rumex acetosa L.	-0.27	-0.32*	-
Caltha palustris L.	-0.39*	-0.13	-
Filipendula vulgaris Moench.	-0.54*	-0.17	-
Geranium pratense L.	-0.55*	-0.29	-
Cruciata glabra (L.) Erhend.	-0.56*	-0.18	-0.25
Geranium palustre L.	-0.49*	-0.38*	-0.22
Lychnis flos-cuculi L.	-0.42*	-0.36*	-0.22
Inula salicina L.	-0.38*	-0.18	-0.51*
Betonica officinalis L. (Trevis)	-0.51*	-0.33*	-0.05
Potentilla erecta (L.) Raeusch.	-0.23	-0.37*	-0.51*
Sanguisorba officinalis L.	-0.74*	-0.78*	-0.28
Selinum carvifolia (L.) L.	-0.33*	-0.40*	-0.31*
Lythrum salicaria L.	-0.53*	-0.51*	-0.65*

Table 4
Comparisons of life history traits related to clonal growth according to [26] in species appearing in seedling pool. Species are ordered according to list of species presented in Table 3.

Species	Clonal growth organ (CGO)	Lateral spread [m/year]	Number of offsprings per parent shoot per year	Lifespan of a shoot [years]
Achillea millefolium L.	Hypogeogenous stems	>0.25	2-10	2
Filipendula ulmaria (L.) Maxim.	Hypogeogenous stems	0.01-0.25	2-10	1
Leucanthemum vulgare Lam.	Epigeogenous stems	0.01-0.25	1	2
Lysimachia vugaris L.	Hypogeogenous stems	0.01-0.25	2-10	1
Cirsium arvense (L.) Scop.	Roots with adventitious buds	>0.25	2-10	1
Galium boreale L.	Hypogeogenous stems	0.01-0.25	2-10	1
Lysimachia nummularia L.	Horizontal above ground stems	0.01-0.25	2-10	1
Iris sibirica L.	Epigeogenous stems	<0.01	1	2
Lotus corniculatus L.	Root-splitters	<0.01	2-10	1
Geum rivale L.	Epigeogenous stems	0.01-0.25	<1	1
Solidago canadensis L.	Hypogeogenous stems	0.01-0.25	2-10	1
Galium verum L.	Hypogeogenous stems	0.01-0.25	1	1
Cirsium rivulare (Jacq.) All.	Epigeogenous stems	0.01-0.25	1	2
Mentha longifolia (L.) L.	Hypogeogenous stems	0.01-0.25	2-10	1
Dianthus superbus L.	Hypogeogenous stems	<0.01	1	2
Ranunculus acris L.	Epigeogenous stems	<0.01	1	2
Valeriana officinalis L.	Hypogeogenous stems	0.01-0.25	1	2
Serratula tinctoria L.	Epigeogenous stems	<0.01	1	2
Centaurea jacea L.	Hypogeogenous stems	<0.01	1	1
Polygonum bistorta L.	Epigeogenous stems	<0.01	<1	1
Succisa pratensis Moench.	Epigeogenous stems	<0.01	<1	1
Rumex acetosa L.	Epigeogenous stems	<0.01	1	2
Caltha palustris L.	Epigeogenous stems	<0.01	1	2
Filipendula vulgaris Moench.	Epigeogenous stems	<0.01	1	2
Geranium pratense L.	Epigeogenous stems	<0.01	1	2
Cruciata glabra (L.) Erhend.	Hypogeogenous stems	0.01-0.25	1	1
Geranium palustre L.	Epigeogenous stems	<0.01	1	2
Lychnis flos-cuculi L.	Epigeogenous stems	0.01-0.25	2-10	2
Inula salicina L.	Hypogeogenous stems	0.01-0.25	1	1
Betonica officinalis L. (Trevis)	Epigeogenous stems	<0.01	<1	1
Potentilla erecta (L.) Raeusch.	Epigeogenous stems	<0.01	<1	1
Sanguisorba officinalis L.	Epigeogenous stems	<0.01	<1	1
Selinum carvifolia (L.) L.	Epigeogenous stems	<0.01	1	2
Lythrum salicaria L.	Epigeogenous stems	<0.01	<1	1

DISCUSSION

The influence of habitat conditions on abundance of species and seedlings

The obtained results show that the number of species and seedlings in patch dominated by small meadow taxa is greater than in patches prevailed by macroforbs and overgrown by macroforbs and shrubs are consistent with previous observations performed in *Molinietum-caeruleae* meadows [7]. Similar phenomenon was observed in *Cirsietum rivulare* meadows being in courseof-succession [27–29]. The abovementioned authors found much weaker recruitment process in patches overgrown by shrub-willows or prevailed by large-tussock sedges, than in patches dominated by low-growing herbs. Furthermore, the decrease of species and seedling number in semi-natural grasslands along the successional gradient was found by V a n d v i k and G o l d b e r g [30].

The observed decrease of number of species and seedlings in the patches representing mid- and late-successional stages might be caused by the prolonged periods of spring flooding. The increase of water table might suppress the seed germination. Such phenomenon was repeatedly observed in several wetland taxa [31–34]. The abovementioned authors argued that the suppression of germination may be due to increased anaerobic metabolism, which could damage diaspore through the buildup of toxic materials. Moreover, the immersion contributes to slow diffusion rates of gases hampering oxygen supply to roots and reducing respiration and photosynthesis rates in submerging plants [35]. The inhibition of growth and ultimately death in waterlogging conditions were observed by Fraser and Karnezis [36], as well as Franczak and Czarnecka [37]. On the other hand, the experiments of Kotowski et al. [38,39] brought evidence, that the high water level usually hampers establishment of seedlings of wetland taxa in a lesser extent, than the darkness. Taking into account the abovementioned findings, it might be assumed that the diminishing abundance of species and seedlings observed in patches with rising height of standing vegetation might be due to the increasing light attenuation by adjacent plants rather than flooding.

Simultaneously, it should be added that the noted diminishing colonization of gaps in successive sites might be a consequence of root competition. So far, several authors observed that the growing density of root system of surrounding vegetation leads to the increasing nutrient uptake that may create local resource depletion zones. Such phenomenon contributes to inhibition of seedling establishment of herbaceous plants [40,41], shrubs [42] and trees [43]**.**

The species diversity in the different-sized gaps in each patch

As expected the species composition in subplots was similar regardless of their dimensions. Such phenomenon suggests that gaps act the role of remarkably efficient "seed traps" and the safe sites for seedling recruitment. Simultaneously, it should be pointed out that performed studies are not consistent with observations of Vandvik [44] carried out in alpine grasslands in course of succession. The aforementioned author argued that gaps of different area are filled with diverse assemblages of species. Also, the observations of herbaceous ground vegetation in artificially-created gaps in a managed beech forest brought evidence that some taxa appeared in large gaps only, whilst the others recruited in small openings [45,46]. Moreover, it is worth to notice that similar phenomenon was observed in the seedlings pool of trees in temperate forest [47]. Also, Fahey and Puettmann [48] showed, that understorey plant community composition differed significantly between large and small openings. Furthermore, the diverse set of species within different-sized gaps was also observed in numerous tropical forest ecosystems [49].

The correlation between gap size and number of seedlings of particular species

Despite of similarity in floristic composition among openings, the obtained results did not uphold the null hypothesis and have showed, that many species present a positive correlation between gap dimensions and seedling number. The performed observations are consistent with the observations of colonization of different-sized openings by seedlings of *Cirsium arvense* [50], *Solidago canadensis* [51,52], as well as *Iris sibirica* [53].

Simultaneously, it should be added that the results of present investigations showing that *Dianthus superbus* may present positive correlation in some habitats and a negative relationship in the other ones, are not consistent with previous findings that regardless of patch character absolute number of generative offsprings increases with augmentation of gap area [54].

The obtained results documented that numerous species show a negative relationship between opening dimensions and the number of seedlings. The performed investigations support the studies of Lepš [55], who has found greater recruitment of *Sanguisorba officinalis* and *Betonica officinalis* in abandoned sites than in mowed ones. The microsite conditions in unmanaged meadows might resemble these ones observed in small openings because of close vicinity of adult plants occurring in existing vegetation. The adjacent mature individuals protect the seedlings from unfavorable factors such as wind and drought but on the other hand they are strong competitors for nutrients, water and light. Such phenomenon isknown as the "nurse effect" [56].The site conditions in mowed patches might be quite similar to occurring in larger openings, where the competition for resources is reduced but seedlings are exposed to unfavorable abiotic conditions, as well as the herbivore activity. Simultaneously, it should be noticed that, contrary to my findings Lepš [55] has documented a positive relationship between intensity of management and recruitment of *Potentilla erecta* and *Selinum carvifolia*. Similar phenomenon was noted by Van der Meer et al. [57], who claimed that the probability of establishment of *Succisa pratensis* seedlings in traditionally managed meadows is much greater than in abandoned sites.

The relationship between opening size and recruitment of taxa adapted to the fast and slow clonal spread

Presented findings showed that species showing positive correlation between seedling abundance and gap size are characterized by traits allowing rapid colonization of open habitat. The creation of hypogeogenous stems enables protection of meristems from destruction due to mechanical damage mainly from animal trampling and digging. The substantial vegetative growth and considerable number of daughter ramets enable also exploration of large gaps and placing descendants in favorable microhabitats, whereas short lifespan of shoots contributes to their fast turnover in large uncrowded places. The formation of epigeogenous stems by taxa showing negative relationship between offspring recruitment and gap dimensions might be connected with low risk of damage of adventitious buds in small openings. The slight values of lateral spread and low number of vegetative offsprings might be linked with restrictions in biomass production in small openings, while the long-lived ramets allow the duration of individuals in small places.

Performed studies support previous observations on the influence of disturbance intensity on recruitment of species with different parameters of selected life history traits relevant to clonality in *Molinietum caeruleae* meadows [58]. The aforementioned author stated that abundance of taxa forming underground clonal growth organs, with considerable vegetative growth, high production of daughter ramets, short lifespan of shoots and not enduring genet integration increased gradually and significantly with growing disturbance gradient. Moreover, the increasing frequency of plants with high vegetative spread in gaps left after moderate and strong disturbances was observed in abandoned grasslands [59,60], mountain pastures [61], as well as old fields [62,63].

Implications for meadow conservation

In light of performed studies it may be stated that the removal of plant canopy and litter leads to the greatest seedling appearance in site representing early successional stage. However, the creation of gaps in places representing mid- and late-successional stages might also contribute to increase of recruitment rates. The creation of different-sized gaps seems to be a very effective way for conservation of *Molinietum caeruleae* meadows. This treatment assures the increase of offspring number of both: taxa showing a positive and a negative correlation between seedling abundance and gap area. The appearance of such species adapted to fast and slow habitat colonization (respectively) assures the taxa heterogeneity, particularly important in the course of succession.

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Wpływ stadium sukcesji i wielkości luk na rekrutację gatunków klonalnych w płatach zarastających łąk trzęślicowych

Streszczenie

W wielu zbiorowiskach roślinnych o zwartej pokrywie roślinnej zaburzenia powstałe na skutek abiotycznych i biotycznych czynników przyczyniają się do powstania luk uważanych za bezpieczne miejsca do kiełkowania. Luki charakteryzują się wieloma cechami, z których wielkość jest powszechnie uważana za najważniejszą. Badania rekrutacji siewek gatunków klonalnych w lukach o odmiennych rozmiarach były prowadzone w latach 2011–2012 w płatach łąk trzęślicowych *Molinietum caeruleae* reprezentujących zróżnicowane stadia sukcesji wtórnej i zdominowanych przez różne gatunki. Płat ES reprezentujący początkowe stadium zarastania był zdominowany przez niewielkie gatunki łąkowe, w Płacie MS reprezentującym pośrednie stadium przeważały wysokie ziołorośla, natomiast Płat LS reprezentujący stadium końcowe był zarośnięty przez ziołorośla i krzewiaste gatunki wierzb. Całkowita liczba gatunków i siewek na kolejnych powierzchniach badawczych stopniowo malała. Zjawisko to może być związane z coraz dłuższym okresem wiosennych podtopień, spadkiem dostępności światła lub zwiększającym się wykorzystaniem zasobów przez gatunki obecne w pokrywie roślinnej. Prawie wszystkie gatunki prezentujące pozytywną korelację pomiędzy liczbą siewek a rozmiarem luk cechują się znacznym wzrostem wegetatywnym i dużą produkcją ramet potomnych umożliwiających szybką kolonizację zasiedlonego miejsca. Większość gatunków wykazujących negatywną

korelację charakteryzuje się wolnym wzrostem wegetatywnym oraz wytwarzaniem niewielkiej liczby długotrwałych ramet potomnych. W świetle przeprowadzonych badań można stwierdzić, że zaburzenia w zwartej pokrywie roślinnej i ściółce mogą przyczynić się do zachowania łąk trzęślicowych. Ponadto tworzenie luk o zróżnicowanych rozmiarach wydaje się szczególnie ważne ze względu na podtrzymanie różnorodności gatunków klonalnych, zwłaszcza w zaawansowanych stadiach sukcesji.

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