THE IMPACT OF DISTURBANCE GRADIENT ON RECRUITMENT OF CLONAL PLANT SPECIES IN MOLINIETUM CAERULEAE MEADOWS

ABSTRACT: The investigations of the impact of disturbance severity on recruitment of clonal plant species were performed in three Molinietum caeruleae patches dominated by small meadow species (MC), or prevailed by tall grasses (GR) or overgrown by willows (SA). The meadows were located in Vistula valley close to Kraków agglomeration, southern Poland. In above mentioned patches ten permanent experimental plots were randomly arranged. Each plot was divided in four subplots measured 900 cm² represented undisturbed control, low level of disturbance (the litter and the moss layer removal), intermediate level of disturbance (the litter, moss and above-ground vegetation removal), high level of disturbance (the litter, moss and the plants removal as well as top soil raking). The colonization of gaps was observed in the years 2008–2010.

Irrespective of patch character, the greatest species richness and seedling abundance were observed in gaps, which occurred in result of intermediate disturbances. Weaker recruitment rates were recorded in openings left after disturbances of low- and high severity, while in fully compact herb layer no seedlings were found. In MC patch, regardless of treatment in all openings similar spectra of life history traits were observed. In seedling pool of all subplots appeared taxa creating below ground organs of clonal growth. In all subplots dominated species with intermediate values of lateral spread, numerous vegetative descendants, short-lasting stems and no persistent genet integration. In sites GR and SA in openings left after weak disturbances appeared species with below- and aboveground organs of clonal growth. The majority of them characterized by slight lateral spread, low number of vegetative offsprings, long lifespan of shoots and persistent genet integration. The abundance of taxa creating underground clonal growth organs, with considerable vegetative spread, high production of daughter ramets, short lifespan of shoots and not enduring genet integration increased gradually and significantly with disturbance gradient.

Although the greatest recruitment rates were found in gaps left after removal of litter, moss and above-ground parts of plants, the most effective way for conservation of Molinietum caeruleae meadows appeared to be creation of different severity disturbances. Such treatment contributes to maintenance of heterogeneity of clonal species composition, especially in patches in advanced successional stages.

KEY WORDS: clonal growth, CLO-PLA 3 database, disturbances, gaps, life-history traits, seedling recruitment

1. INTRODUCTION

The seedling recruitment is the most vulnerable stage in the life histories of plants. The emerging individuals are smaller, less protected against predators, as well as more sensitive to adverse environmental conditions such as
freezing, desiccation and deficiency of nutrients than mature individuals. The successful seedling establishment leads to augmentation of population abundance, facilitates its persistence in occupied site, and maintains genetic diversity. In consequence, the recruitment of new genets influences structure and dynamics of plant communities. According to conventional point of view (c.f Harper and White 1974, Harper 1977, Cook 1985) the clonal species rely chiefly on asexual propagation by means of organs such as stolons, tubers, corms, rhizomes, bulbils or roots and the repeated seedling recruitment in their populations is rare and infrequent. Contrary to traditional thought, Eriksson (1989) asserted that seedling appearance in established populations of adult genets is very common and might occur in temporal openings originated in result of disturbances in plant canopy and litter. Subsequently, the sexual reproduction were recorded in populations of several clonal species representing various life form, i.e. Populus tremula L. (Myking et al. 2011), Rhus L. (Li et al. 1999), Ambrosia tenuifolia Spreng. (Insausti and Grimoldi 2006), Hieracium pilosella L. (Bruun et al. 2007), Geum reptans L. (Pluess and Stocklin 2004) and Iris sibirica L. (Kostrakiewicz 2007).

While considerable body of studies focused on interspecific colonization ability, the intraspecific differences in capacity for seedling establishment received less attention. Until recently, the studies of natural recruitment process were particularly rare. Such investigations were carried out by Borkowska (2004a, b, 2006), who observed the species richness and seedling abundance in artificial gaps corresponding with grazing and rooting in Cirsietum rivularis meadows abandoned at different times. The influence of mowing and litter removal on seedling recruitment was investigated in Molinietum caeruleae meadows by Špačkova et al. (1998), Lepš (1999), as well as Špačkova and Lepš (2004). Studies of influence of site conditions or gap character on proportions of taxa representing different parameters of life-history traits connected with clonal multiplication were equally scarce. Authors have focused on vegetative mobility and observed the performance of species with various rates of lateral spread in relation to soil fertility (Økland 1995), as well as gap origin (Lavorel et al. 1998, 1999, Kohler et al. 2006, Kahmen and Posholdt 2008). Given the inadequate state of knowledge, it should be assumed that research on regularities of clonal species recruitment is still needed. Such investigations are very valuable from an evolutionary point of view, allowing for assessment the mechanisms governing the natural gap colonization. This also has considerable implications for successful ecosystem restoration. Nowadays Molinietum caeruleae meadow is one of the rapidly vanishing communities of Central Europe. During the last decades the blue moor-grass meadows suffer strongly from intensive agricultural use, as well as land abandonment and fragmentation (Fuller 1987, Green 1990, Präh 1993, Joyce and Wade 1998, Muller 2000, Diemer et al. 2001). The Molinon 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 present studies were undertaken to investigate the effect of disturbance severity on recruitment of clonal species in Molinietum caeruleae patches with various site conditions. The detailed goals focused on assessment: (1) the impact of disturbance type on species and seedling abundance, (2) the influence of disturbance character on proportions of species with different parameters of selected life history traits relevant to clonality.

2. STUDY AREA

The studies were carried out in Kostrze district localised on western border of Kraków, on the south of the Vistula River (southern Poland). The research area is at ca 210 m a.s.l, on a low flood terrace of Vistula, 3–6 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 greatest area is taken by Molinietum caeruleae patches, which are relics of vast meadows stretching about 30 km soth from Kraków (Zarzycki 1958). The abandonment of traditional land use for at least a dozen years promoted the development of Phragmites swamps and willow brushwood leading to fragmentation of meadows (Dubiel 1991,
The impact of disturbance gradient on clonal plant recruitment

The studies were carried out simultaneously in three adjacent, abandoned patches *Molinietum caeruleae* with different species composition and habitat conditions.

Patch labeled **MC** (50°01′55.76″N, 19°52′03.06″E) of ca 1 600 m² was dominated by species creating delicate, erect or procumbent stems (i.e. *Lathyrus pratensis* L., *Lotus corniculatus* L.), small-tussock grass (i.e. *Briiza media* L., *Holcus lanatus* L.) and short rosette-forbs (i.e. *Lychnis flos-cuculi* L., *Succisa pratensis* Mchn.). The small-statured meadow species with shallowly rooted underground organs intercepted very low amount of irradiance, contributing to strong insolation of ground surface and fast evaporation of water from soil area.

Patch labeled **GR** (50°01′55.23″N, 19°52′05.48″E) of ca 1 200 m² was prevailed by tall grasses with large tussocks (i.e. *Molinia caerulea* (L.) Moench., *Deschampsia caespitosa* (L.) P.B.) or robuste rhizomes (i.e *Phragmites australis* Trin.). In the plant cover abundantly occurred also tall perennial herbs such as *Chamanerion angustifolium* (L.) Scop., *Lythrum salicaria* L., *Epilobium hirsutum* L. and *Filipendula ulmaria* (L.) Maxim. The high, closely packed shoots, as well as compact tussocks partly shaded the study patch and prevented soil surface from desiccation.

Patch labeled **SA** (50°01′55.60″N, 19°52′04.45″E) of ca 1 500 m² was overgrown by *Salix repens* ssp. *rosmarinifolia* L., *S. cinerea* L., as well as *S. aurita* L. The wide leaf canopy of willows strongly decrease the amount of solar radiation reaching to the soil area and assure the moisture of ground surface.

### 3. MATERIAL AND METHODS

In patches **MC**, **GR** and **SA**, in April 2008 ten permanent experimental plots of 0.5 × 1.6 m were randomly arranged. They were established at least 2.0 metres from the border of patch to avoid edge effect. Each plot was divided in four square-shaped, adjacent subplots of 900 cm². The subplots were subjected to four different disturbance regimes: 1) **no disturbances**; 2) **low level of disturbance**, corresponding with trampling consisted of the litter and moss layer removal; 3) **intermediate level of disturbance**, corresponding with mowing consisted of the litter, moss, and above-ground part of plants removal and 4) **high level of disturbance**, corresponding with rooting by wild mammals consisted of the litter, moss and the pants removal, as well as top soil raking with a metal scraper about 3 cm deep. The design of experiment is shown in Figure 1. The generative offspring establishment was monitored once a week in May, June, July and August, and once every two weeks in April, September and October, from 2008 through 2010. Seedlings were counted in each subplot, using aluminium frame 0.3 × 0.3 m in size. The seedlings and saplings were removed and determined according to Csápos (1968) and Muller (1978) with support of comparative collection. The nomenclature of taxa follows Mirek et al. (2002). The genets of rare and protected plants were replanted and marked with plastic rings and sticks. The effect of disturbance level on gap colonization was character-
ized by mean cumulative number of species and seedlings calculated by adding species (seedlings) that appeared in particular subplots over the course of four years. The statistical analysis done on untransformed data was based on the nonparametric Kruskal-Wallis test, which was applied to examine whether there were significant differences in mean number of taxa and seedlings that appeared in different treatment subplots within each patch.

In order to assess the species response to disturbance level, I selected life-history traits relevant to clonal growth and vegetative multiplication that were thought to be “ecologically meaningful” with regard to grazing or mowing. They were: “clonal growth organ” necessary for plant survival, i.e. occurring in all adult individuals of all populations, “lateral spread”, “number of offspring per parent ramet per year”, “lifespan of a shoot” as well as “persistence of the connection between ramets” (Klimešová et al. 2008). The attribute nomenclature obtained from the database CLO-PLA 3 (Klimešova and Klimeš 2006, Klimešová and de Bello 2009) is given in Table 1. The data for species growing in the experimental plots are presented in APPENDIX. For taxa capable of developing more than one type of necessary clonal growth organ or presented different values of other traits, the most commonly noted data was used in the analysis. Subsequently, the relative abundance of seedlings presenting diverse attributes of each trait were calculated in particular subplots. The chi-square statistics were applied to check whether there were significant differences among subplots within each patch in average percentage of seedlings presenting various parameters of particular features.

Table 1. Plant traits used in analysis (according to Klimeš and Klimešowa 2006).

<table>
<thead>
<tr>
<th>Trait</th>
<th>Attribute</th>
</tr>
</thead>
<tbody>
<tr>
<td>Clonal growth organ</td>
<td></td>
</tr>
<tr>
<td>Above or at soil surface</td>
<td>(rooting horizontal stems at or above soil surface, turions, bulbils and tubers of stem origin at or above soil surface, plantlets, plant fragments of stem origin, budding plants, root tubers at or above soil surface, buds on leaves)</td>
</tr>
<tr>
<td>Below soil surface</td>
<td>(epigeogenous stems, hypogeogenous stems, tuber-splitters, stem tubers, bulbs, root-splitters, roots with adventitious buds, root tubers below-ground, offspring tubers at distal end of above-ground stems)</td>
</tr>
<tr>
<td>Lateral spread (m year⁻¹)</td>
<td>&lt;0.01 0.01–0.25 &gt; 0.25 dispersable</td>
</tr>
<tr>
<td>Number of offsprings per parent ramet per year</td>
<td>1 2 2–10</td>
</tr>
<tr>
<td>Lifespan of a shoot (year)</td>
<td>1 2 &gt;2</td>
</tr>
<tr>
<td>Persistence of the connection between parent and offspring shoots (years)</td>
<td>1 2 &gt;2</td>
</tr>
</tbody>
</table>
4. RESULTS

4.1. The impact of disturbance level on species and seedling abundance

Irrespective of patch character the greatest species richness characterized subplots, where litter, moss layer and above-ground part of plants were uncovered (intermediate disturbance level) (Table 2). The number of species decreased in subplots, where litter, moss, plants and top soil were removed (strong disturbance level). The lowest species richness was found in subplots, where moss layer and decayed organic matter were eliminated (low disturbance level). Additionally, it should be added that species recruitment did not occur in control subplots.

Regardless of site conditions, the greatest recruitment of seedling occurred in openings originated as a result of intermediate disturbance (Table 3). Minor rate of colonization were found in gaps left after strong disturbance. The lowest recruitment of genets was found in openings originated in result of weak disturbance.

4.2. The influence of disturbance character on proportions of species with different parameters of selected life history traits relevant to clonality.

In the seedling pool of all patches were found taxa with various type of clonal growth organs and different rates of lateral spread. There were noted species creating 1, 2, or 2–10 vegetative offsprings, with the lifespan of shoots lasting 1 or 2 years and persistence of connections enduring 1, 2 or more than 2 seasons (APPENDIX).

In seedling pool of all subplots arranged in patch MC were noted only taxa creating below ground organs of clonial growth. The proportions among species with various organs of clonial growth recruited in particular subplots were quite constant (Fig. 2). In sites GR and SA abundance of species forming above ground clonal growth organs decreased, while number of taxa creating below ground organs of clonal growth increased gradually from subplots II, via subplots III to subplots IV (Figs 3 and 4). In the MC patch dominated the taxa, which clonal growth achieved from 0.01 m to 0.25 m per year (Fig. 2). The proportions between species with various rates of vegetative mobility recorded in particular subplots were similar. In patches GR and SA, in subplots II the frequency of species, which lateral spread did not exceed 0.01 m were significantly higher, than taxa presenting greater values of clonal growth (Figs 3 and 4). The aforementioned tendency reversed in subplots III and IV. In MC patch, irrespective of treatment character prevailed species creating numerous vegetative descendants (Fig. 2). In patches GR and SA, the relative abundance of taxa producing several offsprings increased significantly with

<table>
<thead>
<tr>
<th>Patch</th>
<th>Subplot</th>
<th>Average number of species</th>
<th>Statistical significance</th>
</tr>
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<tr>
<td>MC</td>
<td>I</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td></td>
<td>II</td>
<td>9.9±5.1</td>
<td>H=24.48**</td>
</tr>
<tr>
<td></td>
<td>III</td>
<td>20.8±4.2</td>
<td></td>
</tr>
<tr>
<td></td>
<td>IV</td>
<td>19.8±3.6</td>
<td></td>
</tr>
<tr>
<td>GR</td>
<td>I</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td></td>
<td>II</td>
<td>2.0±2.2</td>
<td>H=33.74***</td>
</tr>
<tr>
<td></td>
<td>III</td>
<td>16.9±4.9</td>
<td></td>
</tr>
<tr>
<td></td>
<td>IV</td>
<td>12.5±3.3</td>
<td></td>
</tr>
<tr>
<td>SA</td>
<td>I</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td></td>
<td>II</td>
<td>3.1±4.6</td>
<td>H=34.13***</td>
</tr>
<tr>
<td></td>
<td>III</td>
<td>14.5±3.0</td>
<td></td>
</tr>
<tr>
<td></td>
<td>IV</td>
<td>7.9±2.1</td>
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</table>
disturbance gradient (Figs 3 and 4). Concerning feature "shoot lifespan", it was recorded that, in all subplots arranged in MC patch prevailed taxa producing short-lasting stems (Fig. 2). The proportions between species creating ramets living one season and taxa forming stems lasting two years did not differ among particular subplots. In patches GR and SA, number of taxa with shorter ramet lifespan increased significantly with disturbance level (Figs 3 and 4). In seedling pool of all openings occurred in patch MC dominated taxa with no persistent genet integration. The relative abundance of species presenting long- and short-lasting connection between ramets did not differ among particular subplots. In patches GR and SA, number of taxa with shorter ramet lifespan increased significantly with disturbance level (Figs 3 and 4). In seedling pool of all openings occurred in patch MC dominated taxa with no persistent genet integration. The relative abundance of species presenting long- and short-lasting connection between ramets did not differ among particular subplots. In patches GR and SA, number of taxa with shorter ramet lifespan increased significantly with disturbance level (Figs 3 and 4). In seedling pool of all openings occurred in patch MC dominated taxa with no persistent genet integration. The relative abundance of species presenting long- and short-lasting connection between ramets did not differ among particular subplots. In patches GR and SA, number of taxa with shorter ramet lifespan increased significantly with disturbance level (Figs 3 and 4). In seedling pool of all openings occurred in patch MC dominated taxa with no persistent genet integration. The relative abundance of species presenting long- and short-lasting connection between ramets did not differ among particular subplots. In patches GR and SA, number of taxa with shorter ramet lifespan increased significantly with disturbance level (Figs 3 and 4).

5. DISCUSSION

5.1. The impact of disturbance level on species and seedling recruitment

The performed investigations, demonstrating that weak disturbances lead to appearance of clonal species, stay in accordance with observations of seedling establishment in oligotrophic wet meadows belonging to Molinion alliance (Špačkova et al. 1998, Špačkova and Lepš 2004). Numerous authors asserted that the litter and moss layer inhibit recruitment process. The bryophytes might diminish seedling emergence by mechanical prevention of seeds reaching soil surface, as well as by allelopathic effects (Durting and van Torren 1990, van Torren 1990). The decayed phytomass might change light quality and affect seeds, whose sprouting is controlled by the phytochrome system (Baskin and Baskin 1998), or act as a mechanical filter by allowing only certain species to emerge through its layer (Facelli and Pickett 1991, Xiong et al. 2001).

The recruitment process might be suppressed by standing vegetation. The released diaspores may collide with plant canopy. Pounden (2008) stressed that, seeds with appendages such as kapok, coma or pappus could be trapped by plant elements of low porosity e.g. umbels, densely-needled conifer shoots or stems with fully deployed leaves. Moreover, the standing vegetation might slow wind velocity at the ground level, reduce distance of seeds dispersal and in this way diminish chances for deposition of propagules in gaps. Furthermore, the leaf canopy of established plants absorbs solar radiation and might contribute to diminishing of recruitment rates of light-demanding species. Additionally it should be highlighted, that although intermediate disturbances contribute to increase of recruitment rates, strong disturbances consisting of removal of above-ground vegetation mass and top soil layer lead to inhibition of colonization pro-

<table>
<thead>
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<th>Patch</th>
<th>Subplot</th>
<th>Average seedling number</th>
<th>Statistical significance</th>
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<tr>
<td>MC</td>
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<td>0</td>
<td>H = 29.02***</td>
</tr>
<tr>
<td></td>
<td>II</td>
<td>44.4±4.1</td>
<td></td>
</tr>
<tr>
<td></td>
<td>III</td>
<td>128.2±17.3</td>
<td></td>
</tr>
<tr>
<td></td>
<td>IV</td>
<td>87.5±10.6</td>
<td></td>
</tr>
<tr>
<td>GR</td>
<td>I</td>
<td>0</td>
<td>H = 35.17***</td>
</tr>
<tr>
<td></td>
<td>II</td>
<td>12.0±3.2</td>
<td></td>
</tr>
<tr>
<td></td>
<td>III</td>
<td>69.4±10.2</td>
<td></td>
</tr>
<tr>
<td></td>
<td>IV</td>
<td>55.1±9.4</td>
<td></td>
</tr>
<tr>
<td>SA</td>
<td>I</td>
<td>0</td>
<td>H = 31.81***</td>
</tr>
<tr>
<td></td>
<td>II</td>
<td>9.2±4.5</td>
<td></td>
</tr>
<tr>
<td></td>
<td>III</td>
<td>52.7±7.6</td>
<td></td>
</tr>
<tr>
<td></td>
<td>IV</td>
<td>23.3±4.5</td>
<td></td>
</tr>
</tbody>
</table>
The impact of disturbance gradient on clonal plant recruitment

Fig. 2. The mean percentage of seedlings with different clonal growth organ, lateral spread rate, number of offspring per parent shoot per year, ramet ramet lifespan and value of persistence of connection between ramets in particular subplots established in patch dominated by small meadow species (MC) in subplots with different disturbance regime: II – low level of disturbance, III – intermediate level of disturbance, IV – high level of disturbance.
Fig. 3. The mean percentage of seedlings with different clonal growth organ, lateral spread rate, number of offspring per parent shoot per year, ramet ramet lifespan and value of persistence of connection between ramets in particular subplots established in patch dominated by large-tussocks grasses (GR) in subplots with different disturbance regime: II – low level of disturbance, III – intermediate level of disturbance, IV – high level of disturbance.
The impact of disturbance gradient on clonal plant recruitment

Fig. 4. The mean percentage of seedlings with different clonal growth organ, lateral spread rate, number of offspring per parent shoot per year, ramet ramet lifespan and value of persistence of connection between ramets in particular subplots established in patch dominated by willows (SA) in subplots with different disturbance regime: II – low level of disturbance, III – intermediate level of disturbance, IV – high level of disturbance.
cess. Similar phenomenon was observed by Lepš (1999), who noticed that species and seedling appearance is positively influenced by mowing and, to a lesser extent, by removal of dominant species such as Molinia caerulea. Furthermore, Borkowska (2004a, b, 2006) proved that openings originated as a result of cutting off above-ground vegetation in Cirsietum rivularis patches are much faster colonized than gaps left after removing the plants and 15–20 cm deep layer of soil. Such phenomenon might be caused by partial elimination of seed bank in result of bare ground raking. Several studies (e.g. Lavorel et al. 1993, Kitajima and Tilman 1996, Klug-Pümpel and Scharfetter-Lehrl 2008) confirmed that diaspores density and species richness in soil seed bank is significantly higher in the shallow layer than in the deeper ones.

5.2. The influence of disturbance character on proportions of species with different parameters of selected life history traits relevant to clonality

The similarity of life history trait spectra in all subplots arranged in MC patch, corresponding with distribution recorded in openings left after moderate and strong disturbances in GR and SA patches, confirms the phenomenon observed by Lavorel et al. (1999). The authors found that taxa appearing independently to disturbance in old fields in early successional age, required disturbance to establish in older ones.

The distinct species composition in gaps originated in result of different severity treatments in patches dominated by tall grasses or willows might be caused by various microenvironmental conditions in openings. The appearance of species with above ground- and epigeogenous stems in gaps occurred after weak disturbance could be connected with slight risk of bud bank damage. The augmentation of abundance of species with below ground organs of clonal growth in openings developed in result of intermediate and strong disturbances might be caused by protection of meristems from destruction due to drought, freeze or mechanical damage. Also other authors have claimed that bud bank of plants generally extends from above- to below ground with increasing disturbance severity (Klimešová and Klimeš 2003, 2007), as well as their intensity (Klimkowska et. al 2009).

The observed dominance of species with slight values of lateral spread and low number of vegetative offsprings in openings originated in result of weak disturbances might be caused by restrictions in biomass production in crowded environment. The rise of abundance of species presenting great lateral spread and considerable number of daughter ramets with disturbance severity leads to efficient gap colonization. Also Lavorel et al. (1998) and Kahmen and Poshold (2008) recorded the increase of performance of taxa presenting substantial vegetative growth in openings occurred in result of moderate and strong disturbances. Furthermore, McIntyre and Lavorel (2001) observed the significant augmentation of abundance of taxa presenting large resprouting capacity with acceleration of grazing pressure in grasslands. In contrary, Tamm et al. (2002) assumed that species with low values of clonal growth occurred more abundantly in plant cover of regularly mown meadows, than in overgrown patches.

Performed studies showing the rise of recruitment rates of species with annual ramets with disturbance level gradient is consistent with findings of Tamm et al. (2002). Above mentioned authors found, that long ramet lifespan enables persistence of shoots in small microsites, while short lifespan of ramets assures fast turnover of shoots in uncrowded places occurred in regularly managed patches.

The observed negative relationship between genet integration and disturbance severity is in accordance with predictive models, stated that integration of clonal species is adaptively advantageous in habitats with high productivity, where usually small-sized gaps occur rarely, while splitting is more typical in patches with large canopy gaps or numerous number of small-sized openings (Oborný and Kun 2000, Kun and Oborný 2003). The long lasting connections between ramets facilitate internal transport of water and assimilate from sites of high supply to places of high demand in persistently crowded environment, whereas short genet integration leads to rapid separation of internodes and efficient resource exploitation by autonomous subunits.
5.3 Implications for successful conservation of *Molinietum caeruleae* meadows

It is widely accepted that removal of vegetation and topsoil, providing the "safe sites" for recruitment, contributes to successful conservation and restoration of fen meadows communities (cf. Tallowin and Smith 2001, Isselstein et al. 2002, Klimkowska et al. 2007). Performed studies confirmed the importance of disturbance for the augmentation of clonal species richness as well as for seedling emergence. The highest values of colonization were recorded in patches dominated by small meadow species, but the promising role of disturbances was also observed in places prevailed by tall grasses, as well as in sites overgrown by willows. Although the greatest recruitment rates were noted in openings left after intermediate disturbances, the most effective way for conservation of *Molinietum caeruleae* meadows appeared to be creation disturbances characterized by various severity levels. Such treatment contributes to maintenance of heterogeneity of clonal species composition, especially in patches in advanced successional stages.

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6. REFERENCES


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APPENDIX. Comparisons of life history traits related to clonal growth.

<table>
<thead>
<tr>
<th>Species</th>
<th>Clonal growth organ (CGO)</th>
<th>Lateral spread (m year$^{-1}$)</th>
<th>Number of offspring per parent shoot per year</th>
<th>Lifespan of a shoot (years)</th>
<th>Persistence of the connection between ramets (years)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Achillea millefolium L.</td>
<td>Hypogeogenous stems</td>
<td>&gt;0.25</td>
<td>2–10</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Betonica officinalis L. (Trevis)</td>
<td>Epigeogenous stems</td>
<td>&lt;0.01</td>
<td>&lt;1</td>
<td>1</td>
<td>&gt;2</td>
</tr>
<tr>
<td>Caltha palustris L.</td>
<td>Epigeogenous stems</td>
<td>&lt;0.01</td>
<td>1</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Centaurea jacea L.</td>
<td>Hypogeogenous stems</td>
<td>&lt;0.01</td>
<td>1</td>
<td>1</td>
<td>&gt;2</td>
</tr>
<tr>
<td>Cirsium arvense (L.) Scop.</td>
<td>Roots with adventitious buds</td>
<td>&gt;0.25</td>
<td>2–10</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Cirsium rivulare (Jacq.) All.</td>
<td>Epigeogenous stems</td>
<td>0.01–0.25</td>
<td>1</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Cruciata glabra (L.) Erhend.</td>
<td>Hypogeogenous stems</td>
<td>0.01–0.25</td>
<td>1</td>
<td>1</td>
<td>&gt;2</td>
</tr>
<tr>
<td>Deschampsia cecapitosa (L.) P. Beauv</td>
<td>Epigeogenous stems</td>
<td>&lt;0.01</td>
<td>2–10</td>
<td>1</td>
<td>&gt;2</td>
</tr>
<tr>
<td>Dianthus superbus L.</td>
<td>Hypogeogenous stems</td>
<td>&lt;0.01</td>
<td>1</td>
<td>2</td>
<td>&gt;2</td>
</tr>
<tr>
<td>Filipendula ulmaria (L.) Maxim.</td>
<td>Hypogeogenous stems</td>
<td>0.01–0.25</td>
<td>2–10</td>
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<tr>
<td>Filipendula vulgaris Moench.</td>
<td>Epigeogenous stems</td>
<td>&lt;0.01</td>
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<tr>
<td>Galium boreale L.</td>
<td>Hypogeogenous stems</td>
<td>0.01–0.25</td>
<td>2–10</td>
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<td>Galium verum L.</td>
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<td>Geranium palustre L.</td>
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<td>Geranium pratense L.</td>
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<td>Geum rivale L.</td>
<td>Epigeogenous stems</td>
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<td>&lt;1</td>
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<td>Gladiolus imbricatus L.</td>
<td>Stem tubers</td>
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<td>Heracleum sphondylium L.</td>
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<td>Holcus lanatus L.</td>
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<td>&lt;0.01</td>
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<td>Inula salicina L.</td>
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<td>0.01–0.25</td>
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<td>Iris sibirica L.</td>
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<td>Lathyrus pratensis L.</td>
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<td>Leucanthemum vulgare Lam.</td>
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<td>Lotus corniculatus L.</td>
<td>Root-splitters</td>
<td>&lt;0.01</td>
<td>2–10</td>
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<td>Lychnis flos-cuculi L.</td>
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<td>0.01–0.25</td>
<td>2–10</td>
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<td>Lysimachia nummularia L.</td>
<td>Horizontal above ground stems</td>
<td>0.01–0.25</td>
<td>2–10</td>
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<td>Lysimachia vulgaris L.</td>
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<td>0.01–0.25</td>
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<td>Lythrum salicaria L.</td>
<td>Epigeogenous stems</td>
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<td>Mentha longifolia (L.) L.</td>
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<td>0.01–0.25</td>
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### The impact of disturbance gradient on clonal plant recruitment

<table>
<thead>
<tr>
<th>Species</th>
<th>Clonal growth organ (CGO)</th>
<th>Lateral spread (m year(^{-1}))</th>
<th>Number of offspring per parent shoot per year</th>
<th>Lifespan of a shoot (years)</th>
<th>Persistence of the connection between ramets (years)</th>
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<tbody>
<tr>
<td><em>Molinia caerulea</em> (L.) Moench.</td>
<td>Hypogeogenous stems</td>
<td>&lt;0.01</td>
<td>1</td>
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<tr>
<td><em>Phragmites australis</em> (Cav.) Trin. ex Steud.</td>
<td>Hypogeogenous stems</td>
<td>&gt;0.25</td>
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<td><em>Plantago lanceolata</em> L.</td>
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<td>&lt;0.01</td>
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<tr>
<td><em>Polygonum bistorta</em> L.</td>
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<td>&lt;0.01</td>
<td>&lt;1</td>
<td>1</td>
<td>&gt;2</td>
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<tr>
<td><em>Potentilla erecta</em> (L.) Raesusch.</td>
<td>Epigeogenous stems</td>
<td>&lt;0.01</td>
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<td><em>Primula vulgaris</em> Huds.</td>
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<td>&lt;0.01</td>
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<td><em>Ranunculus acris</em> L.</td>
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<td>&lt;0.01</td>
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<td><em>Ranunculus repens</em> L.</td>
<td>Horizontal above ground stems</td>
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<td><em>Rumex acetosa</em> L.</td>
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<td>&lt;0.01</td>
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<td><em>Sanguisorba officinalis</em> L.</td>
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<td>&lt;0.01</td>
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<td>1</td>
<td>&gt;2</td>
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<tr>
<td><em>Selinum carvifolia</em> (L.) L.</td>
<td>Epigeogenous stems</td>
<td>&lt;0.01</td>
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<td><em>Serratula tinctoria</em> L.</td>
<td>Epigeogenous stems</td>
<td>&lt;0.01</td>
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<td><em>Solidago canadensis</em> L.</td>
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<td>0.01–0.25</td>
<td>2–10</td>
<td>1</td>
<td>&gt;2</td>
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<tr>
<td><em>Succisa pratensis</em> Moench.</td>
<td>Epigeogenous stems</td>
<td>&lt;0.01</td>
<td>&lt;1</td>
<td>1</td>
<td>2</td>
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<tr>
<td><em>Trifolium pratense</em> L.</td>
<td>Root-splitters</td>
<td>&lt;0.01</td>
<td>&lt;1</td>
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<td><em>Trollius europaeus</em> L.</td>
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<td>&lt;0.01</td>
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<tr>
<td><em>Valeriana officinalis</em> L.</td>
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<tr>
<td><em>Viola palustris</em> L.</td>
<td>Epigeogenous stems</td>
<td>&lt;0.01</td>
<td>&lt;1</td>
<td>1</td>
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