ARE *DESCHAMPSIA CAESPITOSA* (L.) BEAUV. TUSsockS SAFE SITES FOR SEEDLING RECRUITMENT IN THE SUCCESSION OF WET MEADOWS?

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ABSTRACT: In stressful and harsh environments, safe sites for seedling recruitment may be created by nurse plants, which accumulate propagules and subsequently facilitate the establishment of individuals. The main goal of the presented studies focused on observations of seedling recruitment in small and large tussocks of *Deschampsia caespitosa* derived from patches of unmanaged *Molinietum caeruleae* meadows situated along the successional gradient and dominated by small meadow species (Patch I), by macroforbs (Patch II), or overgrown by trees and shrubs (Patch III).

The studies showed that, irrespective of patch character, *Serratula tinctoria*, *Selinum carvifolia*, *Lysimachia vulgaris* and *Filipendula ulmaria* are among the best colonizers of *Deschampsia caespitosa* tussocks. The gradual decrease in number of species and offspring abundance along the successional gradient may be connected with a prolonged period of water stagnation accelerating the development of fungal pathogens, a major cause of mortality for buried diaspores. The growing frequency of species present in standing vegetation and the gradually rising contribution of swamp and forest taxa in consecutive patches may be due to the production of non-persistent diaspores by early successional species, as well as reduced seed immigration from neighboring sites.

The obtained results included evidence that, regardless of patch character, the percentage of seedlings representing species present in and absent from existing vegetation as well as taxa with

various vegetation types is similar in small and large tussocks. Furthermore, in small tussocks, regardless of patch character, anemochorous and hydrochorous taxa dominated, the frequency of endo- and epizoochorous taxa was much lower, while the percentage of species characterized by other modes of diaspore dispersal attained the lowest rates. In large tussocks, anemochorous and epizoochorous species prevailed, the share of endozoochorous and hydrochorous taxa was lower, and the contribution of species characterized by other modes of dissemination was very scarce.

On the basis of these studies it might be concluded that, despite the successive decrease of species and seedling abundance, and along with the increase in the recruitment of taxa resident in standing vegetation, especially woody species, the tussocks of *Deschampsia caespitosa* are reservoirs of meadow species even in advanced successional stages and may play a significant role in the process of long-term species turnover.

KEY WORDS: diaspore dispersal, seedling number, habitat conditions, grass tussocks, *Molinietum caeruleae*

1. INTRODUCTION

Seedling recruitment, which leads to increases in population abundance and maintenance of genetic diversity, is also a

critical bottleneck in population dynamics. According to Harper (1977), the emergence and establishment of generative offspring occurs only in safe sites where the environmental conditions are more favorable than in the surrounding area. In stressful and harsh environments, safe sites for recruitment are created by nurse plants buffering habitat conditions through accumulation of nutrients, provision of shade, amelioration of disturbance, or protection against herbivores. The voluminous literature (reviewed by Callaway 1995, 1998, Flores and Jurado 2003, Callaway *et al.* 2005, Brooker *et al.* 2008, Ren *et al.* 2008) has documented numerous benefits for establishment of seedlings under a canopy of shrubs, trees and graminoids. The nurse plants may also accumulate propagules and subsequently facilitate the establishment of seedlings. Such phenomena have been recorded in clonal, rhizomatous species with a phalanx growth strategy (Falińska 1986, 1995), cushion plants (Cavieres *et al.* 2002, Badano *et al.* 2007, Fajardo *et al.* 2008, Yang *et al.* 2010, Dvorský *et al.* 2013), and lichen and moss carpets (Groeneveld and Rochefort, 2005, Groeneveld *et al.* 2007, Casanova-Katny and Cavieres 2012).

Over the past decades, gradually growing interest has been noted in the processes of seedling recruitment in tussock-forming species. This phenomenon has been observed in alpine and subalpine grasslands (Yu *et al.* 2006, 2008, 2010), as well as in habitats subjected to frequent inundations and water disturbances such as freshwater marshes (Lord and Lee 2001, Crain and Bertness 2005), stream edges (Ervin 2007), peatlands (Koyama and Tsuyuzaki, 2010, 2012, Wang *et al.* 2011, 2012) and wet meadows (Brzosko 1991, Falińska 2003, Borkowska 2004). Despite the rising number of investigations, the processes of seedling recruitment in tussocks growing in temporarily flooded meadows remain poorly understood. Such studies may substantially enlarge knowledge of the mechanisms and consequences of colonization processes and could have promising implications for the restoration of meadows designated for conservation by International Conventions (Council Directive 92, Council Directive 97) and included in the NATURA 2000 network (Interpretation 2003).

In response to the insufficiency of present knowledge, investigations of the role of *Deschampsia caespitosa* tussocks as safe sites for seedling recruitment in *Molinietum caeruleae* meadows along the successional gradient were performed. The specific goals of research focused on:

- distinguishing the best colonizers of tussocks in particular patches,
- examining the impact of patch character on species diversity and seedling number on tussocks,
- observing the impact of patch character on the emergence of seedlings representing taxa: (i) present in/absent from standing vegetation, (ii) of different vegetation types, (iii) with various dispersal modes,
- evaluating the impact of the size of tussocks on the emergence of seedlings representing taxa: (i) present in/absent from standing vegetation, (ii) of different vegetation types, (iii) with various dispersal modes.

2. STUDY AREA

The studies were carried out in the Kostrze district, on the western border of Kraków south of the Vistula River (southern Poland). The research area is at ca 210 m a.s.l., on the low flood terrace of the Vistula, 3.0–6.0 m high. The water table is 0–2 m below the ground surface.

The soils in the Vistula River valley consist mostly of black earth and light clay and are covered by *Molinietum caeruleae* patches (Dubiel 2005). The abandonment of traditional land use for at least the past dozen years has favored the encroachment of *Phragmites* swamps and willow brushwood, leading to the fragmentation of meadows (Dubiel 1991, 1996). In the vicinity of meadows, numerous plant communities have formed, from the deciduous forests covering the slopes of the Vistula valley, through the xerothermic calcareous grasslands occurring on limestone and chalk hill slopes, to the ruderal communities appearing near buildings and along the edges of roads.

The studies were carried out simultaneously in three adjacent abandoned patches of *Molinietum caeruleae* with various species compositions and habitat conditions.

Patch I (50°01'48"N, 19°52'63"E), with an area of ca 1600 m², unmanaged for about 12 years (personal observation), is dominated by species creating delicate, erect or procumbent stems (i.e. *Lathyrus pratensis* L., *Lotus corniculatus* L.), small-tussock grass (i.e. *Briza media* L., *Holcus lanatus* L.) and short rosette forbs (i.e. *Lychnis flos-cuculi* L., *Succisa pratensis* Moench.). The elevated water table, the effect of melting snow and rain, falls rapidly during early spring. Small-meadow species with shallowly rooted underground organs intercept a very small amount of irradiance, contributing to the strong insolation of the ground surface and accelerating the evaporation of water from the soil area.

Patch II (50°01'52"N, 19°52'00"E), covering an area of 2000 m², has been abandoned for about 18 years (personal information). It is overgrown by tall macroforbs such as *Lythrum salicaria* L., *Lysimachia vulgaris*, and *Filipendula ulmaria* (L.) Maxim. The groundwater table is elevated during early and mid-spring. Moreover, the high, closely packed shoots partly shade the soil surface and prevent it from rapid desiccation.

Patch III (50°01'53"N, 19°52'75"E) measures ca 1500 m² and has been unmanaged for about 25 years (personal information). It is dominated by the shrub *Salix repens* ssp. *rosmarinifolia* L., as well as trees, i.e. *Betula pendula* L., *Populus tremula*, *S. cinerea* L., and *S. aurita* L. The elevation of the water level in local depressions ensures substantial hydration of the ground until late spring or even early summer. The wide leaf canopy of willows strongly limits the amount of solar radiation reaching the soil area.

3. MATERIAL AND METHODS

3.1. The study species

Deschampsia caespitosa (L.) Beauv. is a coarse, densely tufted perennial clonal grass forming large tussocks with well-defined, more or less circular bases, consisting of densely packed narrow leaves and intravaginal tillers. The tillers and adventitious thin roots arise from a stout branched rootstock. Small individuals have a compact structure due to the close-packed ramets distributed over a small area. After a few years, the in-

creasing distance between shoots weakens the integrity of genet because the spaces between ramets are filled with necrotic plant remains. Iterative growth by tillering contributes to a gradual increase in the dimensions of tussocks. The tussocks are long-lived (up to 30 years). The death of the central part of the tussock leaves two or more adjacent but separate tussocks. *Deschampsia caespitosa* is found in both lowland and mountain habitats throughout Europe and across northern Asia, extending into Central and Southwest Asia. It is also present in the Middle East, China, Japan, the Indian subcontinent, parts of North and Central Africa, Australia, New Zealand, Alaska, Canada, Greenland, the United States and South America. Individuals of *Deschampsia caespitosa* occur over a wide spectrum of habitats, from rough grasslands, through marshes, meadows, and moorlands to forests. The largest and most vigorous tussocks tend to occur in relatively nutrient-rich, seasonally flooded habitats such as marches or meadows, whereas plants inhabiting woodlands are generally smaller (Davy 1980).

3.2. Field trial, laboratory studies and statistical analyses

In 2009, in each patch, 15 small tussocks (720 cm tall, 15–30 cm in diameter, 15–35 cm in height) and 15 large tussocks (30–40 cm tall, 35–50 cm in diameter, 35–50 cm in height) were selected, dug up and transported to a greenhouse. Then, all above-ground parts of plants and necromass were manually removed, while the cores of the tussocks were divided into layers. The recruitment of seedlings and juvenile genets was observed once a week over the period 2009–11. The seedlings and saplings were removed and identified according to Csapodý (1968) and Muller (1978) with the support of a comparative collection. The nomenclature of taxa follows Mirek *et al.* (2002). The genets of rare and protected plants were replanted in the Botanical Garden of Jagiellonian University.

In order to distinguish the best colonizers of *Deschampsia caespitosa* tussocks, the number of seedlings of each species found in all tussocks deriving from particular study sites were counted in 2009, 2010 and 2011. The full census containing the number of

seedlings of particular species is given in Appendix I. Then, to examine the effect of patch character on species diversity and seedling number, the average abundance of species/seedlings found in tussocks inhabiting particular patches were counted for each year separately.

Subsequently, each species found in the seedling pool was assigned to a category, 'present' or 'absent' in standing vegetation. Furthermore, each taxa was assigned to one of five habitat groups after Matuszkiewicz (2012): ruderal, grassland, meadow, swamp, forest species. Next, each species was assigned a dissemination mode *via* wind, animals or water, the principal agents capable of long-distance transport of seeds, particularly important in fragmented communities (Cain *et al.* 2000). The classes of propagule dispersal taken from the Dispersal Diaspore Database (Tackenberg *et al.* 2011) were as follows: 'anemochores' (diaspores with wings or pappi, as well as the smallest unwinged seeds), 'epizoochores' (propagules with hooks, spines or hairs, which adhere to fur or feathers), 'endozoochores' (fruits with fleshy pulp, which are eaten by vertebrates, mainly birds), and 'hydrochores' (seeds with smooth, waterproof coats). The remaining modes of dissemination enabling long-distance dispersal, *e.g.*, bythisochory or chamaechory, were classified as 'other'. For taxa dispersing seeds by more than one mechanism (polychory), the most frequently cited dissemination type was used in the analysis. The full list, containing names of taxa with data on their presence in/absence from the plant composition of studied patches, vegetation type, and dispersal mode, is given in the Appendix II.

Then, the proportions of seedlings representing taxa:

- already present in/absent from existing vegetation of local patches,
- of different vegetation types,
- with different dispersal modes,
- appearing in all tussocks in a given patch, as well as in small and large tussocks in particular patches, were calculated.

The statistical analysis, done on untransformed data, was based on nonparametric tests. The Kruskal-Wallis test was applied to examine whether significant differences ex-

isted in the mean numbers of taxa and seedlings which appeared on tussocks taken from various patches. Chi-square statistics were applied to test whether significant differences existed among patches, as well as among small- and large-sized tussocks within each patch, in the contribution of seedlings representing species:

- already present in/absent from existing vegetation,
- of different vegetation types,
- with different dispersal modes.

4. RESULTS

In the seedling pool of *Deschampsia caespitosa* tussocks growing in all patches, *Selinum carvifolia* and *Serratula tinctoria* appeared most abundantly. Moreover, the tussocks found in Patch I were colonized by *Galium aparine*, *Geum urbanum*, *Lysimachia vulgaris* and *Filipendula ulmaria*. Tussocks occurring in Patch II were colonized by *Solidago canadensis* and *Lysimachia vulgaris*, while tussocks growing in Patch III were colonized by *Filipendula ulmaria* (Table 1). The average number of species noted in the tussocks decreased gradually over successive study sites, from 15.33 to 32.10 in Patch I, from 9.66 to 22.23 in Patch II, and from 5.72 to 17.76 in Patch III. A similar tendency characterized seedling abundance. In Patch I the average number of seedlings ranged from 30.73 to 91.53, in Patch II from 19.06 to 57.06, and in Patch III from 7.46 to 47.53 (Table 2).

In the tussocks occurring in Patch I, the contribution of species present in the plant composition was much lower than the frequency of taxa absent from the established vegetation. This trend was gradually reversed in Patch II and Patch III (Table 3). Moreover, the percentage of swamp and forest species increased, while the frequency of ruderal, grassland and meadow taxa decreased along the successional gradient. Simultaneously it should be added that, irrespective of patch character, the seedling pool was dominated by meadow species, whose contribution ranged from 63.1% to 72.1%. The spectrum of dispersal modes in particular patches was rather similar. The seedling pool was dominated by anemochorous species, which attained 31.1% to 41.8%. A lower contribu-

Table 1. The best colonizers of *Deschampsia caespitosa* (L.) Beauv tussocks growing in patch dominated by small meadow species (I), macroforbs (II) and shrubs and trees (III) in 2009–11

Year	Patch	Species
2009	I	<i>Selinum carvifolia</i> , <i>Serratula tinctoria</i> , <i>Filipendula ulmaria</i>
	II	<i>Selinum carvifolia</i> , <i>Serratula tinctoria</i> , <i>Solidago canadensis</i> , <i>Lysimachia vulgaris</i>
	III	<i>Selinum carvifolia</i> , <i>Serratula tinctoria</i>
2010	I	<i>Selinum carvifolia</i> , <i>Serratula tinctoria</i> , <i>Galium aparine</i> , <i>Geum urbanum</i>
	II	<i>Selinum carvifolia</i> , <i>Serratula tinctoria</i> , <i>Solidago canadensis</i> , <i>Lysimachia vulgaris</i>
	III	<i>Selinum carvifolia</i> , <i>Serratula tinctoria</i> , <i>Filipendula ulmaria</i>
2011	I	<i>Selinum carvifolia</i> , <i>Serratula tinctoria</i> , <i>Lysimachia vulgaris</i>
	II	<i>Serratula tinctoria</i> , <i>Lysimachia vulgaris</i>
	III	<i>Selinum carvifolia</i> , <i>Serratula tinctoria</i> , <i>Filipendula ulmaria</i>

Table 2. The mean number of species and seedlings found inside of *Deschampsia caespitosa* (L.) Beauv. tussocks in patches dominated by small meadow species (I), macroforbs (II) and shrubs and trees (III) in 2009–11. Asterisks indicate that the difference in number of species appearing in Patches I and II (A), I and III (B), II and III (C) are statistically significant at the level * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$

Year	Patch	The mean number of species (SD)	Statistical significance (H Kruskal-Wallis test)	The mean number of seedlings (SD)	Statistical significance (H Kruskal-Wallis test)
2009	I	32.10 (6.42)	A***, B***, C*	91.53 (40.62)	A*, B**, C ^{ns}
	II	22.23 (5.81)		57.06 (24.88)	
	III	17.76 (3.32)		47.53 (18.84)	
2010	I	26.30 (6.06)	A***, B***, C**	65.66 (25.23)	A***, B***, C ^{ns}
	II	16.73 (3.03)		40.76 (15.32)	
	III	13.23 (3.20)		32.40 (8.75)	
2011	I	15.13 (3.75)	A***, B***, C**	30.73 (9.74)	A***, B***, C**
	II	9.66 (2.92)		19.06 (8.73)	
	III	5.72 (2.63)		7.46 (5.77)	

tion was recorded for epizoochorous (21.7 to 33.5%), endozoochorous (12.3 to 19.2%), and hydrochorous species (10.9 to 18.0%). The lowest frequency (2.2 to 10.5%) characterized taxa using other dispersal modes.

The frequency of seedlings representing taxa residing in the plant canopy in large and small tussocks did not differ (Table 4). Also, the contribution of seedlings representing taxa of different vegetation types in large and small tussocks was quite similar. Contrastingly, the percentage of seedlings representing taxa with various dispersal modes differed significantly between large and small tussocks. The seedling pool of small tussocks was dominated by anemochorous and hydrochorous taxa; the frequency of endo- and epizoochorous taxa was much lower; the percentage of species characterized by other modes of diaspore dispersal attained the lowest rates. In large tussocks, anemochorous and epizoochorous species prevailed; the

share of endozoochorous and hydrochorous taxa was lower; the contribution of species characterized by other modes of dissemination was very scarce.

5. DISCUSSION

5.1. The best colonizers of tussocks in particular patches and the influence of patch character on species number and seedling abundance

The studies showed that, regardless of patch character and growing season, *Selinum carvifolia* and *Serratula tinctoria*, regarded as characteristic for the *Molinion caeruleae* alliance and *Molinietalia ordo* (respectively), were the most abundant species in the seedling pool. The observed substantial recruitment of the above-mentioned species corresponds with observations of seedling recruitment in gaps left after mowing in wet meadows

(Špačková *et al.* 1998, Kotorová and Lepš 1999, Stammel *et al.* 2006). Furthermore, the obtained results documented the substantial recruitment of the species *Lysimachia vulgaris* and *Filipendula ulmaria*, considered characteristic for the *Filipendulion* alliance. The considerable recruitment of *Lysimachia vulgaris* corresponds with observations of the colonization of tussocks of *Carex caespitosa* occurring in the overgrowing of wet meadows (Borkowska 2004). However, the same author also found sporadic recruitment of *Filipendula ulmaria* seedlings. At the same time, it should be pointed out that tussocks of *Deschampsia caespitosa* are abundantly colonized by seedlings of taxa not considered characteristic for the *Molinio-Arrhenatheretea* class, such as *Galium aparine*, *Geum urbanum* and *Solidago canadensis*. This phenomenon may be caused by the substantial seed production, effective and long-distant dispersal modes, and considerable germination ability of the above-mentioned taxa, as previously observed by Taylor (1997, 1999), as well as Werner *et al.* (1980).

The observed decrease in species diversity and seedling abundance along the successional gradient may be connected with a gradually increasing period of water stagnation. The prolonged immersion of *Deschampsia caespitosa* tussocks may accelerate the development, longevity, germination and infectivity of fungal pathogens, a major cause of mortality in buried diaspores. According to Blaney and Kotanen (2001), as well as Schafer and Kotanen (2003), an increase in soil moisture in wet habitats accelerates fungal attack and may contribute to reductions in the populations of many species. On the other hand, Bekker *et al.* (1998) claimed that flooding of long duration increases seed survivability in wet meadows.

5.2. The impact of patch character on emergence of seedlings representing taxa present in/absent from standing vegetation, species of different vegetation types and species with various dispersal modes

The findings that the share of taxa resident in existing vegetation rises along the successional gradient are in accordance with investigations of gap colonization in *Molinietum*

Table 3. The contribution (%) of seedlings representing taxa present in and absent from existing vegetation, species of different vegetation types and taxa with various dispersal modes found inside of all tussocks of *Deschampsia caespitosa* (L.) Beauv. in patches dominated by small meadow species (I), macroforbs (II) and shrubs and trees (III) in 2009–11. Asterisks indicate significant differences among patches. * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$ (χ test).

Year	Patch	Percentage of seedlings representing taxa:			Percentage of seedlings representing taxa:					Percentage of seedlings representing taxa:					χ^2 test $df=8$	
		present in existing vegetation	absent from existing vegetation	χ^2 test $df=2$	ruderal	grass-land	meadow	swamp	forest	χ^2 test $df=8$	anemo-chorous	endo-zooch-orous	epizo-chor-ous	hydro-zooch-orous		other
2009	I	35.5	64.5		22.8	6.3	68.9	2.1	0.2		37.9	16.7	31.6	10.9	2.9	
	II	66.4	33.6	21.16***	21.6	5.1	67.1	3.3	2.9	17.80*	31.1	19.2	27.2	13.5	9.0	9.17 ^{ns}
	III	59.5	40.5		15.5	4.9	63.1	11.5	5.0		41.8	12.3	21.7	15.8	8.4	
2010	I	36.0	64.0		20.5	6.7	68.7	1.2	2.9		38.7	17.1	26.2	13.4	4.6	
	II	58.4	41.6	14.62***	16.8	6.7	66.6	5.3	4.6	9.84 ^{ns}	31.6	18.7	29.9	14.3	6.5	5.84 ^{ns}
	III	60.3	39.7		16.9	2.8	64.6	8.8	6.9		35.8	12.9	22.8	18.0	10.5	
2011	I	34.9	61.5		19.5	5.9	72.1	1.4	1.1		36.3	19.1	24.4	15.7	4.5	
	II	61.2	38.8	15.83***	14.3	3.3	70.4	4.7	7.3	15.94*	33.2	14.7	33.5	11.7	6.9	5.64 ^{ns}
	III	56.7	43.3		12.7	2.2	66.3	7.7	11.1		38.4	14.8	29.9	14.7	2.2	

Table 4. The contribution (%) of seedlings representing taxa present in and absent from existing vegetation, species of different vegetation types and taxa with various dispersal modes found inside of small and large tussocks of *Deschampsia caespitosa* (L.) Beauv. in patches dominated by small meadow species (I), macroforbs (II) and shrubs and trees (III) in 2009–11. Asterisks indicate significant differences among tussocks of different sizes. * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$ (χ test).

Patch	Tussock size	Percent- age of seedlings represent- ing taxa:		Percentage of seedlings repre- senting taxa:						Percentage of seedlings representing taxa:						
		present in existing vegetation	absent from existing vegetation	χ^2 test $df=2$	ruderal	grassland	meadow	swamp	forest	χ^2 test $df=8$	anemochorous	endozoochorous	epizoochorous	hydrozoochorous	other	χ^2 test $df=8$
I	small	34.6	65.4	0.02 ^{ns}	19.1	5.6	65.4	8.5	1.4	4.63 ^{ns}	31.3	18.5	25.1	22.7	2.4	14.88**
	large	35.6	64.4		28.9	5.8	57.7	4.3	3.3		41.6	16.6	30.4	7.0	4.4	
II	small	56.5	43.5	2.15 ^{ns}	12.7	4.7	73.7	3.7	5.2	1.99 ^{ns}	24.8	20.8	25.1	21.6	7.7	8.66 ^{ns}
	large	66.6	33.4		19.3	5.7	68.4	2.7	3.9		35.6	16.5	31.0	8.6	8.3	
III	small	60.6	39.4	0.06 ^{ns}	14.0	2.7	70.5	9.0	3.8	1.09 ^{ns}	32.8	13.6	16.4	27.9	9.3	12.44*
	large	58.9	41.1		13.5	4.1	66.5	9.5	6.4		43.0	12.2	26.5	9.9	8.4	

caeruleae meadows (Kostrakiewicz 2011). This phenomenon may be due to the production of non-persistent diaspores by early successional species, which, as a result, disappear from the seed bank as they withdraw from the vegetation, while propagules of taxa established later in the succession are gradually incorporated in the soil. This phenomenon has been observed over a wide range of habitats, from alpine meadows (Ma *et al.* 2011) through dune slacks (Bossyut and Hermy 2004) to hay fields (Bekker *et al.* 2000). Furthermore, the successive increase in similarity, observed in these investigations, between species composition in the seedling pool and standing vegetation may be due to a reduction in seed immigration from neighboring sites. The influx of propagules could be hampered by the growing density and increasing height of plants bordering *Deschampsia caespitosa* individuals, as well as the growing thickness of the litter layer, acting as an effective trap for seeds. A gradual decrease in the share of new colonizers in seed rain along the successional gradient in wet meadows has already been noted by Jensen (1998).

The phenomenon discussed in the previous paragraph is linked with the contribution of seedlings representing species of different vegetation types. The increase in the percentage of swamp and forest species, along with the simultaneous decrease in the frequency of ruderal, grassland and meadow taxa in consecutive patches, is in agreement with observations conducted in alpine grasslands by Vandvik (2004), who documented a decrease in the recruitment of ruderal and alpine taxa seedlings along the successional gradient. The obtained results, showing the greatest share of meadow species in *Deschampsia caespitosa* tussocks growing in different site conditions, are consistent with investigations of seedling recruitment in *Carex caespitosa* tussocks. On the basis of laboratory investigations, Falińska (2003) found that, during succession, the tussocks of *Carex caespitosa* become reservoirs of seeds and niche spaces for species of various vegetation types; however, the most frequent, in terms of the floristic composition of the seedling pool, were meadow species. Furthermore, Falińska (2003) pointed out that sedge mounds are

spatial reservoirs for meadow species even at the time of advanced succession and play a significant role in the process of long-term species turnover. Also, the field observations of Brzosko (1999) documented that tussocks of *Carex caespitosa* may support the development of many meadow species in the course of succession.

Although the frequency of wind-dispersed species in the plant canopy of meadows is rather slight (Willson *et al.* 1990) the current studies showed the domination of anemochorous taxa in the seedling pool of tussocks growing in all patches. This phenomenon may be caused by the very efficient transport of small wind-dispersed seeds, ranging from a few meters to many kilometers (Šerá and Šerý 2004, Tackenberg *et al.* 2003, Soons 2006). The substantial share of epi- and endozoochorous taxa may be an effect of animal activity in all study patches (personal observation). Moreover, temporal floodings occurring from autumn to spring as a result of intense precipitation as well as melting snow may contribute to the efficient transport of water-dispersed diaspores and the presence of hydrochorous species in the seedling pool.

5.3. The impact of the size of tussocks on the emergence of seedlings representing taxa present in/absent from standing vegetation, species of different vegetation types and species with various dispersal modes

The similar percentage of seedlings representing taxa present and not occurring in standing vegetation in different-sized tussocks observed here supports observations of the colonization of gaps in various areas in *Molinietum caeruleae* meadows (Kostrakiewicz 2011). The above-mentioned investigations documented that, in openings in the plant canopy ranging from 0.01 to 0.16 m², the frequency of seedlings representing taxa resident in and absent from standing vegetation is similar. The lack of difference in the contribution of seedlings representing species of various vegetation types in small and large *Deschampsia caespitosa* individuals suggests that tussocks of different sizes may serve as safe sites for the recruitment of ruderal, grassland, meadow, swamp and forest taxa.

The observed domination of anemochorous species in small and large *Deschampsia caespitosa* individuals, irrespective of patch character, corresponds with studies of the colonization of openings in the plant canopy and litter in various communities (Dzwonko and Gawroński 2002, Degen *et al.* 2005 von Blanckenhagen and Poschlod 2005). The substantial share of hydrochorous taxa on small genets of *Deschampsia caespitosa* may be caused by the total or near-total immersion of tussocks during the seasonal floodings in spring and the subsequent decrease in the groundwater table. In effect, the floating seeds may be captured and deposited on emerging clumps. The weaker recruitment of hydrochorous taxa on large tussocks may be caused by their becoming waterlogged only in their basal part, resulting in a scanty accumulation of seeds. The similar share of hydrochorous species in all patches seems to be consistent with the investigations of Hölzel and Otte (2001) and Bissels *et al.* (2004), who documented a quite similar influx of diaspores in the soil seed bank as an effect of both short- and long-term inundation events in alluvial meadows. The considerable percentage of epizoochorous taxa on large tussocks of *Deschampsia caespitosa* and their lower share on small tussocks may be connected with the type and dimensions of the animals dispersing propagules. Birds and smooth-furred small mammals such as rodents, transporting a small number of seeds (Sorensen 1986, Cummings *et al.* 2008, Kulbaba *et al.* 2009), may leave diaspores on both large and small tussocks. Diaspores adhering to the legs of medium and large mammals may be rejected by both large and small tussocks, while propagules attached to the coats of animals are released on large tussocks in particular (personal observation). Simultaneously, it should be pointed out that significantly lower numbers of propagules are retained on the legs and feet of animals than in the fur covering their torsoes, necks and tails (Agnew and Flux 1970, Fischer *et al.* 1993, Kiviniemi 1996). The small and large tussocks of *Deschampsia caespitosa* may be reservoirs and suitable microsites for the germination of endozoochorous diaspores. The similar slight contribution of endozoochorous species in the seedling pool developed on

tussocks derived from all patches observed here is not consistent with the investigations of other authors, such as Cosyns *et al.* (2005), showing the selective use of habitats by wild mammals and livestock animals. These authors claimed that defecation frequencies and depositions of seeds are greater in habitats dominated by small species than in habitats overgrown by tall herbs, shrubs and woodland species.

6. CONCLUSIONS

The gradual decrease in number of species and seedling abundance along the successional gradient suggests that the tussocks of *Deschampsia caespitosa* growing in Patch I are the best reservoirs of diaspores and the best safe sites for recruitment of seedlings representing species of various vegetation types. In spite of the successive increase in the share of taxa resident in standing vegetation, especially swamp and woody species in the seedling pool of Patches II and III, the tussocks of *Deschampsia caespitosa* are reservoirs of meadow species even in advanced successional stages. Moreover, the occurrence of different-sized individuals of *Deschampsia caespitosa* ensures the germination of seeds characterized by diverse modes of dissemination.

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APPENDIX I

The total number of seedlings of species recorded in small and large tussocks in patch dominated by small meadow species (Patch I), macroforbs (Patch II) and shrubs and trees (Patch III) in the years: 2009 (09), 2010 (10) and 2011 (11).

Species	Patch I						Patch II						Patch III					
	Small tussocks			Large tussocks			Small tussocks			Large tussocks			Small tussocks			Large tussocks		
	09	10	11	09	10	11	09	10	11	09	10	11	09	10	11	09	10	11
<i>Achillea millefolium</i>	2	2		6	5		0	0	3	4	2	9	6	7	1	7	5	2
<i>Agrimonia eupatoria</i>							7	7	1	10	9	3						
<i>Alopecurus pratensis</i>							1	8	0	7	6	0	4	2	0	33	21	10
<i>Arctium tomentosum</i>							6			14								
<i>Artemisia vulgaris</i>							6	13	4	23	10	11						
<i>Briza media</i>	48	36	15	82	27	22	13	19	5	25	32	15	11	8	4	6	24	4
<i>Calamagrostis epigejos</i>							4			16			4	10		7	11	
<i>Caltha palustris</i>							23	38	14	10	11	7						
<i>Capsella bursa-pastoris</i>		1																
<i>Cardamine pratensis</i>	6	6		12	4		17	14	9	38	21	15						
<i>Carex flava</i>	37	27	28	88	29	25	28	21	8	17	13	24	30	9	1	17	16	9
<i>Carpinus betulus</i>							1	15	22	13	8	2						
<i>Centaurea jacea</i>	4			32			9	4	1	19	18	19	13		5	54		15
<i>Cerastium holosteoides</i>														12			27	
<i>Cirsium arvense</i>	16	18	18	54	45	9	33	3	1	32	19	30	22	25	2	26	24	7
<i>Cirsium rivulare</i>	26	15		44	41		10	8	5	12	10	8						
<i>Cirsium vulgare</i>	16	16	7	49	34	19							6	3	1	18	16	1
<i>Conyza canadensis</i>	10	10		57	46													
<i>Cruciata glabra</i>	6	6	2	33	30	10	4	2	0	16	10	1	10	7	7	9	11	7
<i>Daucus carota</i>	13	11	9	40	42	13	3	1	3	13	27	15	9	8	1	24	19	4
<i>Epilobium palustre</i>	43	32	5	17	17	13							31	40	0	8	2	1
<i>Erigeron annuus</i>	12	9	7	41	29	13												
<i>Eriophorum latifolium</i>				1														
<i>Filipendula ulmaria</i>	39	39	19	27	21	10	31	21	5	31	4	2	31	26	12	27	26	3
<i>Filipendula vulgaris</i>	47	20	5	90	24	20	11	5	3	16	17	12						
<i>Galium aparine</i>	23	21	0	57	63	40												
<i>Galium boreale</i>	19	15	16	54	19	6	17	10		54	26		12	13	1	67	35	1
<i>Galium uliginosum</i>	3	3	3	22	19	4	9			26			10	4	1	20	24	11
<i>Geum rivale</i>	1	1		21	21		18	14	4	27	17	9						
<i>Geum urbanum</i>	11	10	5	43	64	23												
<i>Hypericum perforatum</i>	16			31														
<i>Inula salicina</i>	7	7	4	32	20	15	23	12	2	36	26	24						
<i>Iris pseudacorus</i>	30	34	21	8	8	5												
<i>Juncus effusus</i>	9	9	4	9	6	4	15	11	2	16	5	1						
<i>Lathyrus pratensis</i>	6	7	6	49	14	8	7	10	0	1	4	0	3	2	0	29	17	3
<i>Leucanthemum vulgare</i>	12	13	12	23	20	11	20	25	4	15	11	7	9	8	3	15	9	3
<i>Lotus corniculatus</i>	17	17	17	30	22	13	9	18	7	9	21	4	7	2		14	9	
<i>Lychnis flos-cuculi</i>	4	4	4	41	42	11	29	12	10	32	22	29	6	2		15	8	
<i>Lysimachia vulgaris</i>	43	37	25	24	22	17	50	31	22	33	22	17	27	17	7	13	19	0

Species	Patch I									Patch II									Patch III								
	Small tussocks			Large tussocks			Small tussocks			Small tussocks			Large tussocks			Small tussocks			Large tussocks			Small tussocks			Large tussocks		
	09	10	11	09	10	11	09	10	11	09	10	11	09	10	11	09	10	11	09	10	11	09	10	11	09	10	11
<i>Myosotis palustris</i>	28	22	22	17	13	6	19	20					13	15		17	14	3	14	3	1						
<i>Pastinaca sativa</i>	10	6	4	21	16	5																					
<i>Peucedanum palustre</i>	6			8																							
<i>Phalaris arundinacea</i>	7	6	1	14	14	7	5	5					16	8		20	20	3	37	8	3						
<i>Phragmites australis</i>	13	17	7	26	20	14	9	10	18	25	5	6	10	8	4	22	11	5									
<i>Plantago lanceolata</i>							2	8	3	10	23	0															
<i>Plantago media</i>	7	6	5	11	12	4																					
<i>Poa annua</i>	5	7	5	7	13	4																					
<i>Populus tremula</i>	6	3	1	15	14	16	10	14		24	6		12	5	0	47	25	4									
<i>Potentilla erecta</i>	7	7	7	12	25	16	16	12		27	32		9	10	1	47	17	4									
<i>Prunella vulgaris</i>	18	15	14	22	22	9	5	6	3	3	10	0															
<i>Ranunculus acris</i>	40	25	17	64	48	10	34	16	8	25	22	15	28	12	1	20	20	2									
<i>Rumex acetosa</i>	4			12			4	2	2	12	23	15	9	8	1	9	9	3									
<i>Rumex acetosella</i>	9			13			28			52																	
<i>Selinum carvifolia</i>	41	62	8	123	95	41	29	24	3	84	59	20	30	6	1	79	39	5									
<i>Senecio vulgaris</i>	12			15																							
<i>Serratula tinctoria</i>	34	44	2	115	88	60	20	31	2	83	79	42	37	32	9	81	51	21									
<i>Solidago canadensis</i>	26	21	11	96	16	10	23	16	0	67	60	18	19	25	6	48	39	13									
<i>Sonchus arvensis</i>	11	11	8	70	30	15	9	4	2	21	20	16															
<i>Tragopogon pratensis</i>	23	13	10	24	22	5									8		2	28		2							
<i>Trifolium pratense</i>	9	9	6	16	16	5										6		3									
<i>Tussilago farfara</i>	10	9	8	19	19	15										7	5	2	21	7	1						
<i>Typha latifolia</i>	10	10	8	17	13	8										16	6		59	12							
<i>Urtica dioica</i>	7	6	7	13	7	10	16			16																	
<i>Valeriana officinalis</i>	4	4	2	7	5	2	16			20						20	26		12	17							

APPENDIX II

The list of species recorded in seedling pool (tussocks) in relation to presence in standing vegetation (field): P – species present; species representing the main vegetation types: R – ruderal species, G – calcareous grassland species, M – meadow species, S – swamp species, F – forest and shrub species; dispersal mode (A – anemochory, EP – epizoochory, EN – endozoochory, H – hydrochory, O – other).

Species	Occurrence of species						Vegetation type	Dispersal mode
	Patch I		Patch II		Patch III			
	Tussock	Field	Tussock	Field	Tussock	Field		
<i>Achillea millefolium</i>	P		P	P	P	P	M	EN
<i>Agrimonia eupatoria</i>	P		P		P		G	EP
<i>Alopecurus pratensis</i>	P		P		P		M	EP
<i>Arctium tomentosum</i>	P		P		P		R	EP
<i>Artemisia vulgaris</i>	P		P		P		R	EP
<i>Briza media</i>	P	P	P	P	P		M	EP
<i>Calamagrostis epigejos</i>	P		P		P	P	R	O
<i>Caltha palustris</i>	P		P		P		M	H
<i>Capsella bursa-pastoris</i>	P		P		P		R	EN
<i>Cardamine pratensis</i>	P	P	P		P		M	EP
<i>Carex flava</i>	P	P	P		P	P	M	EP
<i>Carpinus betulus</i>	P		P		P		F	A
<i>Centaurea jacea</i>	P		P	P	P	P	M	EP
<i>Cerastium holosteoides</i>	P		P		P		M	EN
<i>Cirsium arvense</i>	P		P	P	P	P	R	A
<i>Cirsium rivulare</i>	P	P	P		P		M	EP
<i>Cirsium vulgare</i>	P		P		P		R	A
<i>Conyza canadensis</i>	P		P		P		R	A
<i>Cruciata glabra</i>	P	P	P		P		F	EN
<i>Daucus carota</i>	P		P	P	P	P	M	EP
<i>Epilobium palustre</i>	P		P		P	P	M	H
<i>Erigeron annuus</i>	P		P		P		R	A
<i>Eriophorum latifolium</i>	P		P		P		S	A
<i>Filipendula ulmaria</i>	P		P	P	P		M	H
<i>Filipendula vulgaris</i>	P		P	P	P		G	EP
<i>Galium aparine</i>	P		P		P		R	EP
<i>Galium boreale</i>	P		P	P	P	P	M	EP
<i>Galium uliginosum</i>	P	P	P	P	P		M	EP
<i>Geum rivale</i>	P	P	P		P		M	EP
<i>Geum urbanum</i>	P		P		P		R	EP
<i>Hypericum perforatum</i>	P		P		P		R	EP
<i>Inula salicina</i>	P		P	P	P		M	A
<i>Iris pseudacorus</i>	P		P		P		S	H
<i>Juncus effusus</i>	P		P	P	P	P	M	EN
<i>Lathyrus pratensis</i>	P	P	P		P		M	EN
<i>Leucanthemum</i>	P	P	P	P	P		M	EN
<i>Lotus corniculatus</i>	P	P	P	P	P		M	EN
<i>Lychnis flos-cuculi</i>	P	P	P		P		M	O

Species	Occurrence of species						Vegetation type	Dispersal mode
	Patch I		Patch II		Patch III			
	Tussock	Field	Tussock	Field	Tussock	Field		
<i>Lysimachia vulgaris</i>	P		P	P	P		M	H
<i>Myosotis palustris</i>	P	P	P		P		M	H
<i>Pastinaca sativa</i>	P		P		P		M	A
<i>Peucedanum palustre</i>	P	P	P		P		S	A
<i>Phalaris arundinacea</i>	P		P	P	P	P	S	H
<i>Phragmites australis</i>	P		P		P	P	S	A
<i>Plantago lanceolata</i>	P		P		P		M	EN
<i>Plantago media</i>	P		P		P		G	EN
<i>Poa annua</i>	P		P		P		M	EN
<i>Populus tremula</i>	P		P		P	P	F	A
<i>Potentilla erecta</i>	P	P	P		P		G	O
<i>Prunella vulgaris</i>	P		P		P		M	EN
<i>Ranunculus acris</i>	P	P	P	P	P	P	M	EN
<i>Rumex acetosa</i>	P	P	P		P		M	EN
<i>Rumex acetosella</i>	P	P	P	P	P		R	EN
<i>Selinum carvifolia</i>	P	P	P	P	P	P	M	A
<i>Senecio vulgaris</i>	P		P		P		R	A
<i>Serratula tinctoria</i>	P		P	P	P	P	M	A
<i>Solidago canadensis</i>	P		P	P	P	P	R	A
<i>Sonchus arvensis</i>	P		P		P		R	A
<i>Tragopogon pratensis</i>	P		P		P		M	A
<i>Trifolium pratense</i>	P		P		P		M	EN
<i>Tussilago farfara</i>	P		P		P		R	A
<i>Typha latifolia</i>	P		P		P		S	A
<i>Urtica dioica</i>	P	P	P	P	P	P	R	EN
<i>Valeriana officinalis</i>	P		P	P	P	P	M	O