DO SMALL-SCALE GAPS IN CALCAREOUS GRASSLAND SWARDS FACILITATE SEEDLING ESTABLISHMENT?

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ABSTRACT

In this study we analyzed gaps originated in different seasons of the year vs. places of close vegetation in calcareous grasslands in terms of their suitability for seedling germination and establishment. Gaps, irrespective of the time of their origin, significantly promoted seedling emergence as compared with close swards. However, the season of gap creation influenced the rate of seedling germination/emergence. Seedlings occurred more frequently in autumn and spring gaps than in the summer ones. The highest mean number of seedlings and of their species were noted in autumn openings. However, the subsequent survival of seedlings in autumn gaps was low. On the contrary, in spring gaps juveniles occurred with the significantly highest mean number, frequency and species richness. The above results pointed to the positive, although very limited role of artificially created gaps as places favouring seedlings establishment.

KEY WORDS: gap colonization, phenology, generative reproduction, calcareous grasslands, southern Poland.

INTRODUCTION

The gap concept belongs to one of the most important issues in plant ecology, particularly in seeking to explain the species coexistence, community structure and dynamics (van der Maarel 1988) or to elucidate plant regeneration processes (Grubb 1977; Gibson et al. 1987; Mahdi and Law 1987; Coffin and Lauenroth 1988; Peart 1989; Mitchley 1990; Tilman 1994, 1997; Bullock et al. 1994; Edwards and Crawley 1999; Bullock 2000 and literature cited here; Davies 2002).

Openings in the calcareous grassland turf appear as the result of the natural death of plant individuals or their parts, and different kinds of disturbances (soil erosion, activity of man and animals etc., Bullock 2000 and literature cited here). Many research show the positive role of gaps as "biological space" accessible for germination (Rush, van der Maarel 1992), "safe places for germination" (Harper 1977), "regeneration niche" (Grubb 1977), or "space free from competition" (Bullock 2000 and literature cited here). Some studies have revealed that gaps are more suitable places for both seedling emergence and seedling establishment than compact vegetation (Silvertown 1980; Goldberg and Gross 1988; Winn 1985). It has been shown that the seedling mortality of most annuals and some biennials, which frequently determine the floristic richness of calcareous grasslands, is much higher under a close grassland canopy than in open places (Schenkeveld, Verkaar and Brand 1983; Verkaar and Schenkeveld 1984). Many scientists are of the opinion that gaps creation reduces species dominance within the disturbed patch, which facilitates its colonization by "tiny" species and contributes to an increase in species density (Hillier 1990). Therefore, gap creation and gradual vegetation in-fill is often considered as an effective tool in maintaining the species diversity of grasslands (Grubb 1977; Hillier 1990; Mitchley 1994).

However, the results of other research showed that the role of open spaces as the "safest" place for seedling establishment was not unequivocal (e.g. Ryser 1990, 1993; Bullock 2000) and in some cases there were no differences between the gaps and compact vegetation in reference to seedling establishment (Gross 1984; Garcia-Fayos and Verdu 1998). Additional features of biological space such as: soil texture, nutrient and physical space accessibility, light conditions (Rush, van der Maarel 1992; Silvertown 1980; Silvertovn and Dickie 1980), size and shape of gap

(Goldberg and Werner 1983; Morgan 1997; Bullock et al. 1995; Bullock 2000) are important for success (or lack of it) in gap colonization by particular species.

An interesting, though up to now a little known issue is how does the season of gap appearance in the calcareous grassland swards influence the rate of seedling recruitment and seedling establishment. As far as we know this problem has not yet been investigated by Polish researchers; however the phenology of generative reproduction was investigated in plants of calcareous grasslands communities in the Kraków Jura (Medwecka-Kornaś 1950). In West European literature the similar, comprehensive (community-based) approach to this problem was presented by Rusch (1988), Hillier (1990) and Davies (2002). Rusch (1988) and Hillier (1990) indicated the season of gap appearance during the vegetation period and its durability was an important factor influencing seedling germination. Davies (2002) found that autumn implantation of seedlings into gaps led to their higher survivorship than the spring one.

In view of the great diversity of opinions on the role of open spaces as "places safe for seedling establishment", we decided to aim our study at answering the following questions:

• how does the time of gap appearance during the vegetation period influence: (1) seedling germination/emergence, (2) seedling establishment?

• are there differences between gaps/gap type and places with closed vegetation in calcareous grassland swards in the above mentioned processes?

METHODS

Study area

The research was carried out in the Wąwóz Bolechowicki Nature Reserve [19°46'10''E, 50°46'59''N], southern Poland (Fig. 1A). It is a typical Jurrasic valley with many outcrops built by Upper Jurassic limestone. The prevailing soil type is rendzina. The steep slopes of the valley are covered with calcareous grasslands which belong to the Festucetum pallentis and Origano-Brachypodietum vincetoxicetosum communities (Matuszkiewicz 2001). In 2001, the 30×30 m study plot was established within the latter community. The plot was situated on the south-western slope of the valley, inclined 30-45°. The number of vascular plant species varied from 15 to 20/1 m^2 and 59 to 70/100 m^2. The studied calcareous grassland has not been managed during the last 10-15 years. It is dominated by *Brachypodium pinnatum*, *Origanum vulgare*, *Anthericum ramosum*, *Vincetoxicum hirundinaria* and *Poa angustifolia*.

Experimental design

The research was carried out from September 2001 to June 2003. During this period, 120 quadrats each of 625 cm^2 (20×31.2 cm), were randomly located within the study plot (Fig. 1B). This size of gaps was considered as optimal for seedling establishment on the basis of results of our preliminary studies (Bąba 1997-1999 unpubl.) and similar experiments (Ryser 1990, 1993; Hillier 1990; Davies 2002). Gaps of similar size appeared naturally in the grassland sward as the result of grazing (Hillier 1990, Davies 2002).

The 30 quadrats which were placed in closed vegetation were treated as a control (C). In the remaining 90 quadrats all the above-ground live and dead parts of plants, roots and rhizomes were removed from the upper 5 cm soil layer. The gaps created in this way corresponded to canopy, stem and root gaps sensu Bullock (2000). When the vegetation had been removed the soil's surface was levelled to ensure the uniform microhabitat conditions. The quadrats were separated from each other by 1.5 m wide belts of intact vegetation to ensure sample independency. Around each gap all the vegetation was clipped in the 10 cm wide zone to eliminate the border effect of the surrounding vegetation.

To show the influence of the time of gap emergence on its accessibility for seedling colonization, the experiment was made in 3 series, started in the September 2001 ("autumn" gaps – AU), in March/April 2002 ("spring" gaps – SP) and at the end of June 2002 ("summer gaps" – SU). Each series consisted of 30 quadrats (Fig. 1C).

During the vegetation period, in each quadrat, the number of seedlings and juvenile shoots belonging to particular species were noted. These observations were made six times in each type of gap: at the end of March, in May, June, July, September and October and eleven times in the controls (Fig. 1C). After this period of time, 94% of the created gaps were completely overgrown (i.e. the mean plant cover was similar to that of closed vegetation i.e. 75.4%).

Because of the strong tourist traffic in the reserve it was impossible to mark permanently seedlings emerging in the quadrats. Therefore, in order to distinguish the seedlings, which emerged during a given time period (thus belong to consecutive cohorts), x-y position of each plant individual was noted with the use of a wooden scaled frame, matching gaps/control quadrats. To correct the data gathered by direct field recording, the vertical projection photograph of each quadrate was taken. The photographs were taken with the use of a photographic tripod fixed to permanent points which were marked with plastic tubes buried in the ground (Faliński 2002).

The main criterion of distinction between seedlings and juweniles was the presence or absence of cotyledones. The recognition of grass and sedge seedlings in the field was often impossible without their damage, thus these groups were not taken into consideration. All the seedlings which died at the stage when they couldn't be assigned to species or even genera were included into a separate group ("unspecified").

Data analysis

To obtain the balanced experimental design, of the 330 control quadrates 180 (30 quadrats × six census times) were randomly choosen to further analyses. Together with gaps, 720 floristic records were analysed.

In order to compare the mean frequency of seedling and juveniles in: (1) gap vs. closed sward and (2) SP, SU, AU vs. closed sward (C) a non-parametric U-Whitney-Mann tests with sequential Bonferroni correction for k comparisons were used (Sokal and Rohlf 1995), because the data did not meet the normality assumption, required for ANOVA (Sokal and Rohlf 1995). In the case of the first analysis, the values of frequency in gaps were calculated for 30 randomly choosen quadrats in all gap types in six census times to obtain the equal sample sizes for gap and control.

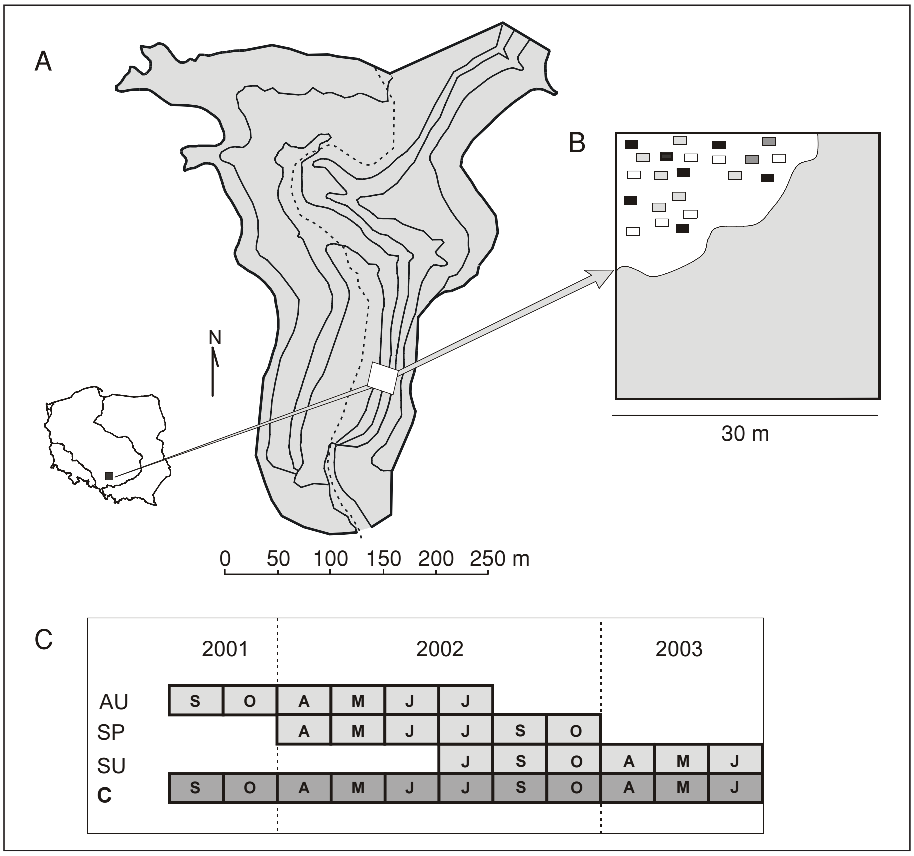

Fig. 1. A – the study area "Wąwóz Bolechowicki" nature reserve with permanent study plot; B – distribution of sample quadrats in study plot (the quadrats represent different types of gaps and closed vegetation were marked with different colours). Only part of study plot are shown; C – experimental design. Letters denote AU – autumn gaps, SP – spring gaps, SU – summer gaps; C – control (closed vegetation).

To test the effects of GAP TYPE (SP, SU, AU, C), TIME (consecutive censuses) and GAP TYPE × TIME interactions on seedling and juveniles (number of individuals and species richness) a Two-way ANCOVA with replication were used (Sokal and Rohlf 1995). Prior to the analysis data were log + 10 – transformed (data on number of seedling and juvenile species/individuals) to meet the normality assumption. A Schaeffe a-posteriori test was used to examine the effects of particular gap types (C, AU, SU and SP). The distribution of quadrats on the slope of the valley, which in spite of their random position had still significant effect, was treated as a covariable. However, there were not significant differences between the months of consecutive years (One-way ANOVA, F = 0.35, p<0.4), thus data from all years were analyzed together.

RESULTS

Altogether 11541 shoots of seedlings and juvenile individuals were noted in the 120 quadrates of 625 cm^2 in the investigated plot. They belonged to 97 species of vascular plants.

Seedlings

Seedlings were found in 486 (69.5%) out of 720 records. They occurred with a higher mean frequency in gaps (0.72±0.23 SD) than in closed turf (0.44±0.18; U-Withney-Man test, U = 2.780, p<0.005). Seedlings were more frequently noted in the AU (0.91±0.34) and SP gaps (0.71±0.38) than in the control ones (U = 3.000, p<0,0085 and U = 26.500, p<0.01020, respectively), but there were not significant differences between the AU and SP gaps (SP vs. AU: U =12.500, p<0.2843). The lowest mean frequency of seedlings was noted in the SU gaps (0.41±0.12). This value was significantly lower than both AU (U = 7.000, p<0.028) and SP (U = 7.000 p<0.048) gaps, but it did not differ significantly from the control (U = 33.500, p<0.7354).

Altogether 6024 seedlings, belonging to 82 vascular plant species were noted. The totals for particular gap types were: 66 in autumn gaps, 45 in spring gaps and 35 in summer gaps, while in the closed vegetation – 49. The mean number of seedlings and the mean number of species they represented, were significantly higher in all types of gaps (AU, SU and SP) than in closed vegetation. In autumn gaps these values were significantly higher than in summer and spring gaps, but between the last two (SU i SP) differences were insignificant in both seedlings' number and species number (Tables 1 and 2).

Juvenile shoots

Juvenile shoots were recorded in 481 out of the 720 analyzed quadrats. They occurred with a slightly higher mean frequency in control plots (0.73±0.53 SD) than in gaps (0.63±0.29), however, these differences were not significant (U-Withney-Man test; U = 3.41995, p<0.7323). Taking into account the time of gap appearance, the mean frequency of juveniles in the SP gaps (0.81±0.35) were significantly higher than in the control (U = 55.000, p<0.0431), AU (U = 14.000, p<0.432) and SU (U = 50.000, p<0.0342). However, there were no significant differences between the AU (0.61±0.25) and SU (0.45±0.04) vs. control (U = 41.000, p<0.1157 and U = 44.5000, p<0.6575 respectively) and AU vs. SU gaps (U = 14.000, p<0.1255).

The total of 5517 juveniles was noted. The mean number of juvenile shoots in autumn and summer gaps was lower than in closed sward; however, these differences were not significant (Table 3). Only in the SP gaps the mean number

TABLE 1. Two-way ANCOVA. (A) The effect of gap type, changes in time and gap type × time interaction on the number of seedlings (B) pairwise comparisons of seedling numbers in particular gap type (Shaeffe test). Distribution of quadrats was treated as a covariable. All the data were log + 10 transformed.
Abbreviations: C – control (closed sward); SP – spring gap; SU – summer gap; AU – autumn gap.

A	df Effect	MS Effect	df Error	MS Error	F	p
Gap type	3	46.08740	116	0.717687	64.21654	0.000000
Time	5	1.65269	580	0.585599	2.82222	0.016017
Gap type × Time	15	6.29830	580	0.585599	10.75531	0.000000

B	SP	SU	AU	C
mean±SD	**7.4805**±2.87	**7.1611**±3.83	**13.0333**±3.65	**3.7500**±1.54
SP		0.423087	0.000145	0.000145
SU	0.423087		0.001153	0.000378
AU	0.000145	0.001153		0.000145
C	0.000145	0.000378	0.000145	

TABLE 2. Two-way ANCOVA. The effect of gap type, changes in time and gap type × time interaction on the number of seedling species (B) pairwise comparisons of numbers seedling species in particular gap type (Shaeffe test). Distribution of quadrats was treated as a covariable. All the data were log + 10 transformed. All abbreviations as in Table 1.

A	df Effect	MS Effect	df Error	MS Error	F	p
Gap type	3	14.27947	116	0.355671	40.14794	0.000000
Time	5	6.02275	580	0.205446	29.31557	0.000000
Gap type × Time	15	3.14219	580	0.205446	15.29451	0.000000

B	SP	SU	AU	C
mean±SD	**3.0944**±1.53	**2.9333**±1.65	**3.6750**±1.42	**1.7444**±0.44
SP		0.827545	0.013546	0.000136
SU	0.827545		0.000902	0.000136
AU	0.013546	0.000902		0.000136
C	0.000136	0.000136	0.000136	

TABLE 3. Two-way ANCOVA. The effect of gap type, changes in time and gap type × time interaction on the number of juveniles (B) pairwise comparisons of numbers of juveniles in particular gap type (Shaeffe test). Distribution of quadrats was treated as a covariable. All the data were log + 10 transformed. All abbreviations as in Table 1.

A	df Effect	MS Effect	df Error	MS Error	F	p
Gap type	3	473.0259	116	33.76253	14.0104	0.000000
Time	5	268.3344	580	5.32934	50.3504	0.000000
Gap type × Time	15	547.0208	580	5.32934	102.6433	0.000000

B	SP	SU	AU	C
mean±SD	**6.9222**±3.38	**4.3972**±2.49	**4.1833**±2.09	**5.5555**±2.22
SP		0.015118	0.005787	0.165716
SU	0.015118		0.673558	0.239513
AU	0.005787	0.673558		0.132653
C	0.165716	0.239513	0.132653	

of juvenile shoots was significantly higher than in other gap types, but there was no difference as compared with closed vegetation (Table 3). The total number of species with juvenile shoots was highest in spring gaps (66) and ranged from 35 in summer gaps and 31 in control plots to 23 in autumn gaps. The mean number of species was also significantly higher in spring gaps than in other types of gaps and in closed vegetation. A difference in the mean number of species between the control and summer gaps was insignificant. On the contrary, in autumn gaps the mean number of species was significantly lower than in the other gap types and closed sward (Table 4).

Changes with time

The analysis of variance showed statistically significant temporal changes in the mean number of seedling species (Tables 1A-4A). However, the detailed analysis of (C, AU, SP, SU) × TIME interactions indicated that they were connected only with spring and autumn gaps. In autumn and to the lower degree in spring gaps the number of seedlings, and the number of species they represented, showed a strong increase from April to May and a consecutive decrease from July to September. The mean numbers of seedlings and their species in closed vegetation and summer gaps showed smaller fluctuations than in other gap types (Fig. 2A, B).

TABLE 4. Two-way ANCOVA. The effect of gap type, changes in time and gap type × time interaction on the number of juvenile species (B) pairwise comparisons of numbers of juvenile species in particular gap type (Shaeffe test). Distribution of quadrats was treated as a covariable. All the data were log + 10 transformed. All abbreviations as in Table 1.

A

	df Effect	MS Effect	df Error	MS Error	F	p
Gap type	3	216.7241	116	2.852679	75.97215	0.000000
Time	5	106.1207	580	1.915979	55.38719	0.000000
Gap type × Time	15	81.9299	580	1.915979	42.76137	0.000000

B

	SP	SU	AU	C
mean±SD	**4.1551**±2.71	**2.1379**±0.34	**1.6034**±0.89	**2.2413**±1.12
SP		0.000000	0.000000	0.000000
SU	0.000000		0.037961	0.954806
AU	0.000000	0.037961		0.008017
C	0.000000	0.954806	0.008017	

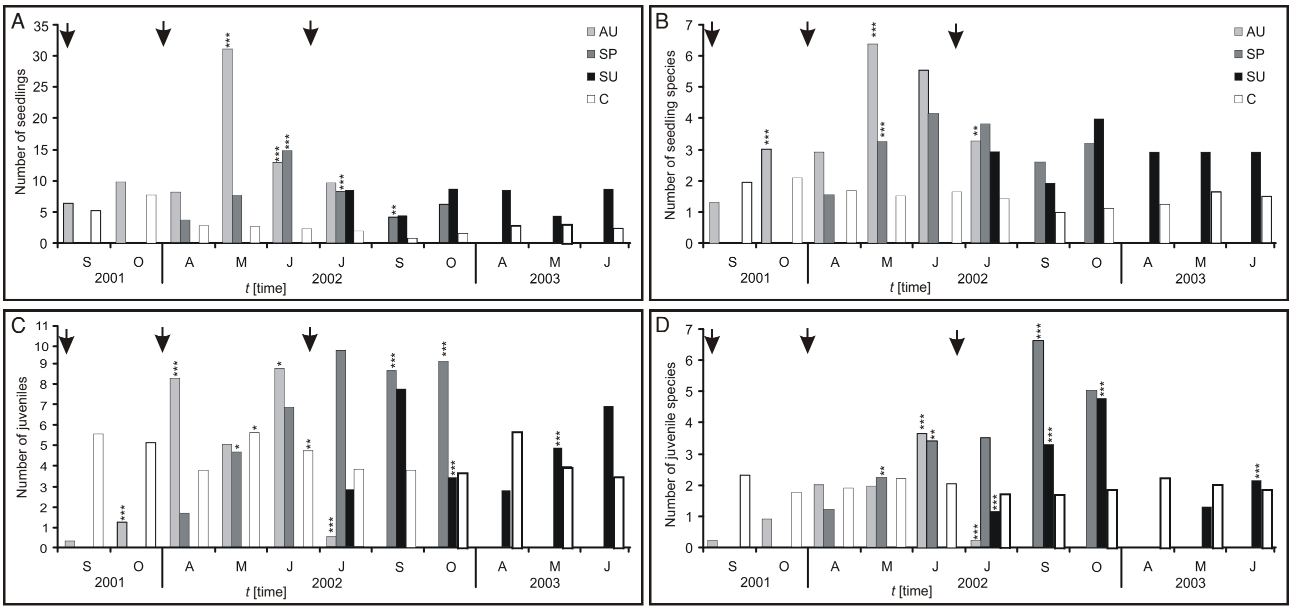

Fig. 2. Changes in mean number of seedling and juvenile individuals (A, B) and seedling and juvenile species (C, D). Only the significance of changes in one census time as compared with the previous one within the particular types of gaps are shown (two-way ANCOVA with Schaeffe a-posterioti test). For further explanation see methods. Arrows indicate time of creation of particular gap type and asterisks denote probability: ***p<0.001; **0.001<p<0.05; *0.05<p<0.01.

In both gap types during the first 2-3 months after they had been created a statistically significant increase in the mean number of juveniles and their species were noted (Fig. 2C, D). In spring gaps, the mean number of juvenile species remained high till the end of vegetation season. On the contrary, in autumn gaps, a sharp decrease in these figures was noted at the end of June.

DISCUSSION

Seedling emergence and establishment in gaps vs. closed vegetation

Our results show that the occurrence of small-scale disturbances, which create open places in closed sward of calcareous grasslands, is an important factor that promotes diaspore germination and seedling emergence. Similar results were obtained in many studies, conducted, i.e. in the intact vegetation of semi-arid grasslands (Aquilera and Lauenroth 1992) and temperate grasslands (Keizer et al. 1985; Bullock et al. 1994; Morgan 1997). They are contradictory to results obtained by Hillier (1990) and Gross (1980). Not only seedlings occurred more frequently in gaps, but also with higher density than in close vegetation. The same pattern was shown by the number of species represented by seedlings.

The higher rate of establishment of seedlings in gaps than in places with close vegetation is frequently observed (Gill and Marks 1991; Goldberg and Werner 1983; Morgan 1997). Contrary to the above-mentioned results and in line with the results of Silvertown and Wilkin (1983), Gross (1984), Ryser (1990), Garcia-Fayos and Verdu (1998), we did not find any significant differences in the mean number of juvenile shoots between gaps and close vegetation. However, there are some difficulties in the interpretation of this phenomenon. The number of juveniles in close vegetation could be slightly overestimated because some individuals which were assigned to juveniles in close vegetation, might have originated from the period before the experiment had been established. Moreover, the prolongation of the juvenile phase of growth of some plant species facing unfavourable environmental conditions, called "Oscar syndrom", is frequently observed in communities with low productivity (Ryser 1990; 1993; Falińska 1998; Bullock 2000).

Effect of time of gap appearance on seedling emergence and establishment

Differences in seedlings emergence between openings and closed sward occurred irrespective of time of gaps origin during the vegetation season. However, among the particular gap types, openings which were created in autumn seemed to be the most suitable for seedling emergence and those created in summer the least. In early autumn the soil moisture deficit is low and light and temperature conditions are sufficient for plants to germinate successfully (Willson and Traveset 2000, Davies 2002). In many publications it was suggested that most calcareous grassland species formed the transient seed bank in soil, i.e. their seeds germinated immediately, or within a year after ripening, from the mother plant (Dutoit and Alard 1995; Thompson et al. 1996, 1997; Davies and Waite 1998; Barbaro et al. 2001). The seed bank diversity, which can be the source of even 50% of the diaspores colonizing gaps in the calcareous grassland sward (Kalamees and Zobel 1998), seem to be at its highest density in autumn and at the lowest in August (Davies 2002). Most of the calcareous grasslands species ripe the diaspore from early summer, with a peak in autumn and winter (Medwecka-Kornaś 1950). However, in summer gaps, although the diaspore might be available from seed rain, the harshness of environmental conditions, especially the strong overdrying of the upper soil profile, hampered seedling germination. In this way the rate of colonization of summer gaps was lower than in the other gaps.

Irrespective of the role, which time of gap creation plays in seedlings germination/emergence, its effect on seedlings establishment is not unequivocal. Only in spring gaps the number of juvenile species was significantly higher than in other types of gaps. These results are in contradiction to the findings of Davies (2002) who pointed out the autumn season as more suitable for seedling establishment. Differences between spring and summer gaps in seedling establishment, like in seedling germination, can be explained by extreme and variable conditions in summer gaps during the period critical to seedling establishment. These explanations were in line with the findings of Ryser (1993) which indicated physical hazards as the main factor controlling seedling survival rather than competition from vegetation. Also Schenkeveld, Verkaar and Brand (1983), Silvertown (1981), Silvertown and Wilkin (1983) argued that in low-productive, nutrient-poor habitats, gaps are not the most favourable microsites for establishment, although germination is often improved in them. In such habitats, in summer period, in gaps which were created in the early spring the juveniles may benefit from the presence of neighbouring plants, which often improve unfavourable moisture and temperature conditions prevailing in open spaces ("shelter effect" – Hillier 1990; "nurse-plant" – Ryser 1993 and cited literature). The low rate of seedling establishment in autumn gaps is more difficult to explain. Since the number of juveniles in that gap type sharply declined in the summer period, the reason probably was the competition with plants which colonized the gaps in a vegetative way. However, the study period was too short, and only a model incorporating the effect of vegetative shoots (in preparation) will enable the determination of the role that vegetatively established plants play in seedling survival in gaps.

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LITERATURE CITED

AQUILERA M.O., LAUENROTH W.K. 1993. Seedling establishment in adult neighbourhoods – intraspecific constraints in the regeneration of the bunchgrass *Bouteloa gracilis*. J. Ecol. 81: 253-261.

BARBARO L., DUTOIT T., COZIC P. 2001. A six-year experimental restoration of biodiversity by shrub-clearing and grazing in calcareous grasslands of the French Prealps. Biodiversity and Conservation 10: 119-135.

BULLOCK J.M. 2000. Gaps and seedling colonization. Seeds: The ecology of regeneration in plant communities. 2nd edition (M. Fenner ed.) CAB International, pp. 375-395.

BULLOCK J.M., HILL C.B, DALE M.P., SILVERTOWN J. 1994. An experimental study of vegetation change due to sheep grazing in a species-poor grassland and the role of the seedling recruitment into gaps. J. Appl. Ecol. 31: 493-507.

BULLOCK J.M., HILL C.B, SILVERTOWN J.A., SUTTON M. 1995. Gap colonization as a source of grassland community change: effects of gap size and grazing on the rate and mode of colonization by different species. Oikos 72: 273-282.

COFFIN D.P., LAUENROTH W.K. 1988. The effects of disturbance size and frequency on a shortgrass plant community. Ecology 69: 1609-1617.

DAVIES A. 2002. The floristic restoration of agriculturally improved grassland. PhD. Thesis, Department of Landscape University of Sheffield, pp. 442.

DAVIES A., WAITE S. 1998. The persistence of calcareous grassland species in the soil seed bank under developing and established shrub. Plant Ecol. 136: 27-39.

DUTOIT T., ALARD D. 1995. Permanent seed banks in chalk grassland under various management regimes: their role in the restoration of species-rich plant communities. Biodiversity and Conservation 4: 939-950..

EDWARDS R.G., CRAWLEY M.J. 1999. Herbivores, seed banks and seedling recruitment in mesic grassland. J. Ecol. 87: 423-435.

FALIŃSKA K. 1998. Patterns of life history for perennial monocarpic. In: Plant population biology and vegetation processes. Falińska K. (ed.), W. Szafer Institute of Botany PAS, Kraków, pp. 51-57.

FALIŃSKI J.B. 2002. Przewodnik do długoterminowych badań ekologicznych [A guide to long-term ecological research]. Vademecum Geobotanicum, Wydawnictwa Naukowe PWN, Warszawa, pp. 672. (in Polish)

GARCIA-FAYOS P., VERDU M. 1998. Soil seed bank, factors controlling germination and establishment of a Mediterranean shrub: *Pistacia lentiscus* L. Acta Oecol. 19: 357-366.

GIBSON C.W.D., WATT T.A., BROWN V.K. 1987. The use of sheep grazing to recreate species-rich grassland from abandoned arable land. Biological Conservation 42: 165-183.

GILL D.S., MARKS P.L. 1991. Tree and shrub seedling colonization of and old-fields in central New York. Ecological Monographs 61: 183-205.

GOLDBERG D.E., GROSS K. L. 1988. Disturbance regimes of midsuccessional old fields. Ecology 69: 1677-1688.

GOLDBERG D.E., WERNER P.A. 1983. The effects of size of opening in vegetation and litter cover on seedling establishment of goldenrods (Solidago ssp.). Oecologia 60: 149-155.

GROSS K.L. 1980. Colonization of *Verbascum thapsus* (mullein) of an old-field in Michigan: experiments of the effects of vegetation. J. Ecol. 68: 919-927.

GROSS K.L. 1984. Effects of seed size and growth form on seedling establishment of six monocarpic perennials. J. Ecol. 72: 369-387.

GRUBB P.J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biol. Rev. 52: 107-145.

HARPER J.L. 1977. Population Biology of Plants. Academic Press, London.

HILLIER S.H. 1990. Gaps, seed banks and plant species diversity in calcareous grasslands Calcareous grasslands – ecology and management. Hillier S.H., Walton D.W.H., Wells D.A. (eds) pp. 57-66.

KALAMEES R., ZOBEL M. 1998. Soil seed bank composition in different successional stages od a species rich wooded meadow in Laelatu, western Estonia Acta Oekologica 19, 2: 175-180.

KEIZER P.J., VAN TOOREN B.F., DURING H.J. 1985. Effects of bryophytes on seedling emergence and establishment of short-lived forbs in chalk grassland. J. Ecol. 73: 493-504.

MAHDI A., LAW R. 1987. On the spatial organization of plant species in a limestone grassland community. J. Ecol. 75: 459-476.

MATUSZKIEWICZ W. 2001. Przewodnik do oznaczania zbiorowisk roślinnych Polski. [Guide to plant communities of Poland]. Vademecum Geobotanicum, Wydawnictwa Naukowe PWN, Warszawa, pp. 520. (in Polish).

MEDWECKA-KORNAŚ A. 1950. Biologia rozsiewania naskalnych zespołów roślinnych Jury Krakowskiej. [The biology of reproduction of rocky plant communities in Cracov Jura]. Rozpr. Wydz. Mat.-Przyr. PAU, Ser. B., 74 (1): 1-41. (in Polish).

MITCHLEY J. 1990. Control of relative abundance of perennial dicotyledons in chalk grasslands Calcareous grasslands – ecology and management. Hiller S.H., Walton D.W.H., Wells D.A. (eds) pp. 67-73.

MITCHLEY J. 1994. Sward structure with regard to conservation. In: Hagger R.J. and Peel S. (eds). Grassland Management and Nature Conservation, Brotish Grassland Society Occasional Symposium 28, pp. 43-53.

MORGAN J.W. 1997. The effect of grassland gap size on establishment, growth and flowering of the endangered *Rutidosis leptorrhynchoides* (*Asteraceae*). J. Appl. Ecol. 34: 566-576.

PEART D.R. 1989. Species interactions in a successional grassland. I. Seed rain and seedling establishment. J. Ecol. 77: 236-251.

RUSCH G. 1988. Reproductive regeneration in grazed and ungrazed limestone grassland communities in Öland. Preliminary Results. Acta Phytogeographica Suecica 76: 113-124.

RUSCH G., VAN DER MAAREL E. 1992. Species turnover and seedling recruitment in limestone grasslands. Oikos 63: 139-146.

RYSER P. 1990. Influence of gaps and neighbouring plants on seedling establishment in limestone grassland Veröff. Geobot. Inst. ETH, Stiftung Rübel, Zürich 104: 1-78.

RYSER P. 1993. Influence of neighbouring plants on seedling establishment in limestone grassland. J. Vegetation Sci. 4: 195-202.

SCHENKEVELD A.J., VERKAAR H.J., BRAND J.M. 1983. On the ecology of short-lived forbs in chalk grasslands: micro-site tolerances in relation to vegetation structure. Vegetatio 52: 91--102.

SILVERTOWN J. 1980. Leaf-canopy induced dormancy in a grassland flora. New Phytologist 85: 109-118.

SILVERTOWN J. 1981. Micro-spatial heterogeneity and seedling demography in species rich grassland. New Phytologist 88: 117-128.

SILVERTOWN J.W., DICKIE J.B. 1980. Seedling survivorship in natural populations of nine perennials chalk grassland plant. New Phytologist 88: 555-558.

SILVERTOWN J.W., WILKIN F.R. 1983. An experimental test of the role of micro-spatial heterogeneity in the coexistence of congeneric plants. Biol. J. Linnean Soc. 19: 1-8.

SOKAL R.R., ROHLF F.J. 1995. Biometry: the principles and practice of statistics in biological research. 3rd edition. W. H. Freeman and Co., New York. 887 pp.

THOMPSON K., HILLIER S.H., GRIME J.P., BOSSARD C.C., BAND S.R. 1996. A functional analysis of a limestone grassland community. J. Vegetation Sci. 7: 371-380.

THOMPSON K., BAKKER J.P., BEKKER R.M. 1997. Soil Seed Banks of North-West Europe: Metodology, Density and Longevity. Cambridge University Press, Cambridge, 276 pp.

TILMAN D. 1994. Competition and biodiversity in spatially structured habitats. Ecology 75: 2-16.

TILMAN D. 1997. Community invasibility, recruitment limitation and grassland biodiversity Ecology 78: 81-92.

VAN DER MAAREL E. 1988. Species diversity in plant communities in relation to structure and dynamics. In: During H.J., Werger M.J.A., Willems J.H (eds) Diversity and pattern in plant communities. SPB Academic Publishing, The Hague, The Netherlands, pp. 1-14.

VERKAAR H.J., SCHENKEVELD A.J. 1984. On the ecology of short-lived forbs in chalk grasslands: seedling development under low photon flux density conditions. Flora 175: 135-141.

WILLSON M.F., TRAVESET A. 2000. The ecology of seed dispersal. Seeds: The ecology of regeneration in plant communities. 2nd edition (M. Fenner ed.) CAB International. pp 85-110.

WINN A.A. 1985. Effects of seed size and microsite on seedling emergence of *Prunella vulgaris* in four habitats. J. Ecol. 73: 831-840.