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Slope aspect affects the seed mass spectrum of grassland vegetation

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Abstract

Seed mass distribution in grassland communities of slopes of contrasting aspect was analysed in dolomite regions of the Pannonian Basin. Species frequencies were obtained for four pairs of data sets, which originated from corresponding south- and north-facing dolomite grasslands, thus forming four independent case studies. The data sets comprised 5–15 sample plots and 51–114 (average 85) species. The species were classified using an eight-class system reflecting their mean seed mass (MSM) records (class 1 being the lowest, MSM $\leqslant 0.2$ mg; class 8 being the highest, MSM > 50 mg). Seed mass class distributions derived from slopes of contrasting aspect showed strong significant differences in chi-square tests for trend for all the four case studies. Small-seeded species (classes 1 and 2) showed a positive balance for the south-facing slopes, whereas large-seeded species (classes 5, 6, 7 and 8) were more frequent on north-facing slopes. Species with intermediate seed mass (classes 3 and 4) were not distinctive between the slopes. These results represent strong evidence of increased seed mass in the vegetation of north-facing grasslands, when compared to their south-facing counterparts. Among the phenomena potentially responsible for the new findings, we discuss the roles of microclimatic effects (especially drought stress and light regime), grass litter, interspecific competition and seed predation.

Keywords: dolomite grassland, seed size, seed weight, slope aspect, vegetation ecology

Introduction

Seed mass of species ranges across ten orders of magnitude in the world flora, and the variation is still seven orders of magnitude for the European vegetation only. Surprisingly, considerable variability may occur among coexisting plants of the same community: average differences may be as much as 5–6 orders of magnitude (Westoby *et al*., 1992; Leishman *et al*., 2000). This extreme variability may explain why the effect of habitat type on seed mass had been unrecognized for a long time. It was Salisbury (1942) who first demonstrated the statistical differences among seed mass distributions of a series of habitats with increasing community maturity. The relationship between seed mass and habitat variables or plant traits has since become known for many cases (Baker, 1972; Thompson and Rabinowitz, 1989; Westoby *et al*., 1992; Leishman and Westoby, 1994; Rees, 1995; Hodkinson and Thompson, 1997; Milberg *et al*., 2000; Azcarate *et al*., 2002; Mazer and Lowry, 2003). However, the effect of slope aspect on the seed mass spectrum of communities has not yet been investigated.

Our interest in this subject was motivated principally by Critchfield (1971; cit. Parker and Kelly, 1989), who reported remarkable contrasts between seed bank properties of vegetation types with different aspect. Species with persistent seed banks expressed higher proportions in the vegetation of south-facing slopes than in that of north-facing slopes of the California chaparral. For species with a transient seed bank, the opposite relationship was detected: they were more abundant on north-facing slopes.

Thompson *et al*. (1993) showed that species of the British flora with persistent seed banks tend to have small, spherical seeds, whereas those with transient seed banks have seeds that are larger in size and less isodiametric in shape. A further seven studies from a wide range of geographical areas confirmed this observation, either for size or shape, or both (e.g. Funes *et al*., 1999; Cerabolini *et al*., 2003), although Leishman and Westoby (1998) could not confirm these findings for 101 species of the Australian flora. From a recent overview of the topic (Peco *et al*., 2003), it is obvious that at least the seed size–seed persistence

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relationship must be accepted as a strongly supported rule of seed ecology.

As a logical consequence of results discussed above, we propose that the vegetation on north-facing slopes is formed by larger-seeded species than that on south-facing slopes. The objective of the present paper is to test the validity of this hypothesis on examples from dry grassland vegetation of Hungary.

Materials and methods

Eroded hills of Triassic dolomite bedrock were selected as study sites. Dolomite hills cover considerable areas in the Pannonian Basin and, due to the physico-chemical characteristics of dolomite, erosion shapes these hills with steep slopes (25–35° in most cases). As a result of the contrasting microclimates, well-distinguishable grassland communities develop on the slopes (Zólyomi, 1942; Draskovits and Kovács-Láng, 1968). The most frequent plant association of the south-facing aspect is *Seseli leucospermi–Festucetum pallentis* (Zólyomi, 1958), which may be replaced by *Poo badensis–Festucetum pallentis* (Maglocky, 1979) in the northernmost part of the Pannonian Basin. On slopes of a north-facing aspect, *Festucetum pallentis–Brometum pannonici* (Zólyomi, 1958) dominates, replaced by *Seslerietum sadlerianae* (Zólyomi, 1936) in some parts of the Budai Hills. These communities develop within a similar altitudinal range on dolomite hills, and are all obligate grasslands, since the shallow soils of their habitats prevent the establishment of woody vegetation (Zólyomi, 1942; Debreczy, 1987). The physiognomic similarity of these communities is important, to eliminate the potential bias that larger plants tend to have larger seeds (Thompson and Rabinowitz, 1989). A further reason for taking dolomite grasslands as study objects was the availability of large field data sets; these communities are favoured by botanists because of their richness in relic and endemic species (Zólyomi, 1987; Csontos and Lőkös, 1992). The data for the present study come from four different sources (= four examples) representing three geographical regions (Table 1). In each example, an equal number of sample plots (relevès) were chosen from the south- and north-facing slopes. The two data sets of Bartha *et al*. (1998) originated from five linear samples of 1200 contiguous micro-quadrats (each 5 cm × 5 cm) along 60-metre-long transects in each of the stands (for more details on sampling, see Bartha *et al*., 1995). The further six data sets were prepared according to the method of the Central-European School of Phytosociology. Quadrat sizes were: 25 m^2 (or 16 m^2 in some cases) for Török and Zólyomi (1998), 8 m^2 for Tamás (1997, 2001) and 16 m^2 for Podani, Tamás and Csontos (unpublished data). In all cases, the flora lists of all spermatophytes found in the quadrats (or linear samples) were used. Further details are given in Table 1.

Table 1. Main features of the data sets from north- and south-facing grasslands of the Pannonian dolomite hills used for seed weight spectrum analyses

Aspect	Community name	Number of quadrats	Total number of species	Total number of occurrences	Geographical region	Reference
North-facing	*Festucetum pallentis–Brometum pannonici*	5	114	234	Transdanubian Central Range	Bartha *et al*. (1998)
North-facing	*Festucetum pallentis–Brometum pannonici*	10	106	363	Transdanubian Central Range	Török and Zólyomi (1998)
North-facing	*Festucetum pallentis–Brometum pannonici*	5	67	211	Nagy-Szénás group, Budai Hills	Tamás (1997, 2001)
North-facing	*Festucetum pallentis–Brometum pannonici* and *Seslerietum sadlerianae*	15	96	680	Sas hill of Budai Hills	Podani *et al*. (unpublished)
South-facing	*Seseli leucospermi–Festucetum pallentis* and *Poo badensis–Festucetum pallentis*	5	75	152	Transdanubian Central Range	Bartha *et al*. (1998)
South-facing	*Seseli leucospermi–Festucetum pallentis*	10	81	293	Transdanubian Central Range	Török and Zólyomi (1998)
South-facing	*Seseli leucospermi–Festucetum pallentis*	5	51	173	Nagy-Szénás group, Budai Hills	Tamás (2001)
South-facing	*Seseli leucospermi–Festucetum pallentis*	15	93	615	Sas hill of Budai Hills	Podani *et al*. (unpublished)

Data processing

Mean seed mass (MSM) data of species were taken from the SEED database (Csontos, 1998) and then converted into eight seed mass classes as follows: 1, ⩽0.20 mg; 2, 0.21–0.50 mg; 3, 0.51–1.00 mg; 4, 1.01–2.00 mg; 5, 2.01–4.00 mg; 6, 4.01–10.00 mg; 7, 10.01–50.00 mg; 8, >50.00 mg. By merging classes 5 and 6, and also classes 7 and 8, this categorization becomes identical to the six-class system of Hodgson *et al*. (1995). The percentage of species with no information on seed mass reached 6–8% in the different data sets. For these species, scores were estimated as follows. If a given species had at least two congeners with direct data in the SEED database, and if their data fell into the same seed mass class, and if the three species had the same life-form and similar fruit morphology, then the same class was assigned to the species in question. If the congeners with known data belonged to different seed mass classes, or obvious morphological differences prevailed, then no estimation was made. In summary, 0–1.97% (mean 0.51%) of species of the data sets were thus excluded from the analyses. For calculating seed mass spectra, species were weighted with their numbers of occurrences in the given data set. Seed mass spectra of the corresponding pairs of south- and north-facing data sets were evaluated statistically by the chi-square test for trend (InStat, 1997).

Results

The frequency distributions of species in the eight seed mass categories are summarized in Table 2, and the distributions of percentage frequencies are shown in Fig. 1a–d. Very similar seed mass spectra and major trends emerged in the four examples.

In all cases, a positive balance occurred for the south-facing vegetation samples in the first two seed mass categories (MSM lighter than or equal to 0.5 mg). In contrast, heavier seed mass classes (classes 5, 6 and 7; MSM between 2.01 mg and 50.00 mg) reached higher quantities for the north-facing vegetation samples. Seed mass classes 3 and 4 proved to be transitional, showing unpredictable proportions in the four examples.

The largest seed mass category was represented only in four of the eight data sets. Species falling into this class (e.g. *Acer campestre* L., *A. platanoides* L. and *Tilia platyphyllos* Scop.) are not regular constituents of the studied communities, but instead they were represented by seedlings only, attempting to colonize the grasslands from neighbouring woods. Sometimes these trees are temporarily successful and can survive in the grasslands for a short period of time, and then they disappear due to the severe abiotic stress (mainly drought) of the habitat (Debreczy, 1987). However, they should not be excluded from the analyses, because their presence (or absence) could also be distinctive to the contrasting aspects. Indeed, tree seedlings were found more frequently in data sets from the north-facing slopes (Fig. 1a, b and c).

The difference between corresponding seed mass distributions proved highly significant for all the examples studied (Table 2).

Discussion

The results demonstrate clearly that the grassland vegetation of north-facing slopes is formed by somewhat heavier-seeded species when compared to

Table 2. Number of species occurrences per seed weight class in the dolomite grassland vegetation samples, and the results of the trend analysis regarding pairs of north- and south-facing vegetation

Seed weight class (mg)	Number of species occurrences							
	Hungarian Central Range (Bartha *et al*.)		Hungarian Central Range (Török and Zólyomi)		Nagy-Szénás group, Budai Hills		Sas hill of Budai Hills	
	North	South	North	South	North	South	North	South
⩽0.20	21	29	47	50	32	36	86	121
0.21–0.50	34	33	50	62	25	37	116	113
0.51–1.00	37	25	56	45	47	31	129	85
1.01–2.00	44	23	59	46	29	24	99	106
2.01–4.00	51	21	71	46	33	21	123	99
4.01–10.00	29	12	54	32	27	15	70	63
10.01–50.00	12	6	21	10	15	9	57	28
>50.00	3	0	2	2	3	0	0	0
n.c.	3	3	3	0	0	0	0	0
cal. χ^2	15.243		10.055		8.210		10.099	
l.s.	$P < 0.0001$		$P < 0.002$		$P < 0.005$		$P < 0.002$	

Abbreviations: n.c., unclassified data; cal. χ^2, calculated chi-squared for trend; l.s., level of significance.

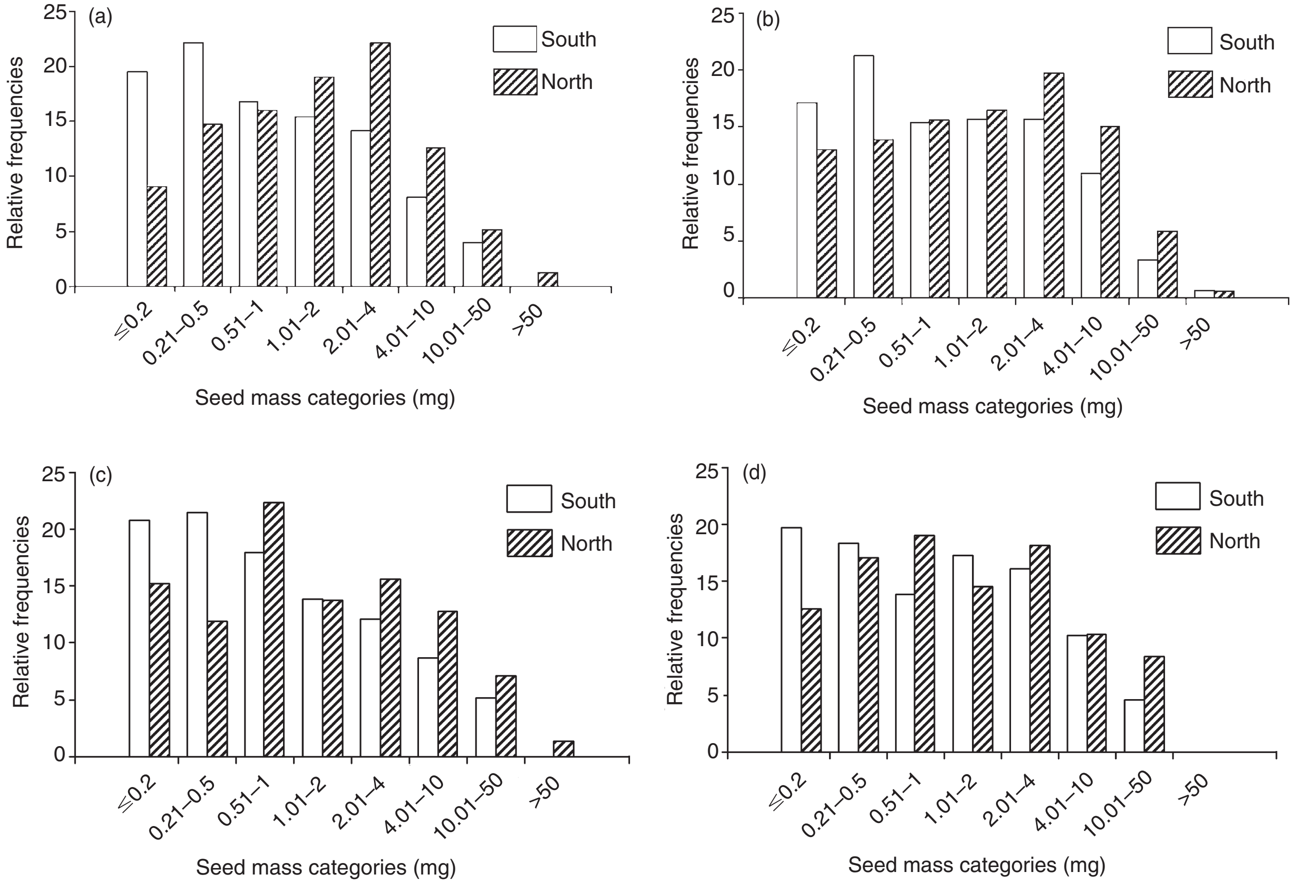

Figure 1. Relative frequencies of species occurrence according to seed mass categories. The corresponding pairs of data sets of rock grassland vegetation originated from south- and north-facing slopes of dolomite hills in various regions of the Pannonian Basin. (a) Transdanubian Central Range (data from Bartha *et al*., 1998); (b) Transdanubian Central Range (data from Török and Zólyomi, 1998); (c) Nagy-Szénás group, Budai Hills; (d) Sas hill of Budai Hills.

that of south-facing slopes of the same geographic area. If we seek to identify background phenomena responsible for the seed mass spectrum differences, the following effects should be considered.

Early microclimatic measurements carried out in the dolomite vegetation of the Budai Hills revealed that daily fluctuations of air temperature at the soil surface, and the soil temperatures at 10 cm depth (the rooting zone) are higher on the south-facing slopes than on the north-facing ones (Draskovits and Kovács-Láng, 1968). Therefore, the south-facing slopes offer habitats of higher abiotic stress for plant life, and of low temporal predictability of environmental conditions. Earlier findings disagree on the effect of such habitats on the seed size of species. (1) In some cases, higher seed mass was detected for species inhabiting drought-prone habitats (Baker, 1972; Salisbury, 1974), allowing the interpretation that larger seed size facilitates seedlings to establish larger root systems early, with a better chance of surviving drought. (2) However, Mazer (1989) did not find a significant relationship between seed size and water availability in the habitat; and, in glasshouse experiments, Jurado and Westoby (1992) could not support the hypothesis that in drying soil large-seeded species would tend to allocate relatively more to roots than small-seeded species. (3) In a British calcareous grassland, a considerably higher proportion of persistent seed bank species was found on the south-facing slope than on the neighbouring north-facing slope. This was claimed to be a general feature in skeletal habitats, where environment rather than management is the primary influence on vegetation (Grime and Hillier, 2000). Because there is a strong negative correlation between seed persistence in soil and seed size (Thompson, 2000; Csontos and Tamás, 2003; Peco *et al*., 2003), Grime and Hillier's finding can be considered as evidence for smaller seed size on south-facing slopes. The present results are compatible with the third case.

In hilly landscapes, the light regime strongly depends on the angle and the aspect of slopes. Considering south-facing slopes of Budai Hills (latitude: 47°30′N) with a slope angle of 24° (the average slope for the region), at noon on the day of the summer solstice (21 June), sunlight reaches the surface at a right angle, as on the level ground at the Tropic of Cancer. However, a similar slope facing to the north at the same latitude has a sunshine inclination angle of 48° on the same day at noon, which corresponds to the level ground near Nordkapp, Lapland. During the vegetation period, clear sky days with direct sunshine are very frequent in the studied region, thus – considering the increased extinction when light reaches the vegetation at a low angle – north-facing slopes receive much less light.

Additionally, on the north-facing dolomite slopes – where microclimatic conditions are less extreme – vegetation cover is higher than on the south-facing slopes (85–100% with average 93%, and 50–80% with average 62%, respectively). This also causes a higher extinction in the canopy, especially if light arrives at a low angle, thus resulting in a further reduction of the relative irradiation at the ground layer. It is known that species adapted to shady habitats tend to have larger (heavier) seeds than species of sunny habitats (Salisbury, 1942; Hodgson and Mackey, 1986; Metcalfe and Grubb, 1995; Hodkinson *et al*., 1998), and the major factor responsible for this could be the higher chance of successful germination of larger seeds in the shade (Grime and Jeffrey, 1965; Milberg *et al*., 2000).

For germination success, the increased amount of grass litter on the north slopes should also be considered, as litter quantity is known to have a remarkable effect on species composition in a wide variety of vegetation types (Xiong and Nilsson, 1999).

Another consequence of the increased vegetation cover on the north-facing slopes could be the increased level of interspecific competition, and this implies a moderate shift of the species' reproductive strategy towards the 'K-end' of the r–K continuum on the north-facing slopes. Since K-strategists are generally known to produce fewer offspring with more parental care, i.e. a larger amount of endosperm in our case, this may lead, again, to an increase in the average seed mass of species coexisting in the north-facing closed dolomite grasslands.

On south-facing slopes (with more open vegetation), small-seededness could also be advantageous in avoidance of seed predation. With reduced ground cover, the number of seedlings of large-seeded species increased significantly in a caged environment (ensuring exclusion of seed predators), whereas small-seeded species were unaffected (Reader, 1993).

It is reasonable to suppose that one or more of the phenomena listed above plays a role in determining seed mass spectra of grasslands on steep slopes with contrasting aspect.

Finally, we would like to emphasize that our new observations come from grasslands occurring intrazonally, due to orographic reasons, in the temperate broadleaved forest belt. However, the same situation could apply to a wider range of vegetation types within this belt. For example, comparable woody vegetation stands may also have this relationship, because (1) evidence suggests the importance of slope aspect in determining the species composition of woody vegetation (Attorre *et al*., 2003); and (2) there are reports of higher proportions of small-seeded species in the herb-layer of forests where the stands were subjected to increased stress (Kenderes and Standovár, 2003). Beyond the broadleaved forest belt, the existence of the same relationship is difficult to predict, and requires a detailed investigation. Under a cool, boreal climate, north-facing slopes may offer very poor habitats for plant life, and the south-facing slopes could be free from summer drought stress; whereas in tropical landscapes, the weakening of an effect of aspect may prevent the manifestation of the seed size differences between slopes.

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