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ECOLOGICAL MEANING OF SEED SIZE AND SHAPE FOR SEED PERSISTENCE AND GERMINABILITY IN SOME MOUNTAIN PLANTS FROM THE COLLECTION OF THE BOTANICAL GARDEN IN LUBLIN

Ekologiczne znaczenie wielkości i kształtu nasion dla ich trwałości i zdolności kiełkowania u niektórych roślin górskich z kolekcji Ogrodu Botanicznego w Lublinie

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STRESZCZENIE

Badania miały na celu odpowiedź na pytania: (1) czy propagule roślin górskich zachowują w warunkach niżowych zdolność do kiełkowania oraz jaka jest ich siła i dynamika kiełkowania; (2) czy istnieją zależności pomiędzy kształtem i wagą nasion a ich zdolnością do tworzenia trwałego banku nasion. Obserwacje prowadzono u 15 gatunków roślin górskich z kolekcji Ogrodu Botanicznego UMCS w Lublinie. Badania nad siłą, dynamiką kiełkowania oraz żywotnością nasion prowadzono w szklarni na diasporach zebranych w sezonie 2004 roku. Nasiona wysiewano na bibule oraz glebie w marcu 2005 i 2006 roku. Nasiona 14 gatunków kiełkowały w warunkach szklarniowych; pomimo stratyfikacji nie wykiełkowały nasiona *Rosa pendulina*. Na podstawie zależności między ciężarem, kształtem i trwałością, nasiona 5 badanych taksonów zaklasyfikowano do kategorii przejściowych (*R. pendulina, Clematis alpina, Centaurea mollis, C. kotschyana*, *C. alpestris*), pozostałe 10 skategoryzowano jako trwałe. Ze względu na przebieg krzywej można wyróżnić trzy wzorce kiełkowania. Propagule gatunków zaliczonych do wzorca *Erisimum wittmannii* kiełkują bardzo szybko, osiągając maksymalną wartość siły kiełkowania (do 100%) w ciągu 6,6–7,9 dni. Siła kiełkowania nasion gatunków należących do wzorca *Aster alpinus* rośnie stopniowo do 68–72%, a średni czas kiełkowania wynosi od 8,4 do 12,3 dni. Przebieg krzywej kiełkowania według wzorca *Hieracium aurantiacum* ma charakter fluktuacyjny; siła kiełkowania w przedziale 18–40% osiągana jest średnio w czasie 5,8–13,7 dni.

SUMMARY

The study aimed to answer to the following questions: (1) if propagules of mountain plants preserve their germinability in lowland conditions, and what is the strength and dynamics of their germination; (2) is there a relationship between the mass and shape of seeds and their ability to form a persistent seed bank. The observation was carried out on 15 mountain species from the collection of the Botanical Garden of Maria Curie-Skłodowska University in Lublin. The studies were conducted in the greenhouse on the diaspores collected in the year 2004. The seeds were sown into tissue paper and into soil in the March of 2005 and 2006. The seeds of 14 species germinated in the greenhouse conditions; despite prior stratification, the seeds of *Rosa pendulina* did not germinate. On the basis of the relationship between seed weight, shape and persistence, seeds of 5 analysed taxa were classified as transient (*R. pendulina, Clematis alpina, Centaurea mollis, C. kotschyana*, *C. alpestris*), while the remaining 10 were categorised as persistent. Taking into account the shape of the germination curve, three patterns could be distinguished. In the pattern of *Erisimum wittmannii* propagules germinate very fast, reaching the maximum values of germination strength (up to 100%) in 6.6–7.9 days. According to the pattern of *Aster alpinus* number of germinating seeds increases gradually to 68–72%, and their mean germination time is 8.4 to 12.3 days. In the pattern of *Hieracium aurantiacum* germination curve is of fluctuating character; the germination strength is 18–40% during the mean time of 5.8–13.7 days.

INTRODUCTION

Plants adapt to changing environmental conditions and develop colonisation abilities due to various adaptive strategies. The latter are a group of genetically encoded mechanisms and features of organisms creating a population, which manifest themselves in various ways, depending on the randomly changing environment (Stace 1993). One of such features is somatic polymorphism of seeds, reflected in the size and shape of seeds, the presence or absence of dispersal structures, the ability to spread and germinate, and the size and survival of seedlings. Somatic polymorphism is usually accompanied by functional polymorphism, decisive for the acceleration or delay of germination (Stace 1993; Czarnecka 1998). Not all the seeds germinate immediately after sowing: a part of them remains in the soil as a reservoir of propagules capable of germination, and forms the so-called seed bank. Its persistence depends on a number of factors such as seed mass and size, or its capability of swift penetration into the soil (Harper et al. 1965; Symonides 1978; Gross 1984; Thompson et al. 1993; Funes et al. 1999; Ghersa et al. 2000; Moles et al. 2000; Cerabolini et al. 2003).

For herbaceous species, Thompson et al. (1993) developed a method of theoretical estimation of the ability of a given species to form a persistent seed bank, based of its seed mass and shape. The authors distinguished 3 groups of seed banks: transient, whose seeds live in soil shorter than 1 year; short-term persistent, whose seeds live between 1–5 years; and long-term persistent, with the seeds staying alive for at least 5 years. Introducing the concept of the longevity index, Bekker et al. (1998) combined the categories of a short-term persistent and long-term persistent seed bank, leaving only two of them: transient and persistent.

STUDY AIM, MATERIALS AND METHODS

The aim of the present study is to answer the following questions:

(1) Do propagules of mountain plants preserve their germinability in lowland conditions, and what is the strength and dynamics of their germination?

(2) Is there a relationship between the mass and shape of seeds and their ability to form a persistent seed bank?

The studies on the seeds' predilection for persistence based on their mass and size, together with the analyses of the strength and dynamics of their germination, were carried out on 15 species (of 7 families), selected from the mountain species collection of the Botanical Garden of Maria Curie-Skłodowska University in Lublin. The plants were earlier observed in order to trace changes in their architecture and flowering phenology (Czarnecka et al. 2006). In the present study, propagules (seeds and fruits) of plants will be further referred to as 'seeds'.

Out of each species, 30 dry seeds were weighted and measured (length, width and thickness). Seed shape was measured with the method of Thompson et al. (1993), as a variance of the length, width and thickness of seeds, after all the values had been transformed in order for the length to equal one. As far as it was possible, the measured seeds were deprived of dispersal structures (e.g. *pappus* in the case of Asteraceae, or fresh parts of fruits). Winged seeds, however (such as *Dianthus nitidus, D. compactus,* and *Alyssum saxatile*), were measured together with their additional structures as their removal could result in the destruction of propagules.

The analysed species were classified according to the theoretical method of seed longevity estimation (Thompson et al. 1993). The seeds whose weight did not exceed 3 mg and whose seed shape was smaller than 0.14 were classified as persistent, while those heavier than 3 mg and of greater variance – as transient.

Depth distribution (*D*) was measured according to Bekker et al. (1998):

$$D = -504.9 \times log\,(M) - 498.9 \times log\,(\sqrt{Vs}) + 521.1\, log\,(M\sqrt{Vs}) + 94.00$$

M – the seed mass

Vs – the variance of seed dimensions (seed shape)

The relationship between horizontal distribution of seeds in soil and their persistence was measured according to the formula of Bekker et al. (1998):

$$L = -0.003023\ D - 0.2065\ log\,(\sqrt{Vs}) + 0.3938$$

L – is the longevity index ranging from 0 (seeds classified as transient) to 1 (those categorised as persistent).

The studies on strength and dynamics of germination, and on the persistence of seeds, were conducted in the greenhouse on the diaspores collected in the year 2004. The seeds were sown into tissue paper and into soil in the March of 2005 and 2006. Because of a small number of available seeds, the experiments were not repeated. Each sample consisted of 50 seeds of a particular taxon. Only in the case of *Clematis alpina* and *Rosa pendulina* three variants of germination were taken into consideration:

(1) seeds stratified during the winter season on a creeper and a shrub;

(2) seeds stratified for two weeks in the refrigerator;
(3) seeds which were not subjected to stratification.
The percentage of germinating seeds was treated as germination strength. The mean time of germination (*Tg*) was measured after Lityński (1977) and expressed in days:

$$T_G = \frac{\Sigma(D \times N_D)}{G}$$

D – subsequent day of germination,
N_D – number of seeds germinated on particular day,
G – germinated seeds as the percentage of the total number of sown seeds.

Table 1. Relation between diaspore size and shape vs. persistence for some mountain species
Tabela 1. Zależność między wielkością, kształtem i trwałością diaspor u niektórych gatunków górskich

Species (n = 30)	Short	Family	Life form	Diaspore	*D*	*L*	Seed mass (mg)	Seed shape (variance)	Persistence
Jovibarba hirta (L.) Opiz subsp. *glabrescens*	Jovhir	Crassulaceae	Herb	Seeds	71.61	0.50	0.08	0.123	p
Hieracium aurantiacum L.	Hieaur	Asteraceae	Herb	Fruits	73.15	0.47	0.10	0.135	p
Erysimum wittmannii Zaw.	Erywit	Brassicaceae	Herb	Seeds	78.69	0.34	0.39	0.108	p
Erysimum pieninicum (Zapał.) Pawł.	Erypie	Brassicaceae	Herb	Seeds	80.65	0.30	0.60	0.105	p
Aster alpinus L.	Astalp	Asteraceae	Herb	Fruits	83.29	0.25	0.89	0.122	p
Dianthus compactus Kit.	Diacom	Caryophyllaceae	Herb	Seeds	83.99	0.23	0.98	0.128	p
Dianthus nitidus Waldst & Kit.	Dianit	Caryophyllaceae	Herb	Seeds	83.99	0.23	0.99	0.124	p
Alyssum saxatile L.	Alysax	Brassicaceae	Herb	Seeds	84.11	0.23	0.96	0.134	p
Mutellina purpura (Poir.) Thell.	Mutpur	Apiaceae	Herb	Fruits	84.38	0.23	1.03	0.132	p
Solidago alpestris Waldst & Kit.	Solalp	Asteraceae	Herb	Fruits	85.03	0.22	0.90	0.173	p
Clematis alpina (L.) Mill.	Clealp	Ranunculaceae	Shrub	Fruits	93.71	0.01	10.96	0.084	t
Rosa pendulina L.	Rospen	Rosaceae	Shrub	Seeds	93.84	0.00	21.37	0.044	t
Centaurea alpestris Hegetschw. & Heer	Cenalp	Asteraceae	Herb	Fruits	95.22	0.00	10.96	0.115	t
Centaurea kotschyana Heuff. Ex W. D. J. Koch	Cenkot	Asteraceae	Herb	Fruits	95.69	0.00	12.29	0.113	t
Centaurea mollis Waldst & Kit.	Cenmol	Asteraceae	Herb	Fruits	95.74	0.00	16.45	0.085	t

Life form classes: Herb – forbs, grasses or sedges; Shrub – shrubs or liana. *D* – depth distribution – the proportion likely to be found in the upper soil layer (0–5 cm); *L* – longevity index calculated according to Bekker et al. (1998); t – transient seeds, p – persistent seeds calculated according to Thompson et al. (1993), Bekker et al. (1998). Species are sorted by decreasing *L*
Formy życiowe: Herb – byliny dwuliścienne, trawy lub turzyce; Shrub – krzewy lub liany. *D* – głębokość zalegania – prawdopodobieństwo znalezienia w górnej warstwie gleby (0–5 cm); *L* – wskaźnik długowieczności obliczony według Bekker et al. (1998); t – nasiona o małej trwałości, p – nasiona o dużej trwałości według Thompson et al. (1993), Bekker et al. (1998). Gatunki uporządkowano według malejącej wartości *L*

RESULTS

The mass of the analysed seeds ranged from 0.08 to 21.37 mg, while the seed variance showed the values between 0.044 and 0.173 (Table 1). On the basis of the relationship between seed weight, shape and persistence, seeds of 5 analysed taxa were classified as transient, while the remaining 10 were categorised as persistent (Fig. 1). The mass of the seeds classified as transient ranged from 10.96 to 21.37 mg, the values of their seed shape from 0.044 to 0.115, and their longevity index was 0 to 0.01 (Table 1). The mass of the seeds categorised as persistent ranged from 0.08 to 1.03 mg, the values of their seed shape reached 0.105 to 0.173, and their longevity index was expressed by the values of the interval between 0.22 and 0.50 (Table 1).

As the differences between the germination of seeds sown onto the tissue paper and those sown into the soil were negligible, the study presents only the results of soil sowing. Out of the 15 analysed species, the seeds of 14 of them germinated in the greenhouse conditions. Despite prior stratification, the seeds of *Rosa pendulina* (Fig. 2) did not germinate; in the case of *Clematis alpina*, whose seeds were also subjected to stratification, only 3 diaspores (those stratified on a creeper) germinated after the period of 30 days, and the strength of their germination did not exceed 6%. The mean time of germination for the remaining seeds sown in 2005 ranged, depending on a species, from ca. 6 days (*Jovibarba hirta* subsp. *glabrescens*) to ca. 14 days (*Dianthus compactus*). For the one-year-old seeds (sown in 2006) the values ranged from 4 days (*Erysimum pieninicum*) to 11 days (*Jovibarba hirta* subsp. *glabrescens*).

Taking into account the shape of the germination curve of the seeds sown in 2005, three patterns could be distinguished (Table 2, Figs. 3–6). The pattern of *Erisimum wittmannii* (Figs. 3, 6) was represented by 5 taxa whose diaspores germinate very fast, reaching in a very short time the maximum values of their

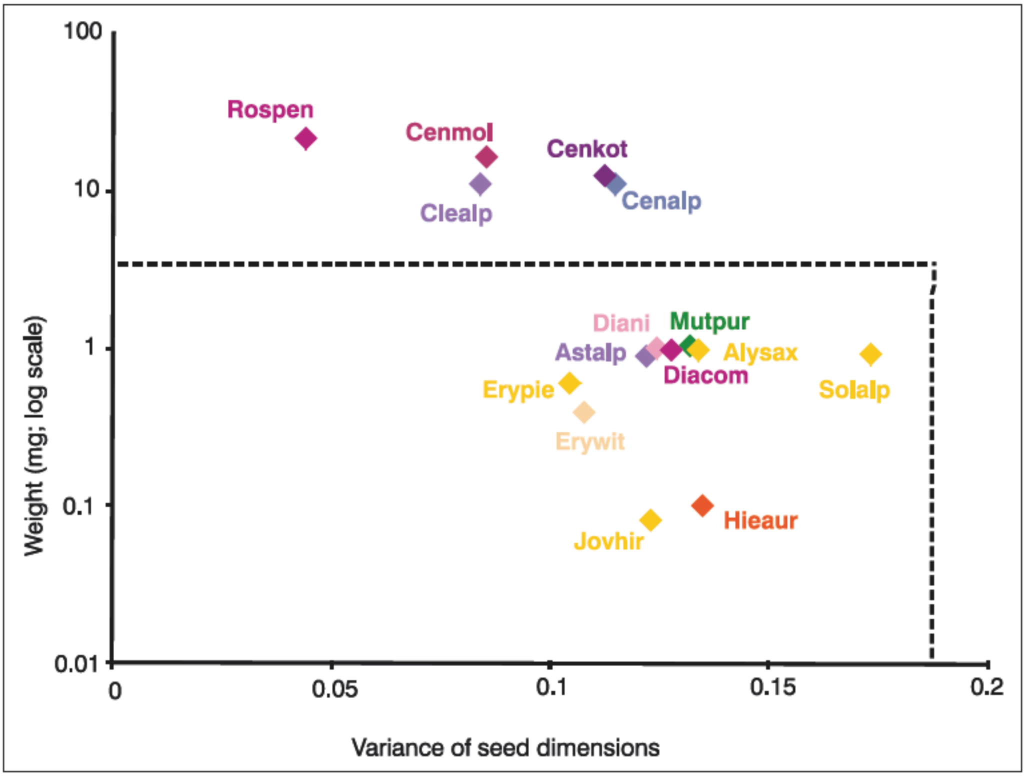

Fig. 1. Relationship between seed weight and variance of seed dimensions in 15 mountain species. The dashed line encloses the region within which all propagules examined are long lived. Shorts as in Table 1.

Ryc. 1. Zależność między ciężarem a wymiarami nasion u 15 gatunków górskich. Linia przerywana wskazuje obszar, w obrębie którego wszystkie badane propagule mają długą żywotność. Skróty jak w Tabeli 1.

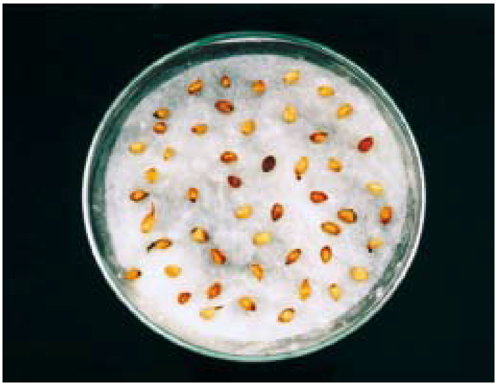

Fig. 2. Seeds of *Rosa pendulina* L. (Photo M. Władyka)
Ryc. 2. Nasiona *Rosa pendulina* L.

Fig. 5. Germinated seeds of *Hieracium aurantiacum* L. (Photo M. Władyka)
Ryc. 5. Kiełkujące nasiona *Hieracium aurantiacum* L.

Fig. 3. Germinated seeds of *Erysimum wittmannii* Zaw. (Photo M. Władyka)
Ryc. 3. Kiełkujące nasiona *Erysimum wittmannii* Zaw.

Fig. 4. Germinated seeds of *Aster alpinus* L. (Photo M. Władyka)
Ryc. 4. Kiełkujące nasiona *Aster alpinus* L.

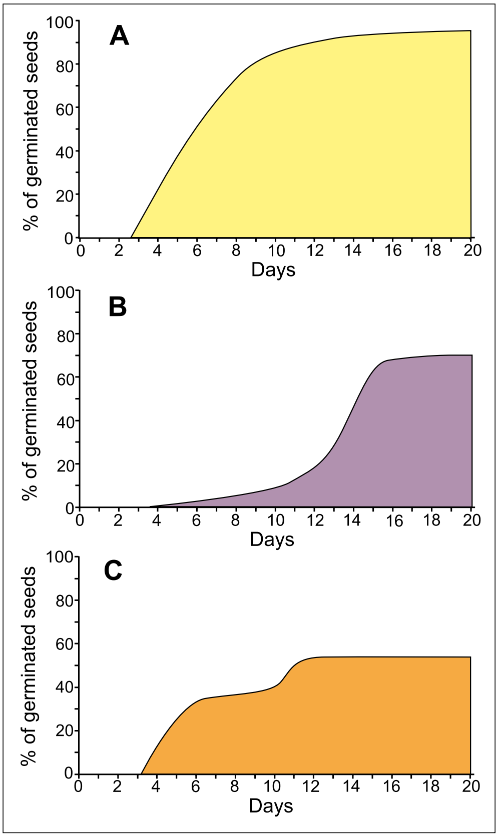

Fig. 6. Seed germination patterns: A – pattern of *Erysimum wittmannii*; B – pattern of *Aster alpinus*; C – pattern of *Hieracium aurantiacum*.
Ryc. 6. Wzorce kiełkowania nasion: A – wzorzec *Erysimum wittmannii*; B – wzorzec *Aster alpinus*; C – wzorzec *Hieracium aurantiacum*.

germination strength (up to 100%), and whose mean germination time ranges from 6.6 to 7.9 days. The pattern of *Aster alpinus* (Figs. 4, 6) included 5 species, too, whose number of germinating seeds is small in the initial stage of germination but increases gradually. The germination strength of these seeds ranges from 68 to 72%, and their mean germination time is 8.4 to 12.3 days. Finally, the pattern of *Hieracium aurantiacum* (Figs. 5,6) is represented by 3 taxa whose germination curve is of fluctuating character. This group is most diverse both as far as the germination strength is concerned (18–40%), and in respect to its mean germination time (5.8–13.7 days).

After a year of storing, the analysed seeds did not lose their germination abilities, and in the case of *Erysimum wittmannii* and *E. pieninicum* the values of their germination strength remained at practically the same level (Table 2). 6 taxa exhibited the lowering of the values of the germination strength (*Aster alpinus, Centaurea mollis, C. alpestris, Solidago alpestris, Mutellina purpurea* and *Alyssum saxatile*), in some cases as serious as 50%. In contrast, in the case of the species *Hieracium aurantiacum, Centaurea kotschyana, Jovibarba hirta* subsp. *glabrescens, Dianthus compactus* and *D. nitidus*, the germination strength increased by over 30% (Table 2).

DISCUSSION

The observation that small and smooth seeds of spherical shape are more capable of forming persistent seed banks than the big, long or flat ones (Thompson et al. 1993) was confirmed by the results of ecological studies carried out on the flora of Europe and Argentina (Bekker et al. 1998; Funes et al. 1999; Cerabolini 2003; Peco et al. 2003). The lack of correspondence between seed shape and seed mass, observed in the vegetation of Australia (Leishman, Westoby 1998) may indicate that this particular method is not universally valid for all plants. However, we have to bear in mind that the

Table 2. Seed germination patterns for some mountain species
Tabela 2. Wzorce kiełkowania nasion u wybranych gatunków górskich

Pattern of	Species	New seeds		One year seeds	
		Germination (%)	T_G	Germination (%)	T_G
A *Erysimum wittmannii*	*Erysimum wittmannii*	92	7.1	90	5.8
	Erysimum pieninicum	100	6.9	98	3.6
	Centaurea kotschyana	88	7.3	100	7.6
	Alyssum saxatile	88	7.9	66	7.9
	Centaurea alpestris	68	6.6	16	7.3
B *Aster alpinus*	*Aster alpinus*	72	9.6	34	8,7
	Centaurea mollis	67	11.3	12	5.6
	Solidago alpestris	76	9.4	36	6.6
	Mutellina purpurea	68	12.3	45	10.0
	Dianthus nitidus	68	8.4	84	5.4
C *Hieracium aurantiacum*	*Hieracium aurantiacum*	40	7.8	58	8.2
	Jovibarba hirta subsp. *glabrescens*	30	5.8	62	10.8
	Dianthus compactus	18	13.7	88	10.2

T_G – mean time of germination in days calculated according to Lityński (1977)
T_G – średni czas kiełkowania w dniach obliczony według Lityński (1977)

studies of Thompson et al. (1993) included herbaceous species only, while Leishman and Westoby (1998) analysed tree and shrub species as well. Most probably, the production of big propagules forming persistent seed banks can be connected with frequent fires and extremely dry climate of Australia (Funes et al. 1999).

Smaller seeds easily penetrate into the soil, and thus 'escape' from early germination; moreover, they are better protected against harmful environmental factors and seed predators. Plants producing big seeds, which after seed dispersal are exposed to devouring by animals, practically do not form seed banks (Jankowska-Błaszczuk 1996; Fenner, Thompson 2005). According to Peco et al. (2003), seed shape is not as decisive for the formation of a persistent seed bank as seed size, because a long and flat shape can be a smaller obstacle to the penetration into the soil for small seeds than for the bigger and longer ones. Among the analysed species of mountain plants, the first group includes, among others, the seeds of *Erisimum wittmannii, Aster alpinus, Hieracium aurantiacum, Jovibarba hirta* subsp. *glabrescens, E. pieninicum, Dianthus compactus, D. nitidus,* and *Alyssum saxatile*, which were classified as persistent. The other group is represented by *Centaurea mollis, C. kotschyana* and *C. alpestris* whose seeds have a lot of store substances and a soft cover, attractive for predators, and thus classified as transient. Cerabolini et al. (2003) point out that a more frequent longevity of small seeds may result from the fact that seed size is inversely proportional to the number of seeds produced by the plant. Thus, it is more possible to detect in the seed bank small propagules than the bigger ones, even if the probability of their penetration into the soil is the same.

The seeds of *Rosa pendulina* (a shrub) and *Clematis alpina* (a creeper) were classified as transient, after Thompson et al. (1993). However, in contrast to the former ones, only the propagules of *Clematis alpina* (stratified on a creeper) germinated after a month, reaching the germination strength of 6%. The reasons for this phenomenon might lie in the extremely hard seed shell which prevents water access and gas exchange.

The ability of seeds to preserve their life force is conditioned by the kind of dormancy they adopt. The latter, in turn, might have an endogenic basis: retardation of embryo development (morphological rest), the presence of airproof and waterproof seed shells (physical rest), as was the case of *Clematis alpina* or *Rosa pendulina*, or the presence of germination inhibitors (physiological rest). In the case of exogenic dormancy we deal with different factors, such as low substratum moisture, inadequate temperature or too high mineral salt content. An adequate amount of water in the seed is essential for the breaking of the spell of rest (Potapczyk 1971; Falińska 2004). A variety of soil surfaces may influence the chance of a seed finding suitable cracks or germination places, so-called 'safe sites' which increase the seed's contact with soil surface and thus enable it to absorb water indispensable for germination (Harper et al. 1965; Harper, Benton 1966; Jankowska-Błaszczuk 1996; Fenner, Thompson 2006). Germination ability of seeds is additionally influenced by the depth of their location in soil. The seeds located deeper have smaller chances of germinating than those lying on the surface or positioned in surface layers (Symonides 1978; Fenner, Thompson 2006). It is a result of the lack of basic germinating factors: adequate temperature, moisture and light, as well as an effect of the loss of nutritive substances by a seedling while attempting to rise to the soil surface (Czerwiński 1978; Grzesiuk, Kula 1981; Czarnecka 1998; Fenner, Thompson 2006).

Seed dispersal mode is also important for the longevity of seeds and their ability to form persistent seed banks. Small seeds transported by wind and animals with the help of dispersal structures (hairs and little hooks enabling them to find cracks and hollows in soil surface) tend to be long-lived and are more frequently met in soil seed banks, while barochores are extremely rare there (Grime et al. 1981; Jankowska-Błaszczuk 1996; Falińska 2004; Fenner, Thompson 2006). Most of the observed seeds of mountain plants are capable of the so-called 'escape in space', chiefly manifested by their adaptation to the spreading over large distances and their ability to germinate quickly as soon as favourable conditions are met. Fast speed of germination can be observed in the case of herbaceous species, mainly annual, while low speed is characteristic of most shrubs and trees. Germination speed tends to decrease together with the increase of seed mass (Harper et al. 1965; Grime et al. 1981; Fenner, Thompson 2006). Mountain vegetation has developed numerous adaptive strategies in order to produce propagules in unfavourable conditions. Among them is the production of a great number of small seeds which increases the chance of finding favourable conditions for germinating or forming a persistent seed bank.

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