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Seed distribution drivers at an early stage of vegetation development in a sand quarry

Distribution of viable seeds on the bare ground slope in a sand quarry located in the vicinity of Saint-Petersburg was studied in relation to the relief of the ground surface, species composition of pioneer communities and surrounding vegetation, as well as the timing of a growing season. Seeds were found even on bare ground and poorly vegetated sites. Ground contains three times more seeds in autumn than in early summer. Most of seeds belonged to perennial grasses (mainly anemochorous, apophytes, and weeds), with a few coming from other life-forms (from annuals to trees), which were spread in the quarry or in the surrounding vegetation. Seeds concentrated on the slope, their number was the lowest in the quarry bottom in both observation periods, since conditions favored to plant germination there. The microrelief of the ground surface can also influence seed distribution: in June, viable seeds mostly located in depressions. We suppose that in dissemination period, seeds of anemochorous plants concentrate on hillocks which trap them; however, more data is needed to conclusively prove this hypothesis.

The paper contains 3 Tables, 3 Figures and 49 References.

Keywords: *seed bank; natural recovery; pioneer vegetation; viable seeds; seasonal dynamics; relief; safe sites.*

Introduction

Seed bank, consisting of all viable seeds present in soil [1, 2] is not only a "common characteristic of many plant species, which allow storage of genetic diversity" [3:29] or "plant regeneration strategy, buffering environmental variation to allow species persistence" [4:201], but also one of the mechanisms of plant communities' self-regulation [5] and the source of their hidden biodiversity.

Seed banks have been studied extensively since the 19-th century (the first publication in 1825 belongs to Dureau de la Malle [6]), and the obtained results showed that the role of the below-ground plant community is much more significant than just the above-ground part we observe. Most research focused on comparison of plant community and seed bank species composition or assessment of its quantifying changes, but "the processes that govern assembly of the soil seed bank following severe habitat disturbance are poorly understood" [7:58]. Little is known about details of seed bank formation process during the early plant community development. E. Chaideftou and co-authors [8] noted that especially little is known about the seed bank inter-annual temporal turnover, and they studied the seed bank composition in permanent plots from year to year. However, the seed bank dynamics during a single year period also has evident ecological importance and must be investigated.

Nowadays, large areas of land are impacted by mechanical disturbances, which destroy their soil and vegetation covers completely. The natural recovery of these bare grounds and the set of colonist-species depend on local flora resources [9-12]. Most of pioneer species are anemochorous [13], so the seed bank should form via "seed rain". Seeds inflow and outflow from the soil bank (via germination, death, water erosion, etc.) happen constantly, so the seed bank is a very dynamic unit.

The species diversity of pioneer communities does not only depend on the success of seed distribution, but also on plant germination, growth, and endurance [14]. The reserve of propagules is always more than the number of seedlings and thriving plants, and the quality of substrate plays an important role in the safety of pioneer species [15]. For example, the high ground density causes a reduction in germination [16] or lack of moisture leads to the death of seedlings [17]. It is well known that natural vegetation recovery is strongly influenced by substrate properties [18, 19]. Open grounds of disturbed sites are unfavorable to plant sprouts because of intensive insolation, extreme fluctuations of soil temperatures, rapid drying of substrate surface, etc. [20]. Plant individuals distribution depends on micro-topography of the ground surface [21, 22], even small depressions contributing to seed accumulation [23, 24]. Seeds gathering in depressions keep their viability better [25], thanks to accumulation of fine material and snow, leading to better moistening. The speed of colonization and pioneer species richness depend on proportion of fine (clay) fractions in the substrate [12, 26-28], due to the fact that the high content of these fractions increases water holding capacity of soil [23]. At the initial stage of primary succession, moistening plays an extremely important role, since plants suffer from nutrient deficit [26, 29], so the colonization process always depends on ground moisture [30, 31].

The territory disturbed by bulldozing or other techniques is often a patchwork of microhabitats (or "microsites"), which differ sharply in their properties (temperature, moisture, nutrients, etc.), including their suitability for settlement, survival, and growth of plants [1, 32]. The favorable microhabitats are referred to as "safe sites" [1]. Natural vegetation recovery is controlled by various abiotic factors, which can be unfavorable to plants (dryness, high temperature of ground surface, excessive solar lighting, strong wind, etc.), and as a result, species are able to survive within safe sites only [24].

The trend of regenerative succession depends on habitat local conditions, according to one point of view [18, 29, 33], or on plant diasporas' distribution at the beginning of colonization, according to another [15, 34]. One of the interpretations of the Egler's Initial Floristic Composition model [35] suggests that seeds from all seral stages are present in the initial vegetation [36], but another scenario (gradual seed bank formation) is possible, as well.

The aim of our research is to receive data on seed distribution on the disturbed territory under influence of the surface relief, the season of the vegetation period and plant cover species composition. The study used the example of a sand quarry, because such quarries are widespread in different regions, which gives an opportunity to compare the obtained results in the future.

Materials and methods

The study was carried out in 2014, in the vicinity of Saint-Petersburg, Russia (southern taiga subzone; 60°05'30"N, 30°26'52"E). A small sand quarry (about 7500 m²) was located on a hill, previously occupied by a grass birch forest. The top of the hill and its eastern slope were completely destroyed by quarrying. In spite of sand extraction ceasing in 2006, even 8 years later there were sites of open ground within the quarry. In 2015, sand extraction was restarted, and we had no possibility to continue our study, so all obtained results were collected during one year.

The data were collected on a sandy slope (eastern exposition, approximately 30-35°, the length about 25 m) covered by patchy vegetation, so the total plant cover varied from 0 to 20% in different places. Adjacent vegetation consisted of a fragment of the birch forest, meadows with grasses and weeds, and communities dominated by *Chamaenerion angustifolium* (L.) Scop. or *Calamagrostis epigeios* (L.) Roth, occurring in spots at the quarry bottom.

We address the following questions: (1) Is the seed bank (consisting of viable seeds) present at disturbed sites with bare ground and poorly developed pioneer vegetation? (2) What is the difference between the seed bank composition in the beginning and the end of a growing season? (3) How is the seed bank composition influenced by the relief of the ground surface and the surrounding vegetation?

Ground samples were taken by core with cross section of 4×4 cm, immersed to the depth of 5 cm [37], their number was determined in accordance with the published recommendations [38] (See below). The samples were placed in craft-paper bags and kept in a dark dry place. The plan of data collection allowed us to assess such factors affecting the seed bank as:

Timing of the growing season. To reveal the dynamics of seeds in the ground, we collected data when most of viable seeds germinated at the end of June (28.06.2014), and at the end of the growing season (7.09.2014), when most of new seeds had already matured.

Location. Ground samples were collected from 4 positions in the relief: top of the slope, its middle and foot, and the bottom of the quarry (Fig. 1).

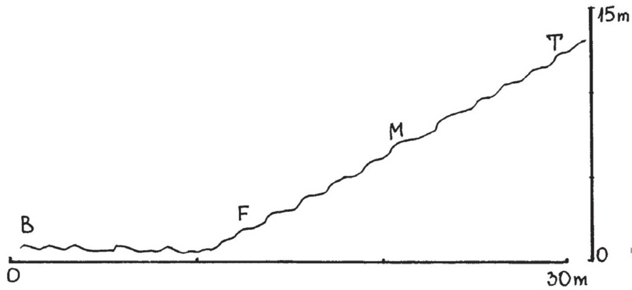

Fig. 1. Sampling scheme: 4 positions in the relief of the quarry: top of the slope (T), its middle (M) and foot (F), and the bottom of the quarry (B). At each position, 3 depressions and 3 hillocks were sampled

Microrelief of ground surface. The surface of sand was not smooth, various hillocks, small ridges as well as dimples and grooves formed an irregular microrelief. Vertical and horizontal sizes of these elements varied from 10 to 40 cm. In each of the aforementioned positions on the slope and quarry bottom, samples were collected from 3 elevated elements of the microrelief (named as "hillocks") and 3 from lower ones ("depressions"). Thus, 24 samples were studied in each from two observation periods. Therefore, the total number of samples was 48.

Vegetation of the slope. Each ground sample was collected inside of 30×30 cm plot, after all plant species were recorded. On 24 plots in June and another 24 plots in September, the total list of species, total plant cover and each species percentage cover estimations were made. As it was mentioned above, study plots were established in correlation with elements of the microrelief, and one of each three plots situated on hillocks or depressions was always located on a bare substrate.

Surrounding vegetation. The total list of species in the surrounding plant communities was made in 2014, also we used the floristic data collected in 2012-2013. Botanical nomenclature for plants is given by SK Cherepanov [39].

The protocol of sample treatment was established on the basis of the published recommendations [40, 41], and the results of our preliminary experimental selection of optimal methods for seed detection and their viability assessment. Each soil sample was stirred diligently and divided into 2 parts. Later, all manipulations were made sequentially with both of them. The ground was sifted through a sieve with a cell diameter of 1mm, and the material remaining in the sieve was examined to find seeds. The sifted ground was split into 2 parts again, and each half was exposed to flotation. Detected seeds were dried at room temperature. A special standard seed collection along with special guides and an atlas [42, 43] to determine the species affiliation of seeds were used.

Without conditions favorable to germination, "dormant" seeds may stay in soil keeping viability for a very long time [3]. Various special manipulations, such as stratification, phytohormones, etc. are applied to force seeds to sprout, but even in this case, we cannot be sure that all viable seeds have germinated and are accounted for. For this reasons, to assess seed viability we used the staining by 0.1% water solution of fuchsine [44]. Seeds were exposed to fuchsine for 1 hour. Viable seeds had uncolored germ and embryo roots or faintly painted spots on roots and cotyledons. Seeds with good colored germ or bright large spots on roots and cotyledons were unviable.

Statistical data processing was carried out by StatSoft STATISTICA 10. Distribution of viable seeds in the relief of the quarry was tested by the Kolmogorov-Smirnov criterion and analyzed using non-parametric tests. So, the Kruskal-Wallis Criterion is used for identification of differences between compared groups of data. Also, we used the Mann-Whitney test (U-test) allowing us to evaluate the performance differences between comparing groups in pairs for a more precise description of the observed trends. We adopted a significance level of $p < 0.05$.

Results of research

Vegetation in the quarry and its neighborhoods

Natural recovery in the quarry developed during 8 years. The densest vegetation occupied the bottom of the quarry, in the other part of disturbed territory plant cover was patchy and absent in some places. The list of vascular plants recorded in quarry in 2012-2014 includes 55 species: trees (*Betula pendula* Roth*, Alnus incana* (L.) Moench, *Populus tremula* L., *Pinus sylvestris* L., *Sorbus aucuparia* L.), shrub (*Salix cinerea* L.), and herbs; dwarf shrubs were absent. Trees were represented by seedlings or young growth.

In the surrounding communities with predominance of *Chamaenerion angustifolium* or *Calamagrostis epigeios*, 16 species of herbs were marked, and only two (*Erigeron acris* L.*, Campanula rotundifolia* L.) supplemented the list obtained in the quarry. Obviously, the fragment of former birch forest differed highly from other communities in species composition, and 5 species more were added to the overall list: *Rubus idaeus* L.*, Arctostaphylos uva-ursi* (L.) Spreng., *Convallaria majalis* L.*, Hypericum maculatum* Crantz, and *Pimpinella saxifraga* L. Thus, in total, 62 species were noted in the quarry and the surrounding vegetation.

Total number of seeds

The total number of seeds collected in 24 samples in September was nearly double the number in June: 513 and 275 seeds, respectively. The percentage of viable seeds became higher by autumn, as well. In the beginning of September, the number of viable seeds revealed in the collected samples increased more than threefold: from 94 to 343. The number of dead seeds was almost unchanged (in June - 181, in September - 170).

Number of species

In relevés of 48 study plots, 20 species of vascular plants were noted. Seeds from 18 of them were found in soil samples. Moreover, 3 species were present as seeds only. Thus, the total number of species present on study plots as either plants or seeds was 23 or 37% of total number of species registered in the quarry and the surrounding vegetation (Table 1). The majority of seeds (including viable and unviable) belonged to perennial grasses, but other life-forms, such as trees (*Betula pendula, Sorbus aucuparia*), dwarf-shrubs (*Arctostaphylos uva-ursi*), and short-lived (annuals and biennials) herbs (*Berteroa incana* (L.) DC., *Veronica verna* L. et al.) were present as well.

Table 1

Frequency of plants and/or seeds (viable and unviable) on study plots, %

No	Species	June (24 plots)		September (24 plots)	
		plants	seeds	plants	seeds
1	*Artemisia campestris*	63	25	29	21
2	*Calamagrostis epigeois*	46	17	42	54
3	*Festuca rubra*	17	58*	33	50
4	*Rumex acetosella*	21	38	17	17
5	*Hieracium pilosella*	13	17	21	8
6	*Betula pendula*	4	75	4	83
7	*Berteroa incana*	4	42*	0	33*
8	*Chamaenerion angustifolium*	8	17*	0	13
9	*Tussilago farfara*	17	0	13	4*
10	*Achillea millefolium*	13	0	8	8
11	*Cirsium arvense*	0	17	8	13
12	*Erigeron acris*	4	0	17	25
13	*Artemisia vulgaris*	4	0	13	0
14	*Linaria vulgaris*	17	0	0	0
15	*Veronica verna*	4	0	0	8
Noted on 1 plot					
16	*Sorbus aucuparia*	4	4	0	0
17	*Hippophaë rhamnoides*	4	0	0	0
18	*Knautia arvensis*	4	0	0	0
19	*Taraxacum officinale*	4	0	0	4
20	*Arctostaphylos uva-ursi*	0	4	0	0
21	*Convallaria majalis*	0	0	0	4
22	*Phleum pratense*	0	0	0	4
23	*Agrostis tenuis*	0	0	4	0
	Total number of species	20		18	
	Seeds and plants	9		10	
	Plants only	9	-	2	-
	Seeds only	-	2	-	6

Note: * Only unviable seeds were found.

Vegetation on study plots

On 32 plots where vascular plants were noted (unlike other 16 plots located on bare sand), the total plant cover varied from 5 to 20% in June, and from 1 to 10% in September. *Artemisia campestris* L., *Calamagrostis epigeois, Festuca rubra* L., *Rumex acetosella* L., and *Hieracium pilosella* L. were the most frequent in plots, but only two of them (field sagewort and chee reedgrass) were the most widespread all over the slope. Other plants distribution can be described as irregular mosaic. There were no real dominants between species. The maximal abundance (10%) was registered very rarely and for plants with large leaves or rosettes.

There was no distinction in species composition between two elements of the microrelief. No species was exclusive to only hillocks or depressions. On hillocks the number of species per plot (excluding plots on bare ground) varied from 1-2 to 5 in both observation periods. In depressions, this parameter changed from 2-6 species in June to 3-4 species in September. The mode is equal for hillocks and depressions: 4 species in June, and 3 in September. The average number of species (3.5) was identical for different elements of the microrelief and months. The average total cover on plots on both hillocks and depressions was 12-13% in June and 7-8% in September.

Plant and seed composition on study plots

Five aforementioned species had the highest frequency in above-ground vegetation, and their seeds were frequently found in soil samples as well, but the maximum frequency (about 80%) was noted in seeds of *Betula pendula*, despite the fact that the young growth of birch was only observed on 2 of 48 plots. The plants of *Berteroa incana* were registered on 1 plot in June, and their unviable seeds were contained in 30-40% of samples in both observation periods. Viable seed absence of short-lived weeds (from Brassicaceae and Chenopodiacea, for example) is caused by 8 years of vegetation development: in 2014, pioneer species were rare in the quarry unlike grass communities belonging to the next stage of succession.

Seeds of 5 species (*Artemisia vulgaris* L., *Linaria vulgaris* Mill., *Hippophaë rhamnoides* L., *Knautia arvensis* (L.) J.M. Coult., *Agrostis tenuis* Sibth.) which had been noted in relevés were not found in soil samples. 3 species (*Phleum pratense* L., *Convallaria majalis, Arctostaphylos uva-ursi*) were present only as a single seed, and their plants were very rare in the quarry outside the plots. It should be emphasized that *Convallaria majalis* and *Arctostaphylos uva-ursi* are typical species of forest communities, and *Phleum pratense* is one of a few grass species (Poaceae), which are not pioneer plants on disturbed lands.

About a half of all species noted in relevés was found as seeds in ground samples in both observation periods. In June, seeds of 9 species were absent, and 2 species were present only as seeds. In September, the situation reversed (Table 1).

The simultaneous presence of plants and seeds on the same plot was revealed for *Calamagrostis epigeios* and *Festuca rubra* (in both observation periods), and *Erigeron acris* (in September). The number of such plots was low and varied from 2 to 6 for the mentioned species.

Even on bare ground plots, the seeds of 2-4 species were present, and only twice on 1 plot in June, and on 1 plot in September none was found, and the both of the empty plots were located at the bottom of the quarry.

Viable seeds

In September, the total number of seeds increased, together with the number of viable ones, and practically all species had a relatively larger proportion of viable seeds than in June (Table 2).

Table 2

Proportion of viable seeds of different species in soil samples, %

No	Species	June (24 samples)	September (24 samples)
1	*Betula pendula*	47	65
2	*Festuca rubra*	0	77
3	*Artemisia campestris*	43	60
4	*Rumex acetosella*	82	100
5	*Calamagrostis epigeios*	0	72
6	*Hieracium pilosella*	13	67
7	*Chamaenerion angustifolium*	0	100
8	*Cirsium arvense*	(100)	(100)
9	*Arctostaphylos uva-ursi*	(100)	0
10	*Sorbus aucuparia*	(100)	0
11	*Erigeron acris*	0	80
12	*Veronica verna*	0	100
13	*Phleum pratense*	0	(100)
14	*Achillea millefolium*	0	100
15	*Taraxacum officinale*	0	(100)
16	*Convallaria majalis*	0	(100)

Note: Data are shown in parentheses, if the number of seeds per 1 sample is less than 4.

Only 16 out of 23 species noted on study plots contributed viable seeds to the seed bank. *Arctostaphylos uva-ursi, Convallaria majalis, Sorbus aucuparia* were represented by a single seed only, and *Phleum pratense* by 4 seeds. Such weeds as *Taraxacum officinale* F.H. Wigg. and *Cirsium arvense* (L.) Scop. also had a very low number (1-4) of viable seeds in the soil bank due to their high germination capacity. No viable seed of *Berteroa incana* and *Tussilago farfara* L. was found. The first species is a pioneer annual plant, which was in the quarry in 2012, but it became very rare in 2014: we marked unique specimen on 1 plot in June. The second one mainly follows the vegetative form of reproduction, and its seeds stay viable for less than one year [45, 46]. Thus, the core of the seed bank consists of seeds of 10 species (Table 2).

The viable seeds of many species (*Festuca rubra, Calamagrostis epigeios, Chamaenerion angustifolium, Erigeron acris* et al.) were noted in autumn, only. We can assume that all viable seeds of these species germinated in June. The main stock of seeds was formed by *Betula pendula*, *Calamagrostis epigeios*, *Artemisia campestris*, *Festuca rubra*, *Rumex acetosella*, which are typical colonizers of disturbed lands. In the seed bank, the proportion of viable seeds of the aforementioned plants reached 93% in June and 86% in September. These high values were determined by a large number of birch seeds (62 and 65% of the seed bank, respectively). Adjusting for 30×30 cm plot size, the maximal number of viable seeds of *Betula pendula* was more than 500 in June and about 3500 in September.

Viable seeds distribution in the relief

Viable seeds of *Betula pendula* and *Festuca rubra* were widespread along the slope and at the bottom of the quarry (Table 3). Seeds of 4 species (*Artemisia campestris, Calamagrostis epigeios, Cirsium arvense, Rumex acetosella*) were noted in 3 out of 4 positions in the relief, and most of them had a high frequency in the vegetation of the study plots. Viable seeds of other species demonstrated more a narrow distribution in 1-2 positions.

Table 3

Seed bank (viable seeds) distribution in connection with the position in the relief

No	Species	Bottom of quarry		Foot of slope		Middle part of slope		Top of slope	
		June	September	June	September	June	September	June	September
1	*Betula pendula*	225	394	1350	1406	900	5794	788	4894
2	*Festuca rubra*	0	113	0	281	0	338	0	1350
3	*Artemisia campestris*	113	225	0	225	731	225	0	0
4	*Rumex acetosella*	0	0	338	56	225	0	225	281
5	*Cirsium arvense*	0	0	113	56	0	169	113	0
6	*Calamagrostis epigeios*	0	113	0	0	0	675	0	225
7	*Chamaenerion angustifolium*	0	0	0	0	0	56	0	281
8	*Erigeron acris*	0	0	0	0	0	731	0	169
9	*Veronica verna*	0	0	0	0	0	113	0	169
10	*Achillea millefolium*	0	0	0	0	0	506	0	0
11	*Taraxacum campylodes*	0	0	0	0	0	56	0	0
12	*Convallaria majalis*	0	0	0	0	0	56	0	0
13	*Hieracium pilosella*	0	0	0	0	0	0	56	113
14	*Arctostaphylos uva-ursi*	0	0	0	0	0	0	56	0
15	*Sorbus aucuparia*	0	0	0	0	0	0	56	0
16	*Phleum pratense*	0	225	0	0	0	0	0	0
Total number of seeds		338	1 070	1 801	2 024	1 856	8 719	1 294	7 482
Number of species		2	5	3	5	3	11	6	8

Note: Number of seeds is given as recalculation on 30×30cm plots.

Full data from collected samples on the distribution of seeds according to locations in the relief and microrelief are shown in Figure 2.

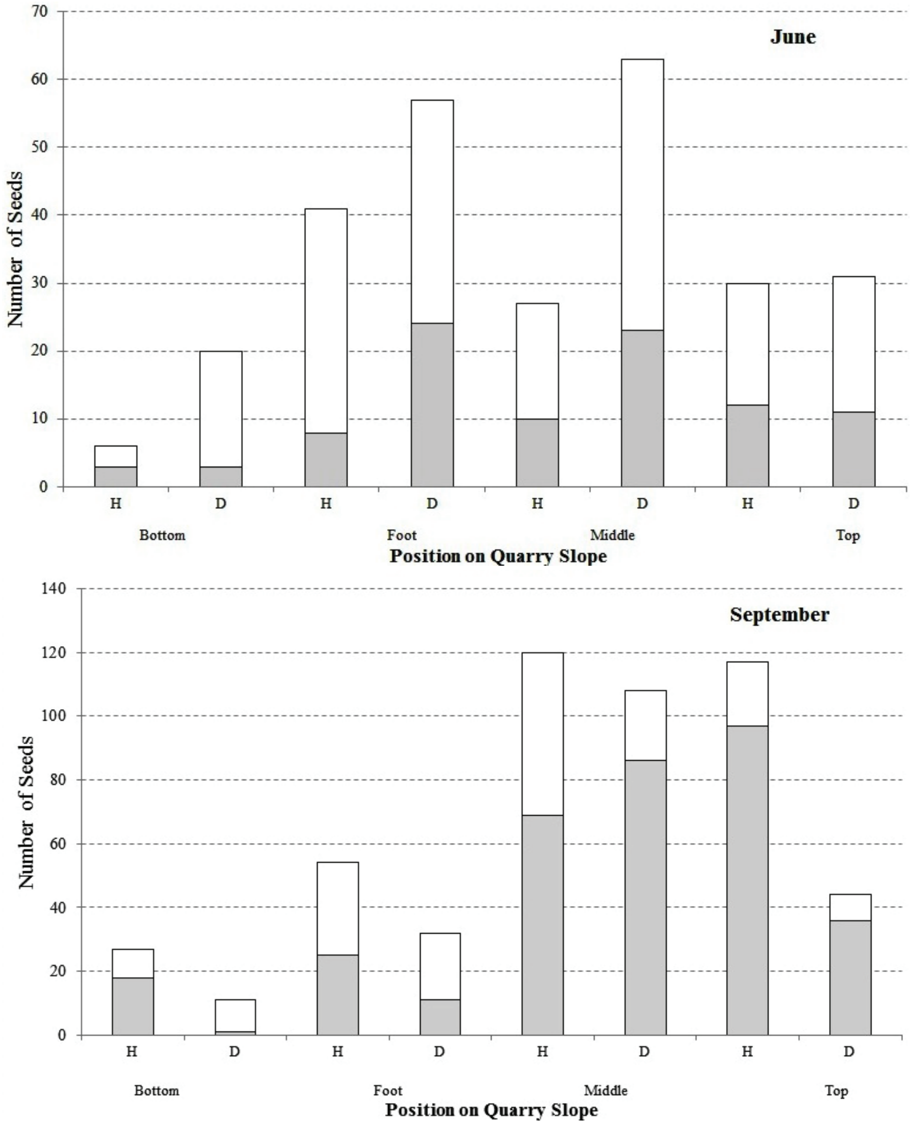

Fig. 2. Seasonal distribution of viable and unviable seeds between elements of the microrelief across the slope profile. Bar heights are numbers of seeds; grey parts of bars are numbers of viable seeds. H - Hillocks, D - Depressions

In general, the position factor has an impact on the distribution of viable seeds (Kruskal-Wallis test: $p = 0.0405$). The number of seeds at the quarry bottom was the lowest in both observation periods. However, statistically significant differences between the bottom and other slope positions are revealed in the pairwise comparison by means of the Mann-Whitney test and only in June ($p_{bottom/foot} = 0.0259$; $p_{bottom/middle} = 0.0283$; $p_{bottom/top} = 0.0393$). In

September, there were no differences (p = 0.1127) in the distribution of seeds on the relief because the number of seeds in samples varied greatly (Fig. 3).

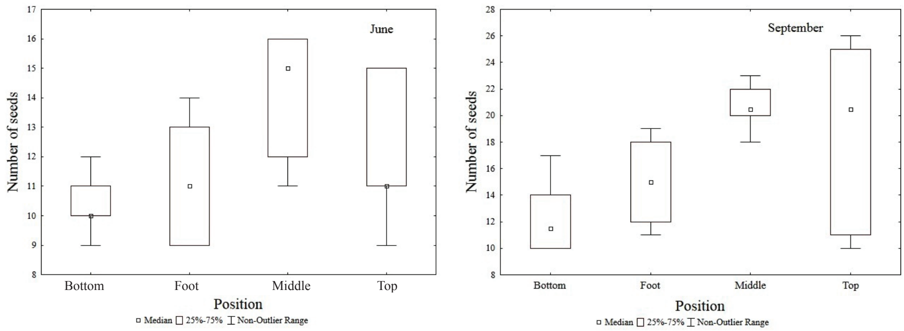

Fig. 3. Viable seeds distribution on slope and quarry bottom in two observation periods. The first and third quartiles (25th and 75th percentiles, respectively), the median (50th percentile) and the edges of the statistically significant sample are shown in the Box Plot

Influence of the microrelief

Analysis of the data by distribution of viable seeds on the microrelief showed that the difference between hillocks and depressions is significant in June, only (U-test p = 0.0278). The samples collected in September revealed no influence of the microrelief.

Discussion of research

23 species of vascular plants were recorded on study plots, and only 10 of them (*Betula pendula, Festuca rubra, Artemisia campestris, Rumex acetosella, Calamagrostis epigeios, Hieracium pilosella, Chamaenerion angustifolium, Erigeron acris, Veronica verna,* and *Achillea millefolium* L.) had viable seeds in soil. Among these vasculars forming the seed bank there were 1 deciduous tree and 2 annual-biennial species, but most of them were perennial herbs, which are mostly typical colonizers of open ground, sandy dunes and other habitats with infertile soil. Many of them are considered weeds, and they have biological traits (large number of seeds, light seeds, early germination etc.) that facilitate rapid colonization and survival in such habitats.

The absence of viable seeds of the annual weed *Berteroa incana* in soil is an example of started changes in the seed bank composition - a decrease in the number of therophytes - observed in plant communities following restoration [47, 48]. The presence of species belonging to different life-forms in the seed bank lend credibility to the suggestion that the Egler's Initial Floristic Composition model [36] works.

Among 10 aforementioned species contributing to the seed bank on study plots, only 5 species are in the majority, with *Betula pendula* being the most prominent. The influence of vegetation surrounding the quarry also appeared as the seed bank enrichment by seeds of some species (forest plants *Convallaria majalis* and *Arctostaphylos uva-ursi*, for example). Even the low number of such seeds can be effective if their inflow to quarry is annual.

The conclusion of M. Kalin with coauthors [49] that compositional similarity and spatial matching between the seed bank and the standing vegetation is not high was confirmed by our data. The presence of any species in the above-ground plant community was not directly connected to its stock in the seed bank. 4 species (*Artemisia campestris*, *Calamagrostis epigeios*, *Festuca rubra*, and *Rumex acetosella*) had relatively high abundance on study plots, but the overwhelming majority of the seed bank (more than 60%) belonged to *Betula pendula*, whose young growths were observed on 2 plots out of 48.

The fact that the majority of the seed bank is formed by birch, despite this species being present in the quarry only in unfruitful young growth birches, can be an indirect confirmation of the Egler's Initial Floristic Composition model.

The seed bank is influenced by many stochastic processes, habitat configuration, land use etc. [7]. The relief of the quarry influences seed distribution. In September, the greatest number of viable seeds was found on the top and in the middle part of the slope. It is easy to explain, because during the dissemination period, seeds of anemochorous plants land at first on the elevated terrain. Later, they can move gradually down the slope under the influence of rain, wind, crumbling sand, and snow. *A priori* assumption that seeds will always concentrate in the lowest part of the quarry was not confirmed: the minimum number of seeds was marked at the bottom of the quarry in both observation periods. There are the most favorable conditions for plants in this lowest part of the quarry [12, 25], therefore seed germination is very active there.

Different factors (rain, wind, erosion etc.) cause seed redistribution and change viable seed pattern, which has no direct reflection in the above-ground vegetation. The influence of the microrelief was statistically significant in one of two observation periods.

The suggestion that in September seeds of anemochorous species primarily filled the hillocks and afterwards moved to depressions seems most likely, and we hypothesize that in dissemination period, seeds of anemochorous plants concentrate not at "safe sites" (depressions), but on hillocks which trap them. In the future, more data collection would be necessary to prove this hypothesis with a statistically significant result. In June, the seed bank was significantly more present in depressions.

The obtained data do not completely confirm the idea that species can survive only within "safe sites" [1, 24]. Although in June, viable seeds concentrate in depressions, we observed neither germination as active as that at the bottom of the quarry, nor a difference between poor vegetation in either element of the microrelief.

Conclusion

Our results suggest that in the sand quarry the seed bank as a pool of viable seeds exists even at sites with bare ground or less developed plant cover. The bank includes seeds of species, which are spread in the quarry and the surrounding vegetation, and consists of seeds belonging to plants of different life-forms. The seed bank has temporal and spatial dynamics during a single year period. The number of seeds varied greatly in the beginning and the end of summer. The seed bank also changed in terms of its species diversity during the growing season. It also demonstrated heterogeneity in seed distribution with regards to the quarry relief and microrelief. A "paradoxical" result is that at the bottom of the quarry the number of viable seeds is always minimal (because of favorable conditions for germination there). Our results do not contradict the Egler's Initial Floristic Composition model, but do not support the hypothesis of plants survival at "safe sites".

The seed bank comprising viable seeds with different time and strategy of development is a complex composition. Obviously, in the field research we could not consider all its specific and diverse features. Our goal, to reveal the influence of the relief and season on seed distribution, was achieved, and the obtained data show how complex in space and time the seed bank is, as well as allow us to clarify some previously published information. We believe that our research of the seed bank short-term dynamics adds new data to study seed redistribution patterns.

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