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Seed rain on alpine ski runs in Switzerland

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Abstract

Urbanska K. M., Fattorini M., Thiele K. and Pflugshaupt K. 1999. Seed rain on alpine ski runs in Switzerland. *Bot. Helv.* 109: 199–216.

Spatial and temporal variation in seed rain was studied in two un-restored ski runs at the Jakobshorn Mtn. (NE Swiss Alps), at ca. 2500 m a. s. l. The study carried out from 1996 to 1998 included density per m², alpha diversity (species richness), and species composition of the seed rain vs. that of the resident vegetation. This is the first detailed study of seed rain on machine-graded ski runs at high elevation.

Density of seed rain peaked mostly in late summer; on the other hand, alpha diversity varied most frequently with one peak after spring snowmelt and another towards the end of the growth period. Distribution of seeds among dry traps was patchy. Between-plot differences within one year, and also differences between years were not always significant.

Between-slope differences were very clear. Seed rain in 1998 was significantly higher in the SW ski run than in the NE run (2467 ± 418 vs. 900 ± 202 seeds/m², 3.1 ± 0.3 vs. 1.9 ± 0.2 species per trap). Seed rain on the SW ski run totalled 23 species; on the other hand, total alpha diversity of seed rain on the NE run amounted to only 16 species. Only few species prevailed in seed rain, the others provided small contributions. Seed rain was largely dominated by forbs, whereas graminoids amounted to only ca. one-third of all species and less than 10% of all seeds. Species included in seed rain represented mostly seed shadow and bore no clear relationship to successional stages.

The results suggest that seed rain in high-alpine ski runs strongly depends on local conditions such as neighbouring vegetation, slope incline and microrelief; general landscape context is apparently important, too. Data on seed rain in disturbed sites show potential for assessment of impact levels, and are thus relevant for the planning and implementation of restoration schemes.

Key words: Seed rain, downhill ski run, alpha diversity, seed shadow, seed input.

Introduction

Intensive recreation and overgrazing by cattle leave persistent scars in high-alpine and subalpine landscape (e.g., Marchand and Roach 1980, Florineth 1988, Cole and Hall 1992,

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Zabinski and Gannon 1997). The worst damage is done by activities which involve loss of topsoil e.g., road construction (Keigley 1988, Chambers 1993, Williams and Marvel 1990), open-pit mining (Brown et al. 1984, Moller 1996) or creation of machine-graded downhill ski runs (Etra and Johnson 1986, Meisterhans 1988). Unassisted recovery of such sites does not occur within a reasonable time-span. For instance, graded ski runs at high altitude offer a desolate picture of erosion-endangered, only sparsely colonised soil even after several decades (Urbanska et al. 1987, Wood 1987, Delarze 1994, Urbanska 1995a, Bayfield 1996, Urbanska and Fattorini 1998b).

Seed deposition represents the first step in colonisation of disturbed areas (Ash et al. 1994, Urbanska 1997b). It is therefore very important to know spatial and temporal patterns of seed rain. Understanding of these site-specific components is particularly relevant to self-recovery assessment, and to restoration of ecosystems at high altitude. Seed rain in alpine sites has been very little studied (Ryvarden 1970, Marchand and Roach 1980, Spence 1990, Chambers 1993), and man-disturbed sites above the timberline are virtually unknown in this respect. Preliminary comparisons between intact grassland and machine-graded ski runs (Urbanska et al. 1998) indicated dramatic differences. In natural alpine grassland we found significant differences in seed rain between two opposite slopes of the same mountain (Urbanska et al. in preparation).

This paper deals with un-restored downhill ski runs. The following questions are asked:

- (i) Does seed rain in high-alpine ski runs vary seasonally?
- (ii) Are within-year differences between sites on one slope or between slopes significant?
- (iii) Are between-year differences significant?
- (iv) Is the species composition of seed rain the same as that of resident vegetation? Are any spatial or time-related aspects recognisable?

Materials and methods

Studies on seed rain were carried out at the Jakobshorn Mountain, in the alpine surroundings of Davos (Canton of Grisons, NE Swiss Alps). Ski runs within the area have been machine-graded for the most part ca. 30 years ago; more recently, a snowboard piste and further ski lifts were added at SW slope. The ski runs are bordered by intact grassland and boulder fields.

Human land use in the Jakobshorn area is rather diversified: in addition to winter exploitation and daily maintenance of the ski area, slopes are heavily frequented by tourists who often damage the vegetation by walking off the marked paths. Service vehicles of the cable-car company are mostly used on roads but also driven across the landscape. The area is also grazed by large herds of domestic cattle.

The studied plots were located at ca. 2430–2500 m. a. s. l. on two opposite slopes of the Jakobshorn (Figs. 1–2). The steep NE slope represents the highest difficulty grade (black diamond ski run), whereas the gentle SW slope is used both as downhill run and exercise area for ski classes. Resident vegetation on ski runs was very sparse (Table 1) and the scattered plants did not form any distinct community (Table 2). No soil horizons were developed; the mineral soil was partly non-stabilised.

The plots NSO, NSM and NSU located on the NE ski run were established in 1996, the plots SSO, SSM and SSU on the SW run in 1997. Each plot consisted of two 5 m × 5 m subplots, separated from each other by ca. 0.5 m, and subdivided into 0.5 m grids. Ten dry traps per plot were positioned on randomly selected grid intersections, but not on the marginal points. Each trap unit included a plastic coffee filter of 11.5 cm diameter and ca. 10 cm depth; the filters were weighted with small stones and placed inside PVC funnels of the same dimensions with the bottom closed by a dense steel mesh. The trap units were covered with a metal grid of medium size and dug into the ground leaving about 0.5 cm rim above ground level. The trapping surface of a single unit amounted to 104 cm².

Traps were checked for seeds in intervals of ca. two weeks with occasional longer intervals caused by snowfall. The contents of each trap were emptied into plastic bags with a small brush. In rainy weath-

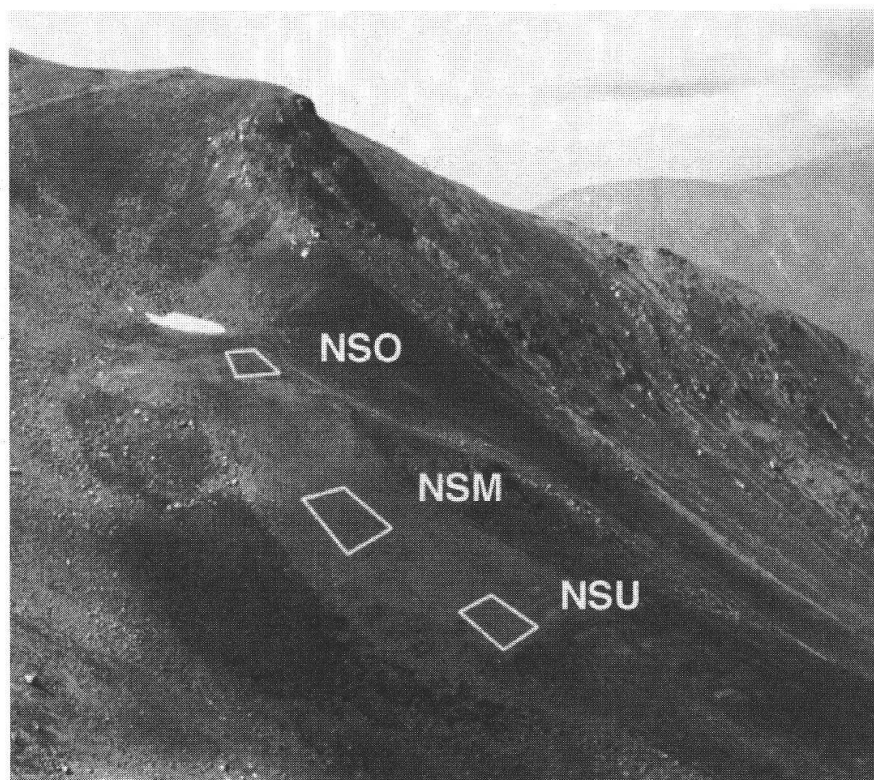


Fig. 1. NE ski run at the Jakobshorn (2500 m a. s. l.) with the location of studied plots.

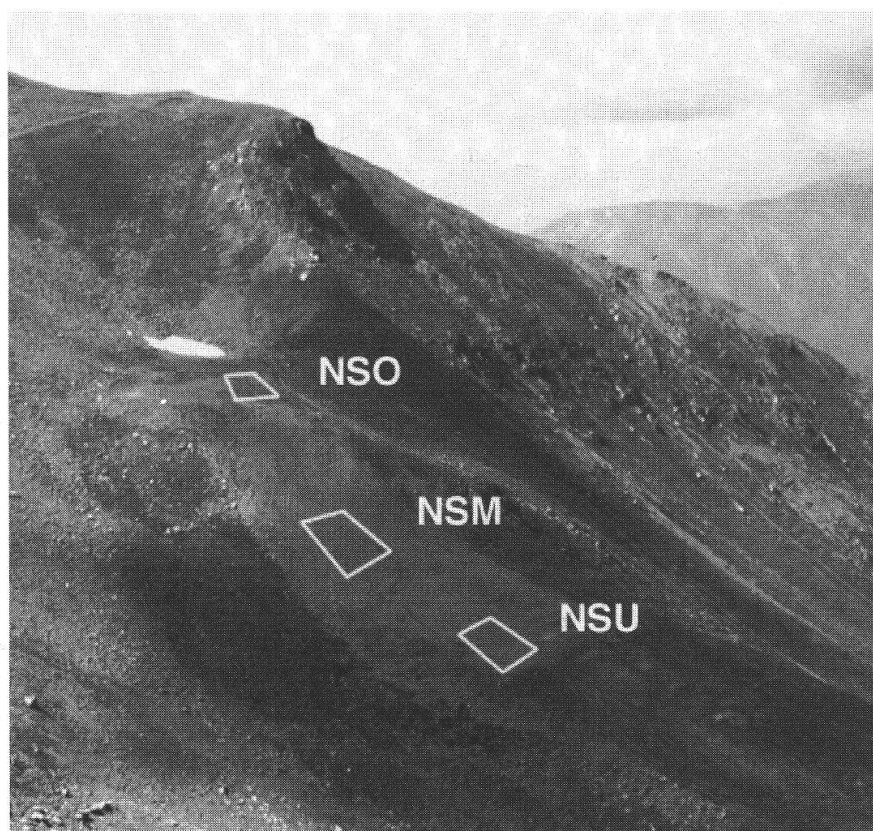


Fig. 2. SW ski run at the Jakobshorn (2500 m a. s. l.) with the location of studied plots. Note that the landscape is largely wind-exposed.

Table 1. Slope incline and aerial cover (both %) of the study plots. Status as of August 1996. Total cover values do not always correspond to an exact 100% because rough estimations of rocks vs. bare soil cover were rounded off within 5 per cent bracket (Landolt, personal communication).

Variable	NE ski run			SW ski run		
	NSO	NSM	NSU	SSO	SSM	SSU
Slope	20	40	40	5	10	10
Rocks	55	65	60	75	80	80
Bare soil	15	30	25	5	5	5
Cryptogams	5	5	5	7	5	5
Phanerogams	10	2	7	15	10	10

Table 2. Phytosociological relevés of the study plots including the combined estimation scale of abundance and cover (method of Braun-Blanquet). • = species absent; + = < 20 plants and < 1% cover; 1 = 20–100 plants or 1–5% cover; 2 = <100 plants or 5–25% cover.

Species	NSO	NSM	NSU	SSO	SSM	SSU
<i>Agrostis rupestris</i>	1	•	+	+	1	+
<i>Agrostis schraderiana</i>	•	•	•	+	•	•
<i>Arabis alpina</i>	•	•	•	•	•	+
<i>Arenaria biflora</i>	•	•	•	+	•	+
<i>Cardamine resedifolia</i>	1	+	+	1	+	1
<i>Carex curvula</i>	•	•	•	+	+	+
<i>Cerastium trigynum</i>	•	•	•	•	•	+
<i>Chrysanthemum alpinum</i>	1	1	2	1	1	1
<i>Deschampsia flexuosa</i>	+	•	•	•	•	•
<i>Doronicum clusii</i>	1	•	+	+	+	+
<i>Euphrasia minima</i>	+	•	•	•	•	•
<i>Festuca rubra</i>	•	•	+	•	•	+
<i>Gnaphalium supinum</i>	+	•	•	•	+	+
<i>Helictotrichon versicolor</i>	+	•	•	+	•	+
<i>Hieracium alpinum</i>	+	•	•	+	•	•
<i>Homogyne alpina</i>	+	•	•	•	+	•
<i>Leontodon helveticus</i>	•	•	•	+	+	+
<i>Linaria alpina</i>	+	+	+	+	•	+
<i>Luzula lutea</i>	•	•	•	+	•	•
<i>Luzula spadicea</i>	+	•	+	+	+	+
<i>Poa alpina</i>	+	•	•	+	+	2
<i>Poa laxa</i>	1	+	+	+	1	+
<i>Salix herbacea</i>	+	•	•	•	•	•
<i>Saxifraga bryoides</i>	+	•	•	•	•	•
<i>Saxifraga stellaris</i>	+	+	•	•	•	•
<i>Sedum alpestre</i>	•	•	•	•	•	+
<i>Senecio carniolicus</i>	+	•	+	+	+	1
<i>Sesleria disticha</i>	+	•	•	+	•	•
<i>Sibbaldia procumbens</i>	•	•	•	+	+	+
<i>Veronica alpina</i>	+	•	•	•	•	•
Species number	20	5	9	18	13	19

er, traps were rinsed with distilled water and the rinse was collected in the bags. Dried samples were studied under a dissecting microscope. Undamaged filled seeds were counted and identified to species or genus with the help of our reference collection, and also the descriptions given in the literature (Hess et al. 1967–1972, Müller-Schneider 1986). One sample of dicotyledonous seeds differed morphologically from all determined species recorded in seed rain but could not be identified. It was coded as Di* and included in the assessments. Seed numbers were converted to density (number per m²). Alpha diversity in a given year was evaluated on two levels viz. (i) mean species number per trap, and (ii) total species number per plot/year. Species identified in seed rain were compared to those listed in phytosociological relevés. To estimate spatial patchiness in seed rain, the ratio of variance to mean s^2/\bar{x} was used according to Grieg Smith (1957).

Differences between samples were tested with the two-way Mann-Whitney *U*-test and partly also with the Wilcoxon paired rank test, both including the Bonferroni's correction. Correlation between contribution of species to seed rain and their phytosociological status was tested with Spearman's correlation coefficient r_s . The significance level was set at $p = 0.05$. The statistical software used was Systat®, the software for scanning the photographs was Photoshop®.

Terminology

As in our previous papers on seed banks (Urbanska and Fattorini 1998a, b), the term “seeds” used in this paper applies to all diaspore types i.e. genuine seeds and various fruit types. The species names follow Hess *et al.* (1967–1972).

Results

Seasonal variation in seed rain density and alpha diversity

Pattern of seasonal variation of seed rain density was mostly unimodal with peak density registered towards the end of summer. A distinctly bimodal variation pattern was observed only once in 1997 in plot NSO, where a considerable accumulation of seeds just after the spring snowmelt was followed by a strong decrease in density which peaked again by the end of summer. On the other hand, the actual timing of maximum seed rain flush varied between plots, the earliest peak being registered by mid July, the latest one – by late September.

Species richness also varied seasonally, but fluctuations within plots and between-plot differences in species number were on the whole stronger than those of density. The general pattern was bimodal: one peak occurred immediately after spring snowmelt and was followed by a decrease in species number which later increased again. The timing of maximum alpha diversity differed slightly among plots. Most frequently, the highest species number was registered in the second half of summer but a late peak corresponding to the end of season was found once (1998) in SSU.

Within- and between-year differences

Seed rain density. Mean density of seed rain in NSO amounted in 1996 to 202 ± 75 seeds per m²; it was considerably lower in NSM and NSU (57 ± 21 , and 77 ± 23 seeds per m², respectively) but the differences between plots were not significant and remained so in 1997. On the other hand, seed rain in NSO increased in 1998 to 1451 ± 171 seeds per m²; it differed significantly from NSU (499 ± 190 seeds per m²) but not from NSM (749 ± 525 seeds per m²). The high density of seed rain in NSO influenced the significance of between-year differences when data from all plots were pooled (Fig. 3).

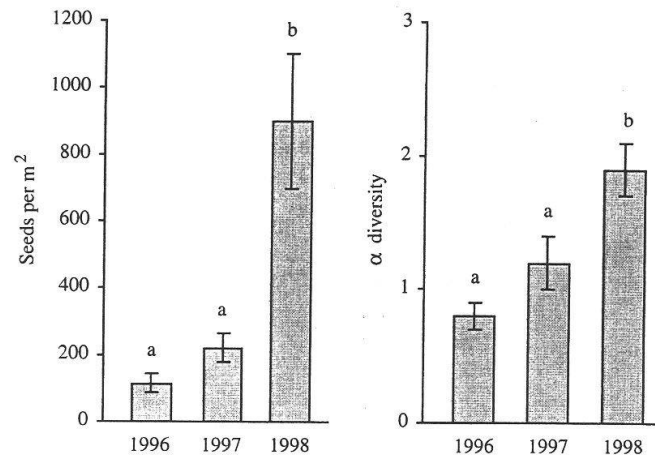


Fig. 3. Between-year changes in seed rain density per m² (left) and alpha diversity per trap (right). Wilcoxon paired rank sum test ($N = 30$). Different letters denote significantly different means (seed rain density: 1996 vs. 1998: $p < 0.0001$; 1997 vs. 1998: $p = 0.0003$. Alpha diversity: 1996 vs. 1998: $p = 0.0003$; 1997 vs. 1998: $p = 0.0108$). Bars are SE.

On the opposite slope, the mean density of seed rain in 1998 ranged from 893 ± 287 seeds/m² in SSM to 4807 ± 587 seeds/m² in SSO; the latter plot differed significantly from SSM but not from SSU (Fig. 4). According to an unpublished report of Kofler, SSO differed significantly from both other plots in 1997; regrettably enough, raw data from this year were not available for comparison but a general increase in seed rain density between 1997 and 1998 was considerable (1695 vs. 2467 seeds per m²).

Table 3. Patchiness index s^2/\bar{x} of seed number (upper rows) and species number (lower rows) per trap in study year 1998. Sampling dates given in the table head. Sample size $n = 10$. <1 = regular distribution; 1 = random distribution; >1 = clumped distribution (bold print); no = traps covered with snow, hence no sampling; – = mean equal zero.

Plot code	24 Jun	4 Jul	19 Jul	3 Aug	16 Aug	31 Aug	23 Sept
NSO	1.53	1.52	–	–	14.49	4.02	3.35
	1.03	0.89	–	–	0.33	0.60	0.52
NSM	0.78	1.00	–	–	12.33	38.94	1.60
	0.78	1.00	–	–	0.67	1.19	1.00
NSU	1.52	1.00	–	–	1.60	3.67	1.19
	0.89	1.00	–	–	0.82	1.19	0.67
SSO	1.73	1.29	0.89	0.89	8.19	4.20	4.11
	1.11	0.68	0.89	0.86	0.34	0.17	0.18
SSM	no	1.52	–	1.22	3.89	4.48	3.77
	no	1.52	–	1.22	0.82	1.09	0.67
SSU	2.81	3.12	–	0.78	20.93	2.37	5.61
	0.52	0.82	–	0.78	0.97	0.92	0.63

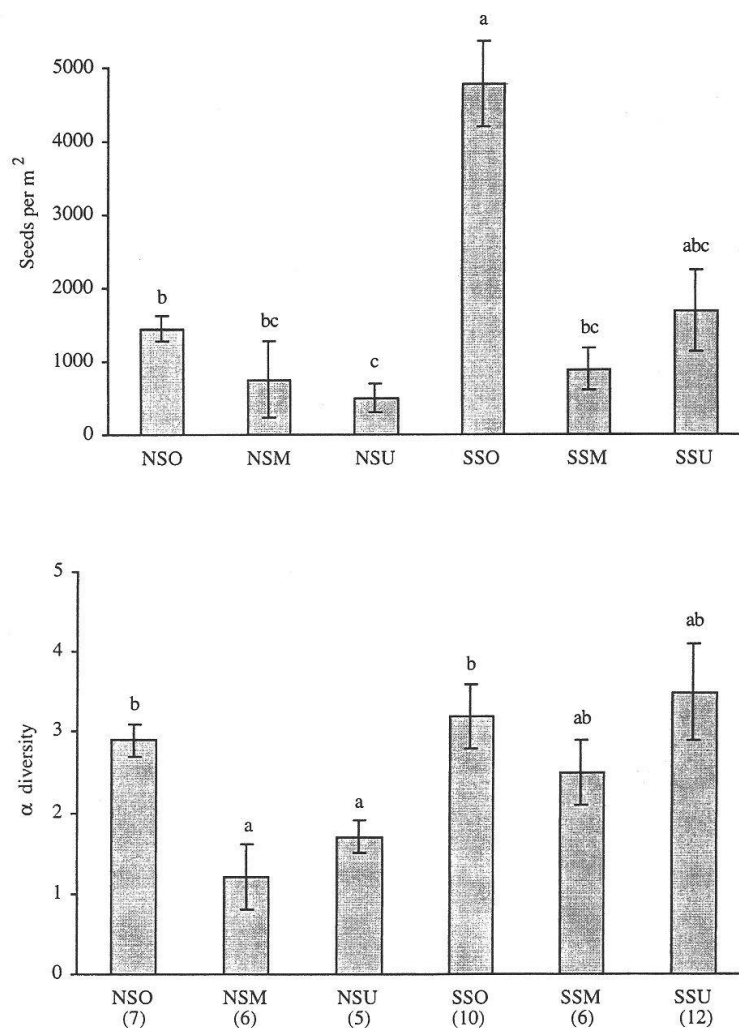


Fig. 4. Study year 1998: density of seed rain per m² (above) and alpha diversity per trap (below) in all plots studied ($N = 6$). U -test of Mann-Whitney ($n = 10$). Means \pm SE. Different letters denote significant differences. For seed rain density: NSO vs. SSO: $p = 0.006$; NSM vs. SSO: $p = 0.0165$; NSU vs. SSO: $p = 0.003$; SSO vs. SSM: $p = 0.006$; SO vs. NSU: $p = 0.0465$. For alpha diversity: NSM vs. NSO: $p = 0.0495$; NSM vs. SSO: $p = 0.045$; NSU vs. NSO: $p = 0.0195$; NSU vs. SSO: $p = 0.042$. Total species number in plots given in parentheses.

Alpha diversity per trap. Plots on NE ski run differed only slightly from each other during the first two years; the lowest mean value of 0.5 ± 0.2 species was registered in 1996 in NSM, the highest (1.3 ± 0.3 species) occurred in NSO one year later. In 1998, however, difference between NSO and both other plots was significant (2.9 ± 0.2 vs. 1.2 ± 0.4 and 1.7 ± 0.2 species, respectively). Between-plot differences on SW ski run were not significant in 1998 (Fig. 4).

Total species number per plot and year. In 1996, seed rain included 5 species in NSO and 3 species both in NSU and NSM. In 1997, alpha diversity in NSO and NSU increased by one species, but more than doubled in NSM. One year later one more species appeared in seed rain of NSO, whereas the species number in NSU remained stable and that in NSM decreased to 5 species. Evaluated for the whole three-year study period, alpha diversity in NSO amounted to 9 species, and that in NSU to 7 species; on the other hand, total seed rain in NSM included 12 species.

Species number in SSO increased from 8 to 10 between 1997 and 1998, whereas that in SSM decreased from 7 to 6. Between-year increase of alpha diversity was most pronounced in SSU (8–12). Total alpha diversity per plot recorded over the two years of study included 15 species in SSO, 9 in SSM and 14 in SSU.

Patchiness in seed rain

Density of seed rain was most frequently patchy. Of 76 available records, 48 (63.1%) indicated clumping, whereas 10 (13.2%) corresponded to randomness and 18 (23.7%) to a uniform distribution. On the whole, clumping was particularly strong in late summer and towards the end of the growing period but relatively weak or replaced by random/uniform distribution at the beginning and in the middle of the growing period (Table 3).

Contrary to density, distribution of species in seed rain was mostly regular or approached randomness. No seasonal patterns were detected (Table 3).

Seed rain species and their respective contributions (%)

The large majority of the 29 species registered in seed rain on ski runs represented dicotyledonous plants (Table 4, Fig. 5); most of them were forbs. The monocotyledonous group consisted of seven graminoids.

Table 4. Species which contributed less than 2% each to seed rain throughout three-year study period. Di* = undetermined dicotyledonous species.

Species	Seeds	%
<i>Agrostis rupestris</i>	11	0.66
<i>Arabis alpina</i>	6	0.36
<i>Arenaria biflora</i>	11	0.66
<i>Campanula scheuchzeri</i>	1	0.06
<i>Carex curvula</i>	3	0.18
<i>Cerastium trigynum</i>	7	0.42
<i>Doronicum clusii</i>	16	1.00
<i>Gentiana punctata</i>	1	0.06
<i>Gnaphalium supinum</i>	21	1.25
<i>Helictotrichon versicolor</i>	2	0.12
<i>Hieracium alpinum</i>	1	0.06
<i>Leontodon helveticus</i>	7	0.42
<i>Linaria alpina</i>	1	0.06
<i>Luzula spadicea</i>	4	0.24
<i>Minuartia verna</i>	1	0.06
<i>Poa alpina</i>	22	1.31
<i>Rhododendron ferrugineum</i>	1	0.06
<i>Salix herbacea</i>	4	0.24
<i>Saxifraga stellaris</i>	1	0.06
<i>Sedum alpestre</i>	22	1.31
<i>Sesleria disticha</i>	2	0.12
<i>Sibbaldia procumbens</i>	6	0.36
<i>Silene rupestris</i>	3	0.18
<i>Taraxacum alpinum</i>	2	0.12
<i>Veronica alpina</i>	1	0.06
Di*	1	0.06

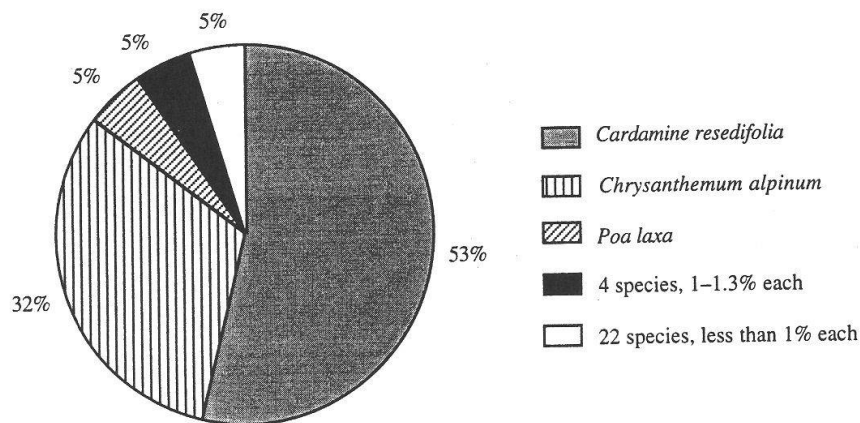


Fig. 5. Total alpha diversity, and contribution (%) of species to seed rain. The species which contributed very little (black and white field, respectively) are listed in Table 4.

Table 5. Occurrence of species in seed rain of the studied plots grouped by aspect. Di* = undetermined dicotyledonous species. OC = occasional contributor; SP = stable-presence contributor; EC = episodic contributor. For explanations regarding contributor types and rare species see text. Data on all species ($N = 29$) from the study period 1996–1998.

Species	Number of records/aspect	Contributor	Records total
<i>Cardamine resedifolia</i>	8 NE, 6 SW	SP	14
<i>Chrysanthemum alpinum</i>	9 NE, 5 SW	SP	14
<i>Gnaphalium supinum</i>	3 NE, 4 SW	SP	7
<i>Poa laxa</i>	4 NE, 3 SW	SP	7
<i>Agrostis rupestris</i>	3 NE, 3 SW	SP/EC	6
<i>Leontodon helveticus</i>	2 NE, 3 SW	SP	5
<i>Salix herbacea</i>	4 NE	SP	5
<i>Cerastium trigynum</i>	4 SW	SP/EC	4
<i>Doronicum clusii</i>	3 NE, 1 SW	SP/EC	4
<i>Poa alpina</i>	1 NE, 3 SW	SP	4
<i>Arabis alpina</i>	3 SW	SP	3
<i>Carex curvula</i>	2 SW	SP	2
<i>Luzula spadicea</i>	1 NE, 1 SW	OC	2
<i>Sesleria disticha</i>	2 NE	OC	2
<i>Sibbaldia procumbens</i>	2 SW	OC	2
<i>Silene rupestris</i>	2 SW	OC	2
<i>Taraxacum alpinum</i>	1 NE, 1 SW	OC	2
<i>Arenaria biflora</i>	rare SW	OC	1
<i>Campanula scheuchzeri</i>	rare SW	OC	1
<i>Gentiana punctata</i>	rare SW	OC	1
<i>Helictotrichon versicolor</i>	rare SW	OC	1
<i>Hieracium alpinum</i>	rare SW	OC	1
<i>Linaria alpina</i>	rare NE	OC	1
<i>Minuartia verna</i>	rare NE	OC	1
<i>Rhododendron ferrugineum</i>	rare SW	OC	1
<i>Saxifraga stellaris</i>	rare NE	OC	1
<i>Sedum alpestre</i>	rare SW	EC	1
<i>Veronica alpina</i>	rare SW	OC	1
Di*	rare NE	OC	1

Distribution of species was largely asymmetric (Fig. 5). *Cardamine resedifolia* and *Chrysanthemum alpinum* formed together most of the seed rain; *Poa laxa* was the third most frequent species but represented only few per cent. Twenty six other species provided minor contributions each (Table 4). Species composition of seed rain varied in space and time.

Within- and between-year variations. On the whole, data on alpha diversity per plot and year gathered throughout the study totalled 15 records (Table 5). *Cardamine resedifolia* and *Chrysanthemum alpinum* were recorded 14 times each. Of the remaining 27 species, 15 were registered 2 to 7 times, and twelve rare species were confined to a single record each.

Species in seed rain represented three main contributor groups (Table 5). Occasional contributors (OC) with inconsistent and negligible contributions to seed rain formed the largest group (16 species); all but one rare species belonged to this category. Stable-presence contributors (SP) which regularly occurred in seed rain throughout a given study period formed a rather small group (9 species). Other three species behaved as stable-presence contributors in some plots but qualified as episodic in the others. Episodic contributors (EC) which provided a good number of seeds in one year but none in preceding or following year(s) were represented only by *Sedum alpestre* which appeared once in 1998 in a single plot.

Species within seed rain vs. resident vegetation

Species in seed rain apparently originated from different sources and were accordingly assigned to three separate categories:

- (1) Seed shadow consisted of species registered both in seed rain and resident plant cover of the respective plots;
- (2) Near seed input included species which did not grow in a given plot but occurred in vegetation of other plots on the slope;
- (3) Distant seed input was provided by species which did not occur in resident vegetation of any studied plots but mostly occurred in natural sites or on ski runs nearby. This group included also species not observed in our study area.

Seed shadow largely prevailed in seed rain but its relative proportion varied over the years (Table 6). This variation was largely influenced by between-plot differences in near seed input recorded in a given year and also by year-to-year variation. For example, *Cerastium trigynum* on the SW ski run occurred in 1997 as seed shadow in SSU but represented near input in SSM. One year later it still represented seed shadow in SSU but was not anymore recorded in SSM and appeared instead as seed input in SSO.

Seed input in 1996 included only two species; of those, *Minuartia verna* represented distant input in NSU, and *Linaria alpina* - near input in NSM. In the following year 7 species

Table 6. Seed rain categories (see text for descriptions) grouped by aspect and year. Numbers of records given in rows. NE = NE ski run; SW = SW ski run.

Aspect and year	Seed shadow	Near seed input	Distant seed input
NE 1996	9	1	1
NE 1997	11	6	1
NE 1998	11	2	3
SW 1997	19	2	2
SW 1998	21	2	5

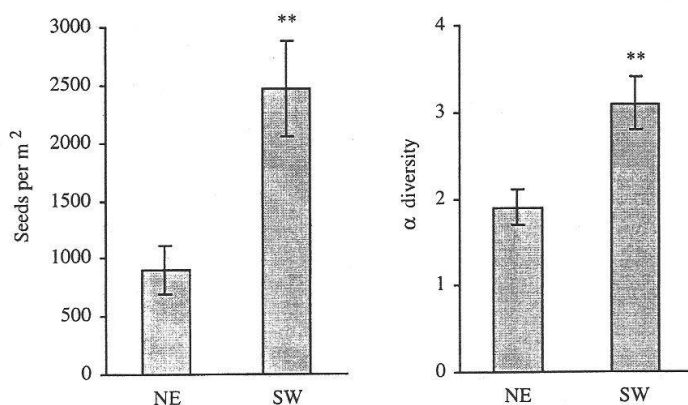


Fig. 6. Mean seed rain density per m² and alpha diversity per trap grouped by aspect. *U*-test of Mann-Whitney ($n=30$). Means \pm SE. Asterisks denote significant differences (seed rain: NE vs. SW: $p=0.0023$; alpha diversity: NE vs. SW: $p=0.0052$).

were found. Five species were registered in NSM, two of them occurred also in NSU. Except for *Taraxacum alpinum*, which apparently originated from a more distant source, all species on the NE ski run represented near input. Of the four immigrant species registered in seed rain on the SW ski run, two each occurred in the SSO and SSM where they respectively represented one distant input and one near input.

In 1998, seed input included 12 species. The two species in NSO represented distant input, whereas NSM received near input from two species and distant input from one species. The four immigrant species in SSO corresponded in equal proportions to near and distant input. On the other hand, SSU received only distant input from three species.

Seed rain and aspect

On the whole, seed rain density on SW ski run was consistently higher by ca. 1500 seeds per m² than that on the NE slope (1695 vs. 218 in 1997, 2468 vs. 900 in 1998). The assessment of data from 1998 revealed highly significant differences between slopes both in mean density and mean alpha diversity per trap (Fig. 6).

Distinct between-slope differences in total alpha diversity per year (16 vs. 10 species in 1997, 17 vs. 9 species in 1998), were also confirmed in the overall assessment: 23 species

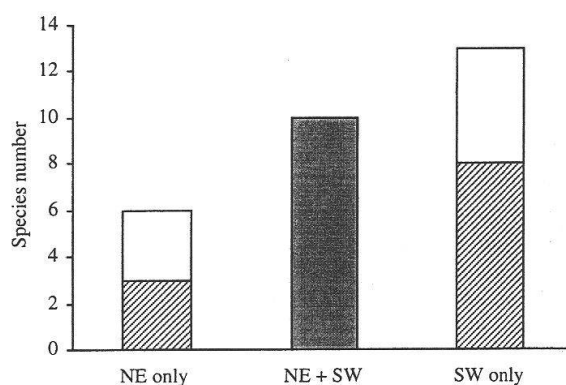


Fig. 7. Aspect and number of species in seed rain. Open parts of the bars denote species found in more than one plot, hatched parts correspond to rare species recorded only once in a single plot each.

Table 7. Seed rain in 1997 and 1998: Relatively frequent contributors (ten seeds and more per year) grouped by aspect. NE \neq SW = nearly equal occurrence; NE > SW = more seeds on NE ski run; NE < SW = more seeds on SW ski run.

Species	NE \neq SW	NE only	SW only	NE > SW	NE < SW
1997:					
<i>Arenaria biflora</i>	.	.	11	.	.
<i>Cardamine resedifolia</i>	36/310
<i>Chrysanthemum alpinum</i>	11/147
<i>Doronicum clusii</i>	.	.	10	.	.
1998:					
<i>Cardamine resedifolia</i>	77/475
<i>Chrysanthemum alpinum</i>	175/184
<i>Poa alpina</i>	.	.	20	.	.
<i>Poa laxa</i>	16/29
<i>Sedum alpestre</i>	.	.	22	.	.

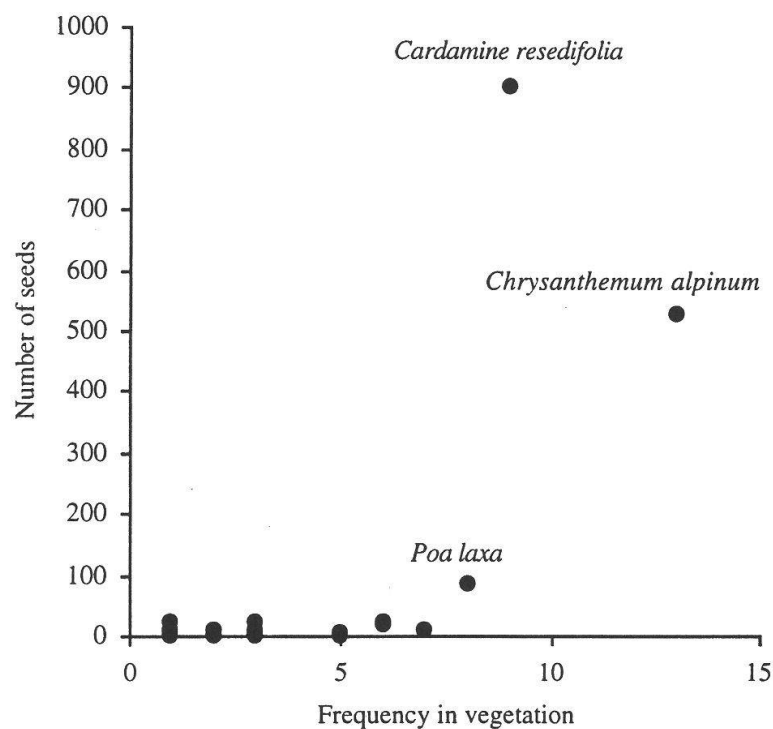


Fig. 8. Relationship between number of contributed seeds vs. frequency of species in vegetation. Pooled variables from the whole study period ($N = 21$). Spearman's correlation coefficient $r_s = 0.54$, Bartlett Chi-square test: $\chi^2 = 6.254$, $df = 1$, $p = 0.012$.

occurred in the two-year study on the SW ski run but only 16 were registered on the NE ski run studied for three years. Of all species in seed rain, only 10 occurred on both ski runs; the remaining species were unequally distributed between slopes: the number of species occurring only on the SW ski run was more than twice as high as that on the opposite slope, and the relative proportion of rare species was also higher (Table 5, Fig. 7). Larger annual con-

tributions of ten seeds or more were generally recorded on SW ski run, although *Chrysanthemum alpinum* which performed considerably better on the SW slope in 1997 was found one year later in nearly equal proportion in seed rain on both sides of the Jakobshorn (Table 7).

Phytosociological status of species vs. their contribution to seed rain

Species which frequently occurred in plant cover (Table 2) were also relatively good contributors to seed rain. Correlation coefficient calculated for the ranked data was significantly positive ($r_s = 0.54$, $p = 0.0123$, $N = 21$, Fig. 8). This result should be regarded as tendency, because the phytosociological status of the species was based on their presence and did not relate to reproductive behaviour.

Discussion

The results of this study extend the information on population and community processes in high-alpine sites. They show that some features of seed rain above the timberline are rather general. They also reveal patterns of spatial and temporal variation, and implications for restoration.

General features of seed rain

Seed rain in ski runs was characterised by (i) clumped distribution of seeds among traps, (ii) unequal species distribution, (iii) predominance of seed shadow, and (iv) occurrence of species representing various seral stages.

As far as the patchiness of seed rain is concerned, degraded ski runs are generally comparable to intact grassland studied in the same area (Urbanska et al. 1998). Similar problems were previously encountered by Spence (1990) in natural alpine communities in New Zealand. No further detailed data on seed rain are available; on the other hand, we observed clumping in our previous study on soil seed reserve both in intact alpine grassland and un-restored ski runs (Urbanska and Fattorini 1998a, b). Clumped distribution of seeds means that they may be under-represented in the material. We regard therefore the density registered in our study as a minimum value and accept a possibility that there may have been more seeds.

Seed rain in ski runs was dominated by only few species. The results corroborate the previous reports from various alpine sites (Ryvarden 1971, Marchand and Roach 1980, Stöcklin and Bäumler 1996, Urbanska et al. 1998). Uneven species distribution in seed rain possibly represents an individual response of species towards environmental constraints, but seems not to be specifically related to disturbance.

A large majority of species registered in seed rain of ski runs represented forbs. Graminoids were less frequent (one-third of all species) and provided less than ten per cent of the whole seed rain. In this respect, ski runs were similar to intact alpine grassland (Urbanska et al. 1998), as well as glacier foreland in the Swiss Alps (Stöcklin and Bäumler 1996) and Norway (Ryvarden 1971). On the other hand, substantial amounts of graminoid seeds were recorded in various alpine communities in the New Zealand Alps (Spence 1990). In disturbed Appalachian grassland, two graminoid species formed between them more than 50% of seed rain (Marchand and Roach 1980); however, seed rain in this study area totalled only four species so that the results are not conclusive. Many alpine graminoids produce late-maturing seeds (Müller-Schneider 1986); since seed rain in this group peaks often by the end of the growing period or perhaps even after spring snowmelt, it may be particularly sensitive to weather fluctuations.

Seed rain in the studied sites represented mostly seed shadow i.e. seeds were for the most part produced *in situ*. Our results are consistent with the previously reported short distances of dispersal and colonisation in the alpine vegetation belt (Ryvarden 1971, Marchand and Roach 1980, Spence, 1990, Urbanska 1997a, b). Species occurring in the alpine vegetation belt of the Swiss Alps have been mostly classified as anemochorous (Müller-Schneider 1986) but events of long-distance dispersal apparently are isolated. The behaviour of high-alpine plants contradicts the widely held view that the presence of specific adaptations for dispersal ought to promote travel over long distances (Howe and Smallwood 1982, Fenner 1985, Olatunde Akinola et al. 1998). On the other hand, our data strongly suggest that most species in the study area are far more polychorous than previously assumed.

Species composition of seed rain in ski runs bore no clear relationship to successional stages. A comparable trend was revealed in seed bank build-up (Urbanska and Fattorini 1998a), and also in colonisation of ski run and restoration plots (Urbanska 1994, 1995a, b, 1997a, b). Occurrence of so-called late seral dominants in colonisation of disturbed alpine sites was also reported from North America (Chambers et al. 1987).

In high-alpine areas, one species may often be found in several adjacent communities representing different seral stages and the classical concept of succession is often not directly applicable (Urbanska 1997b, c). Species registered in seed rain, seed bank, or resident vegetation of alpine disturbances should thus be regarded in the context of neighbouring vegetation and dispersal distance rather than automatically assigned to the traditional seral stages.

Spatial and temporal patterns of seed rain

Temporal and spatial variation of seed rain was reflected both in density and species richness as well as species composition. The unpredictable weather above the timberline undoubtedly influenced the patterns of dispersal both indirectly and directly.

Weather conditions influence the health of plants in a given growing period and thus their reproductive performance in the following year (Urbanska and Schütz 1986). Year-to-year variations in seed rain density observed in our study clearly indicate the importance of this factor although the annual fluctuations were not always as strong as those reported e.g., by Chambers (1993). A direct influence of weather on seed rain within one growing period may be recognised in phenological fluctuations, and particularly in timing of species-specific dispersal pulses. Our study supports in this respect an earlier report of Marchand and Roach (1980), and also our recent data on alpine grassland (Urbanska et al. 1998).

Spatial variation of seed rain was registered both locally and in medium-scale patterns. The small-scale variation occurring among sites located close to each other further documented the strong heterogeneity of high-alpine areas reported previously e.g., in studies on vegetation (Vetterli 1982). The greatly varying soil stability and the largely scattered vegetation clumps on machine-graded ski runs suggest that alpine disturbances may be still more heterogeneous than intact areas; accordingly local variation is to be expected. Much more intriguing are the highly significant differences in seed rain found between two ski runs located on opposite slopes of the same mountain. When the results of the present study are compared to those obtained in adjacent grassland (Urbanska et al., in preparation), contrasting patterns emerge: on the NE slope, seed rain was more abundant in grassland than in degraded ski run but a reverse trend occurred on the SW slope, and these differences were again highly significant ($p = 0.0003$ and 0.0119 , respectively). The ecologically meaningful patterns remain to be further investigated as our results are the first of the kind, but it seems that (a) intraspecific responses may vary spatially, and (b) the whole landscape context has to be considered. Differences in the landscape configuration as e.g., incline, exposure to wind, surface micro-

relief or general formation of surrounding mountain slopes, may be of utmost importance. As far as the steep NE ski run at the Jakobshorn is concerned, low rates of seed entrapment may well render an already limited seed rain still less effective; in this respect, our results are partly comparable to those of Fort and Richards (1998). On the other hand, the gentle SW ski run may offer better conditions to entrapment of seeds.

The above comments are helpful for an assessment of seed fates but they do not explain sufficiently well the puzzling differences in seed rain density. Since both ski runs at the Jakobshorn are surrounded by vegetation-rich slopes, abundance of the produced seeds should be basically comparable. Land use (recreation, grazing by domestic cattle) on the SW slope is more intensive than on the NE slope; it apparently affected seed rain in grassland situated close to ski runs. Less seed rain should accordingly be expected on the SW ski run but our findings demonstrate just the contrary. Different aspects should decidedly be included in future studies on seed rain in high-alpine sites; seed production should also be investigated, although it may be difficult to disentangle effects of land use from those of landscape morphology and weather conditions. For instance, grazing is likely to be a relevant factor limiting reproduction by seed, but the duration of winter snow cover undoubtedly has an important influence, especially on seed output and dispersal in late-flowering species.

The results of the study support the conclusion that seed rain does not always represent the limiting factor in colonisation of degraded ski runs. They also show that seed rain alone does not suffice to ensure a successful colonisation if safe sites are not available (Urbanska 1997 a). Our data from the NE slope coupled with seed bank data from the same site (Urbanska and Fattorini 1998 a) clearly indicate a deficient seed deposition but also safe sites are apparently rare and far between. On the other hand, the unsuccessful colonisation of the SW ski run is apparently influenced in the first place by recruitment constraints and not by lack of seed rain. Colonising ability of a species is expressed in the number of seeds that eventually result in successful recruitment (but see Eriksson and Jakobsson 1998), and colonisation might be enhanced by a build-up of soil seed reserve.

Implications for restoration

Our results confirm the usefulness of monitoring seed rain for damage assessment in degraded sites. The data may have an important bearing on the subsequent planning of restoration schemes. As far as high-alpine sites are concerned, we recommend the use of entrapment structures, e.g., geotextile mats, in restoration schemes (Urbanska and Hasler 1992, Urbanska 1994, 1997 a). In this way, deficient seed rain may be counterbalanced to some extent by a better entrapment, whereas good seed rain may be further improved.

The study shows that seed rain in some disturbed sites may be satisfactory; however, the sparse vegetation indicates that unassisted recovery does not follow. This result points out again towards the importance of recruitment phase and the necessity to provide safe sites which require much attention in restoration of alpine disturbances. Safe sites above the timberline should be provided both by biodegradable covers and local re-introduction of transplants of native species as population founders and nurses (see the concept of safety islands, Urbanska 1997 a).

Zusammenfassung

In zwei alpinen planierten Skipisten am Jakobshorn (ca. 2500 m ü. M., NE Schweizer Alpen) wurden 1996–1998 räumliche und zeitliche Schwankungen im Samenregen untersucht.

Die Studie befaßte sich mit der Samendichte pro m², der Alpha-Diversität (Artenvielfalt), und einem Vergleich zwischen Artenzusammensetzung des Samenregens mit jener der bestehenden Vegetation.

Die höchste Dichte des Samenregens wurde meistens im Spätsommer registriert. Die Artenvielfalt variierte hauptsächlich bimodal mit einem Maximum nach der Frühjahr-Schneeschmelze und einem gegen das Ende der Vegetationsperiode. Die Verteilung der Samen in Fallen war meistens gehäuft. Teilweise erwiesen sich die Unterschiede zwischen den Flächen innerhalb eines Jahres und auch jene zwischen Untersuchungsjahren als signifikant.

Es zeigten sich sehr deutliche Unterschiede zwischen verschiedenen Hängen. Auf der SW-Skipiste war 1998 sowohl die Dichte des Samenregen wie auch die Anzahl der Arten pro Falle signifikant höher als auf der NE-Piste. Der Samenregen auf der SW-Skipiste umfaßte im ganzen 23 Arten gegenüber nur 16 Arten auf der NE-Piste.

Nur wenige Arten dominierten im Samenregen, die Mehrheit war sehr schwach vertreten. Der Samenregen bestand hauptsächlich aus Kräutern; die Graminoiden betrugen weniger als ein Drittel aller Arten und weniger als 10% aller Samen. Die im Samenregen vorkommenden Arten entsprachen meistens dem Samenschatten und zeigten keine klare Beziehung zu Sukzessions-Phasen.

Die Ergebnisse lassen vermuten, daß der Samenregen in hochalpinen Skipisten stark von örtlichen Verhältnissen wie z. B. benachbarten Vegetationen, Hangneigung sowie Mikrorelief abhängig ist, und dass die allgemeine Landschaftskonfiguration auch eine wichtige Rolle spielt. Die Angaben über Samenregen an gestörten Standorten erweisen sich bei Erfassung des Störungsgrades als relevant und sind somit wichtig für die Planung und Durchführung der Renaturierung.

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