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Seed bank studies in the Swiss Alps. I. Un-restored ski run and the adjacent intact grassland at high elevation

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Abstract

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This preliminary study investigated soil seed banks in two high-alpine sites to assess the potential for unassisted recovery after disturbance. Comparisons were drawn between an un-restored ski run which was machine-graded about 27 years before, and the adjacent intact grassland. This is the first report on seed banks in the former site type.

The soil seed reserve in the un-restored ski run included only 52±20 seeds per m^2, in spite of the fact that the ski run was graded ca. 27 years earlier, and intact vegetation occurred in close proximity; on the other hand, the seed reserve in the adjacent natural grassland averaged 2401±336 seeds per m^2. Only 3 species were identified in the seed banks of the un-restored ski run, whereas the number of species identified in the seed banks of grassland totalled 9. Distribution of species in the seed reserve was irregular. Not all species found in the soil cores contributed to the plant cover of the respective sites; discrepancies in frequency of species in the soil seed reserve vs. that in standing vegetation were a lso recorded.

The results indicate that in the graded ski run no unassisted recovery of vegetation from seed banks may be expected within a reasonable time period. It is concluded that improving seed deposition and seed production in situ should be considered a major issue in restoration schemes.

Key words: Sed bank, soil seed reserve, unassisted recovery, restoration, high-alpine grassland, machine-graded ski run.

Introduction

The seed reserve in soil is a characteristic feature of self-supporting plant communities. On the one hand, seed banks form an important constituent of regeneration niche and population turnover in undisturbed sites; in the other hand, they represent the potential for spontaneous recovery after disturbance (Grubb 1977, Grime 1979, Thompson 1992, Urbanska 1992). Knowledge of how much unassisted recovery of vegetation may be expected is important not only for a general assessment of the ecosystem resilience (Urbanska 1997c) but also for the planning and implementation of the restoration work in disturbed areas.

Data on plant populations in cold-influenced alpine areas may be decisive in this respect, and it is necessary to know as much as possible about seed reserves in soil of high-alpine sites. However, the data available are so far few. As far as the Alps are concerned, there are only four published reports (Hatt 1991, Diemer and Prock 1993, Niederfrinninger-Schlag and Erschbamer 1995, Bernhardt 1996). Two of these studies refer to grassland seed banks in silicaceous soils.

Machine-graded downhill ski runs and snowboards tracks in high-alpine sites represent extreme environmental disturbance (Cernusca 1977, Hasler 1992, Urbanska 1995a, b, 1997a, b, Urbanska, unpublished data, Klug-Pumpel and Krampitz 1996). The particularly severe damage was inflicted upon the alpine ecosystem in the early 1970s by extensive grading of ski runs accompanied by removal of the topsoil together with the extant vegetation. Colonization of graded sites by native plants from neighbouring areas is very limited (Stolz 1984, Meisterhans 1988, Urbanska, in press) and the resulting scars in the alpine landscape have remained virtually bare and thus erosion-exposed until today despite commercial revegetation attempts. Our recent study revealed an extremely restricted diaspore deposition on machine-graded and un-restored ski runs (Urbanska et al., in press). However, these results are based on data from one growth period only, and it might be supposed that some diaspores have actually accumulated in the soil over years.

This preliminary study is part of a research programme including soil seed reserves in different high-alpine sites. The present paper deals with the first results obtained in un-restored ski run and in natural grassland. Its aim is (1) to test for the first time a possible development of seed banks in an un-restored alpine ski run within ca. three decades after machine-grading, and (2) to provide information about the seed reserves in an adjacent undamaged high-alpine grassland with abundant standing vegetation. The principal questions asked here are as follows:

(1) Are there soil seed banks in an un-restored degraded ski run and in an intact high-alpine grassland?

(2) Are there significant differences in seed bank density, alpha diversity (species number), species composition, and species frequency between these two sites?

(3) Are there differences between the occurrence and frequency of species in the seed reserve and those represented in the standing vegetation in either site?

Material and methods

The soil cores were collected in the northern slope of Jakobshorn Mountain at ca. 2500 m.a.s.l., in alpine surroundings of Davos, Grisons, NE Swiss Alps. The Jakobshorn Mountain consists of silicaceous substrata. Its natural high-alpine landscape includes grassland with *Carex curvula* as the dominant species, cliff faces and rocky ledges, snow-beds, as well as mostly half-stabilized scree and boulder slopes.

The area is very heterogeneous with relief and plant cover varying over small distance. The downhill ski run, very steep in some parts, was machine-graded in the early 1970s, and mostly traced across the grassland. The vegetation and topsoil were then removed and discarded leaving the mineral soil exposed.

Two ski run plots and one grassland plot were selected for the study (Fig. 1). Growing vegetation in these sites was recorded in phytosociological releves (Table 1) made according to the method of Braun-Blanquet (1964).

The grassland plot virtually bordered the ski run and was separated by only ca. 1 m from the upper ski run plot; the lower ski run plot was situated about 10 m below the upper one. On account of the

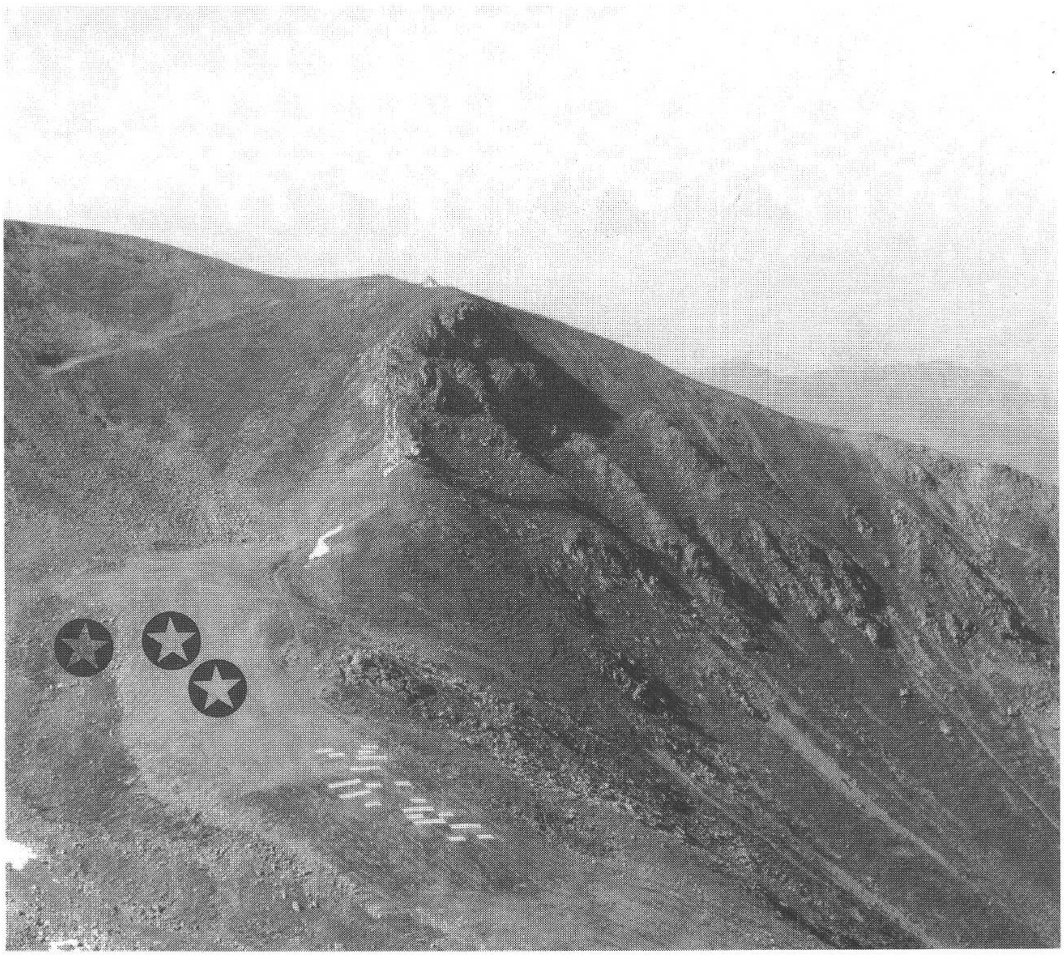

Fig. 1. Jakobshorn Mountain: uppermost part of the northern slope showing an approximate situation of the studied plots marked by asterisks. Note the natural grassland bordering the machine-graded ski run.

pronounced site heterogeneity, each plot was divided into two adjacent but not contiguous sub-plots of 5 m×5 m each. Each sub-plot was further divided into 0.50×0.50 m sections.

Soil cores were taken on July 4, 1996, at randomly selected positions within subplots (Fig. 2). The winter snowmelt occurred about three weeks before sampling, but it was followed by intermittent snowfall so that the vegetation was still dormant. One hundred soil samples were taken in the ski run, whereas those collected in the grassland totalled 50. Each circular core measured 5.4 cm in diameter and 5 cm in depth and included the plant litter on the surface. The soil volume of one core was 114.5 cm^3. Each sample was air-dried before being passed through two sieves of 0.4 cm and 0.2 cm mesh, respectively, to remove stones and debris. The 0.4 cm fraction was discarded. The sieved soil was thoroughly mixed and spread to an approximate depth of 0.7 cm in Petri dishes.

The samples were placed on a well-lit table in a room with a mean temperature of ca. 18 °C under approximate 16:8 light-dark regime. After 66 days they were transferred to a growth chamber with the same light-dark regime, controlled air humidity and day/night temperature (17.3 °C/8.7 °C). The Petri dishes were regularly watered from above with tap water. Abundant mosses appearing in some samples throughout the incubation period were removed.

Many high-alpine species require light for germination. In order to bring buried seeds close to the soil surface, the samples were thoroughly re-mixed three times in ca. 7-week-interval, the first time on the 37^{th} day of the trial. Seedlings were counted, identified to species or genus level whenever possible,

Table 1. Phytosociological releves of the vegetation in grassland and un-restored ski run plots according to the method of Braun-Blanquet (1964). Status as of July 1996. Only two species occurred within the lower ski run plot.

Species	Grassland	Upper ski run	Lower ski run
Agrostis rupestris	2	1	.
Anthoxanthum alpinum	.	.	.
Arnica montana	.	.	.
Bartsia alpina	+	.	.
Cardamine resedifolia	.	1	.
Carex curvula	2	.	.
Chrysanthemum alpinum	2	1	1
Deschampsia flexuosa	.	+	.
Doronicum clusii	+	1	.
Euphrasia minima	2	+	.
Gentiana kochiana	.	.	.
Gnaphalium supinum	1	+	.
Helictotrichon versicolor	.	+	.
Hieracium alpinum	+	+	.
Homogyne alpina	1	+	.
Leontodon helveticus	1	.	.
Linaria alpina	.	+	+
Luzula spadicea	2	+	.
Phyteuma hemisphaericum	+	.	.
Poa alpina	+	+	.
Poa laxa	.	1	.
Primula integrifolia	+	.	.
Rhododendron ferrugineum	+	.	.
Salix herbacea	2	+	.
Saxifraga bryoides	.	+	.
Senecio carniolicus	2	+	.
Sesleria disticha	.	+	.
Soldanella pusilla	2	.	.
Veronica alpina	1	+	.
Cover (%)	65	25	5

otherwise registered as mono- or dicotyledons. Some seedlings not identifiable at early developmental stages were potted and grown until determination.

After the germination trial was concluded, six randomly selected soil samples per site were examined in detail under the disssecting microscope to detect possible dormant or unviable diaspores.

Data for seedlings were converted to seedlings per square metre for comparison. Since the cores were non-stratified, the data for unit area of soil surface also represented the density of seedlings per unit volume. The standard non-parametric test used to assess differences between sub-plots of a given plot, and also between sites was the two-tailed Mann-Whitney *U*-test; statistical significance was set at $p=0.05$. For estimates of spatial patchiness in the seed distribution in samples, the patchiness index (variance to mean ratio) was calculated according to Greig-Smith (1957). In this test the ratio >1 indicates spatial patchiness among soil samples whereas ratios <1 indicate uniform seed distribution among the samples.

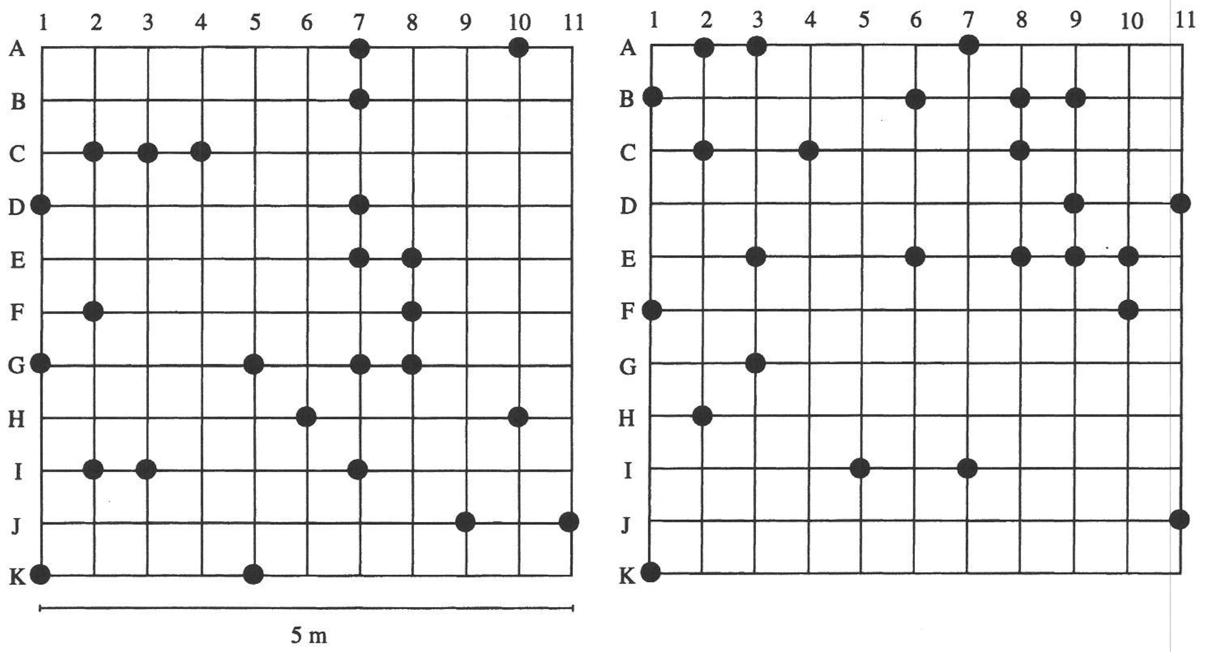

Fig. 2. Pattern of sampling exemplified by the grassland plot. Situation of soil cores randomized by drawing lots marked with black points on intersections of the 50 cm×50 cm grid.

Terminology

Following the classification proposed earlier by the senior author (Urbanska 1992), the terms "seed bank" and "seed reserve" used in this study refer respectively to the seeds representing a single species (=seed population), and to all seeds occurring in a given soil sample (=seed community). The term "seeds" is not restricted to genuine seeds but includes all diaspore types. The species names follow Hess et al. (1967–1972). Seedlings were characterized as forbs or graminoids, where graminoids denote Gramineae, Cyperaceae, and Juncaceae, and forbs include all herbaceous but not graminoid species.

Results

Data and estimations presented in the following part of the paper are based on the seedlings retrieved in germination trial. Most of them emerged within the first two months of the trial. No diaspores, dormant or otherwise, were found in soil samples examined under dissecting microscope after the trial was concluded. The numbers of the emerged seedlings are accordingly considered representative of the whole soil seed reserves in the studied sites.

Seedling density per unit area

The total number of seedlings in 100 samples from the un-restored ski run amounted to a mean of only 52 seedlings per m^2 (±SE 20, Fig. 3). Differences among sub-plots were sometimes considerable but not significant; no seedlings at all were recovered from one sub-plot (Table 2).

The number of seedlings recovered from 50 soil cores sampled in natural grassland amounted to a mean density of 2401±336 seedlings per m^2 (Fig. 3). The number of seedlings

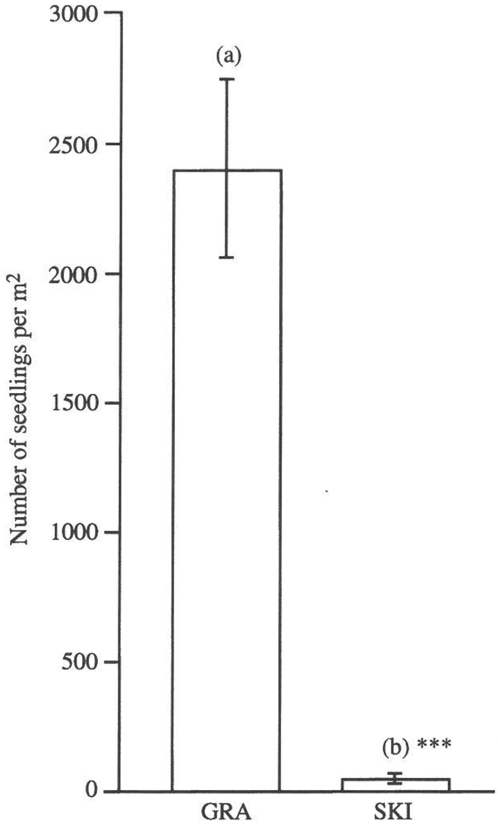

Fig. 3. Seedling density per unit area of soil surface in grassland (GRA) and in ski run (SKI). Means ± SE. Different letters above bars refer to statistically significant differences. *** $p<0.001$. Mann-Whitney test.

Table 2. Seed density per unit area of soil surface and patchiness index. G=grassland; SO=upper ski run plot; SM=lower ski run plot. "a" and "b" refer to sub-plots of each plot studied. Means±SE. * = no seds found within this sub-plot. Sample size, i.e. number of soil cores per sub-plot $n=25$.

Code	Seeds · m^{-2}	$s^2/\bar{x}$
Ga	1658±273	2.6
Gb	3143±582	6.1
SOa	122± 64	2.0
SOb	34± 24	1.1
SMa	*	*
SMb	52± 38	1.7

in one of the two grassland sub-plots studied was nearly twice as high as that in the second sub-plot (Tables 2 and 3); this difference was virtually at the limit of statistical significance ($p=0.0507$, Mann-Whitney test).

The difference in seedling density between grassland and the degraded ski run was highly significant ($p<0.001$, Mann-Whitney test; Fig. 3).

Table 3. Total number of seedlings recorded throughout the trial (duration: 142 days). See Table 2 for plot/sub-plot codes and number of soil samples per sub-plot. * both *Cardamine alpina* and *C. resedifolia* were identified but not all seedlings were determined to species level.

Species	Ga	Gb	SOa	SOb	SMa	SMb
Cardamine sp. *	40	49	1	1	0	0
Chrysanthemum alpinum	0	2	0	0	0	0
Gnaphalium supinum	12	19	0	0	0	0
Luzula spadicea	8	16	0	0	0	0
Poa alpina	1	2	0	0	0	0
Poa laxa	22	58	3	1	0	0
Soldanella pusilla	0	1	0	0	0	0
Veronica alpina	0	1	0	0	0	0
unidentified dicots	11	30	1	0	0	2
unidentified monocots	0	0	2	0	0	1
Total	95	180	7	2	0	3

Patchiness

The distribution of seeds in samples was uneven and generally clumped with the patchiness index ranging from 1.1 to 6.1 (Table 2). The most pronounced clumping was found in one grassland sub-plot. The negligible numbers of seeds found in the cores from non-restored ski run clearly influenced the patchiness.

Alpha diversity and species composition of seed reserves

Only three species were identified among the very few seedlings recovered from soil cores sampled in the un-restored ski run (Tables 3 and 4). The sub-plots of the ski run differed from each other in respect to the species number, an no seedling at all emerged in one sub-plot from the lower ski run plot. All three species determined in the soil seed reserve of the ski run also occurred in the soil cores from the grassland.

Identified species in the seed reserve of grassland totalled 9 with *Poa laxa* clearly prevailing (Tables 3 and 4). The two grassland sub-plots had most of the species in common. Monocotyledons were represented by three graminoids; dicotyledons included six determined forbs and also several unidentified seedlings. Both *Cardamine alpina* and *C. resedifolia* were identified in the studied samples, but an exact proportion of either species could not be determined on account of the high seedling mortality in early life stages. Four seedlings were so deformed that they could not be determined even as monocotyledons or dicotyledons.

Species diversity in soil seed reserves vs. standing vegetation

The comparisons drawn between the data obtained in germination trials and the species lists in phytosociological releves clearly show discrepancies in alpha diversity between standing vegetation and soil seed reserves in the studied sites.

The plants scattered within the upper plot of the un-restored ski run totalled nineteen species (Table 1), but the six identified seedlings in the soil samples represented only three species (Table 3). On the other hand, the three seedlings from the lower plot of the ski run

Table 4. Identified species in soil seed reserve of grassland (G) and ski run (S), and their respective occurrence in natural vegetation. Framed "yes" refers to relatively frequent occurrence in the seed reserve and/or in the standing vegetation; numbers given in brackets refer to codes of abundance-dominance according to Braun-Blanquet (1964). * Both *Cardamine alpina* and *C. resedifolia* occurred in the seed reserve, but only *C. resedifolia* was recorded in the natural vegetation.

Species	Soil seed reserve		Natural vegetation	
	G	S	G	S
Cardamine sp. *	[yes]	yes	no	[yes (1)]
Chrysanthemum alpinum	yes	no	[yes (2)]	[yes (1)]
Gnaphalium supinum	[yes]	no	[yes (1)]	yes
Luzula spadicea	[yes]	no	[yes (2)]	yes
Poa alpina	yes	no	yes	yes
Poa laxa	[yes]	yes	no	[yes (1)]
Soldanella pusilla	yes	no	[yes (2)]	no
Veronica alpina	yes	no	[yes (1)]	yes

remained unidentified but positively did not represent *Chrysanthemum alpinum* or *Linaria alpina* recorded as the only species in the scarce vegetation (Tables 1 and 3).

Of the 19 species listed in the phytosociological releve made in the grassland (Table 1), six were identified in the soil seed reserve (Table 3); in addition, three species not listed in the standing vegetation were found in soil cores (Table 4). Of the five species well represented in soil seed reserve of grassland, only two attained the respective abundance-dominance codes 2 and 1 in the releves; curiously enough, *Poa laxa* which prevailed in the soil cores, did not occur at all in the standing vegetation. Of the three species identified in the soil seed reserve of the un-restored ski run, two were among the most frequent in the scanty vegetation of the site.

Discussion

Our preliminary study has several shortcomings which limit the interpretation of the results: (i) the number of replicate plots and subplots was insufficient for more detailed statistical analysis, (ii) sampling was made only once, and (iii) not all seedlings could have been identified to species. These limitations notwithstanding, the study clearly shows some within-site patterns, and also differences occurring between the intact and the strongly damaged site.

Degraded ski run

The un-restored ski run studied was virtually devoid of seed banks. A direct comparison with another site of this type is not possible given the lack of the available data. However, studies on high-altitude disturbances at the Beartooth Plateau, Montana (Chambers 1993, 1995a, b, 1997) indicate that soil conditions and, in particular, the soil surface characteristics may be decisive in the build-up of the seed reserve in the soil; they may also influence its species richness.

The soil of the studied ski run was still partly unstable. Even ca. 27 years after grading when the topsoil has been discarded, it apparently does not provide suitable conditions for the development of soil seed banks. The site may accordingly be regarded as "no invasion window" (see van der Valk 1992 for the concept) which does not permit the build-up of soil seed reserve and establishment, although natural vegetation is close by.

Older machine-graded ski runs at high elevations may be compared in their general outlook with natural half-stabilized scree slopes. However, the only paper available on soil seed reserve of a high-alpine scree slope, dealing with a site in the Austrian Alps (Diemer and Prock 1993), reported differences in seed number and species composition which are not even roughly comparable. The number of seeds in the soil cores of the ski run studied in our project corresponded to less than 3% of that in the natural site, and the number of species identified corresponded to only ca. 20% of the species assemblage in the Austrian Alps. It should be noted, however, that plants largely scattered over the studied ski run represented only ca. 26% of the species growing in the natural scree slope (Diemer and Prock 1993).

Differences in seed density per unit area between the un-restored ski run and the grassland were highly significant. Established plants were very sparse on the studied ski run so that only the few seeds produced in situ might contribute to seed banks in soil. A recent study in seed rain in the same site revealed a severely limited seed deposition (Urbanska et al. in press); these results suggest that virtually no acquisition of diaspores by seed banks can be expected from outside. The drastic environmental damage of the ski run apparently destroyed the potential for unassisted recovery of vegetation within a reasonable time span. The soil seed reserves of high-alpine plant communities are the signature of their resilience; however, once the site structure and the topsoil is destroyed, the resilience threshold has been crossed so that no unassisted recovery may be expected within decades (Urbanska, in press).

The soil seed reserve of the ski run was studied in a rather extreme, N-facing slope. There may be local or regional differences among graded ski runs situated in different high-alpine landscapes, and further studies are urgently needed to clarify this problem. The studied ski run sector has not been commercially "revegetated"; it would be interesting to compare our results with data from sites in which commercial efforts failed. To the best of our knowledge, however, no such data are available so far.

Soil seed reserve in alpine grassland

The seed banks in the intact grassland were well developed. This result was expected as the *Caricion curvulae* represents vegetation of considerable age. Our data in seed density per unit area conform to the report from another site in the alpine surroundings of Davos (Hatt 1991) but differ from the results obtained in the South Tyrolean Alps (Niederfrinniger-Schlag and Erschbamer 1995). The differences are not surprising because the Alps extend over a vast territory which includes various floristic, edaphic, and climatic regions. Reports from other parts of the world also show large local and regional size differences of soil seed reserve in alpine or high-subalpine grassland (Archibold 1984, Chambers 1993, Ingersoll and Wilson 1993, Roach 1983, Morin and Payette 1988, McGraw and Vavrek 1989, Semenova and Onipchenko 1994, Spence, unpublished data). More studies from well-spaced sites are needed to obtain a better understanding of a possible variation occurring within the whole territory of the Alps.

The species number in the soil seed reserve of the grassland was rather limited. It should be remembered, however, that not all dicotyledonous seedlings were identified. Our results are generally comparable to the data from the Southern Alps and do not seem to be influenced by number of samples or duration of the germination trial. On the other hand, nearly twice as many species were previously found in the soil seed reserve of a grassland also situated in the surroundings of Davos (Hatt 1991), but the plant cover of that grassland included many more species than the vegetation in our plots (44 vs. 19). A strong positive correlation between species richness in the soil seed reserve and that in the standing vegetation have been sometimes observed (McGraw and Vavrek 1989, Roach 1983), but discrepancies between species number in growing vegetation and the soil samples have also been reported, both from high elevation sites (Ingersoll and Wilson 1993, Morin and Payette 1988, Weidman 1983) as well as lowland ecosystems (see e.g., Hutchings and Booth 1996). Soil seed reserves are likely to change in space and time; these changes may show a large-scale pattern but they may also be very local. It would thus be very desirable to study the seed banks of the species occurring in the *Caricion curvulae* over a period of time, preferably over several consecutive years. For a better assessment of the seed bank dynamics, sampling at the beginning and towards the end of the growth period would be recommended.

Highly significant differences between the intact grassland and the adjacent un-restored ski run demonstrate that colonization of disturbances at high elevation largely depends on conditions suitable for diaspore trapping and seedling establishment (Chambers 1995a, b, Chambers et al. 1991, Urbanska, 1997b). Enhancing in situ seed production and colonization should accordingly be considered a major issue in restoration of dramatically disturbed alpine sites. Of a special interest in this respect are studies on sil seed reserves in restoration plots in which conditions for diaspore entrapment and seedling recruitment have been provided; they will be considered in the second paper in this series (Urbanska and Fattorini, in preparation).

We are grateful to Professor Elias Landolt who made the phytosociological releves in the field and greatly helped with determination of young seedlings. Thanks are also due to Silvia Erdt who took good care of the soil samples during their incubation at the field station in Davos, as well as to Anita Hegi and Stefan Locher for their technical assistance. Helpful comments on the manuscript contents and the linguistics offered by Jeanne C. Chambers and Nigel R. Webb are very much appreciated. An anonymous reviewer provided constructive critics of the paper.

Zusammenfassung

Diese Pilot-Studie untersucht Samenbanken in Böden von zwei hochalpinen Standorten, um das Potential for die spontane Erholung nach einer Beschädigung zu erfassen. Die Verhältnisse in einer nicht renaturierten, vor rund 27 Jahren planierten Skipiste wurden mit jenen im benachbarten ungestörten Grasland verglichen. Dies ist der erste Bericht über Samenbanken in einer degradierten hochalpinen Skipiste.

In den Skipistenböden umfaßte die mittlere Dichte des Samenvorrates lediglich 52±20 Samen pro m^2, obwohl die Piste fast drei Dekaden vorher planiert wurde und eine ungestörte Pflanzendecke in nächstger Nähe vorkam. Der entsprechende Wert für benachbartes intaktes Grasland lag dagegen bei 2401±336 Samen pro m^2. Nur drei Arten wurden im Samenvorrat der Skipiste identifiziert, während im Grasland neun Arten auftraten. Die Verteilung der Arten im Bodenvorrat war unregelmäßig. Nicht alle in Bodenproben gefundene Arten haben zur Pflanzendecke der entsprechenden Standorte beigetragen. Das Muster der Arten-Dominanz im Samenvorrat des Bodens entsprach nicht demjenigen der bestehenden Vegetation.

Die Ergebnisse lassen vermuten, daß keine spontane Erholung der Pflanzendecke der Skipiste aus dem Samenvorrat im Boden in einer absehbaren Zeit erwartet werden kann. Es wird daraus geschlossen, daß ein verbesserter Sameneintrag sowie die Samenproduktion an Ort und Stelle als eine wichtige Komponente der Renaturierung solcher Standorte betrachtet werden muß.

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