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Reproduction by seed in alpine plants and revegetation research above timberline

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Abstract

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The paper deals with various aspects of reproduction by seed in plants inhabiting extreme ecosystems above timberline and their relevance to alpine revegetation research.

Seeds represent a largely maternal investment; their production is environmentally controlled, either indirectly via resources the mother plant is supplied with or/and directly via meteorological conditions during seed formation. Seed dormancy in alpine plants may be innate, induced or enforced; the latter type, appearing at the end of growing season, may obscure the former mechanisms. Seed coat-influenced innate dormancy seems to be rather frequent in alpine plants the seeds of which often respond well to scarification.

Establishment represents a further risk-exposed phase of life cycle in alpine plants and safe sites are of primary importance. The authors argue that safe sites not only are taxon-specific and habitat-specific but also ecosystem-specific, and propose a general concept of safe site above timberline. Differences between areas above and below timberline are emphasized. Alpine ecosystems have a low-nutrient budget but plants apparently are well-adapted to these conditions; a safe site in the alpine belt is therefore not expected to have an excessively nutrient-rich soil, other features apparently being more relevant. The safe site concept proposed by the authors is therefore valid for alpine plants only.

The importance of alpine revegetation research focusing upon native plants of high altitudes as a potential material for biological erosion control in the Swiss Alps is stressed.

Key words: seed formation – germination – dormancy – establishment – safe site – revegetation research

Introduction

This paper is the second in a series dealing with life history strategies in plants, especially in taxa inhabiting extreme ecosystems. In the previous publication on asexu-

ally reproducing plants and their population structure, the senior author referred to numerous arctic-alpine plants (Urbanska 1985). In the present contribution special attention is paid to reproduction by seed without specific distinction between sexual and asexual reproduction; except for a single case, the present paper deals with taxa occurring above timberline in the Swiss Alps. Not only true seeds but also specialized forms of fruits, e.g., achenes and/or caryopses, function as units of dispersal and survival in the Angiosperms. They are hereafter simply referred to as seeds.

Revegetation research focused on native plants of the alpine vegetation belt as potential materials for biological erosion control above timberline is exceedingly rare in Europe; to the best knowledge of the authors, the Geobotanical Department of SFIT Zürich is the only institution carrying out the experimental revegetation studies with alpine plants at high altitudes. The aim of the present paper is to point out some aspects of reproduction by seed in alpine plants that may prove useful for further revegetation research, urgently needed if revegetation above timberline is to succeed in the long run.

Seed – a maternal investment and an environmental control

Reproductive success in seminiferous Angiosperms can be defined as the production of sporophyte progeny by the mother sporophyte. The developing embryo depends on its mother plant for nourishment and protection.

Seeds may be produced sexually or asexually; depending on particular mechanisms involved in seed formation, maternal investment in seeds largely prevails over paternal contribution or is even exclusive (Table 1), but in all cases reproduction by seed proceeds at the expense of the mother plant. The more limited the budget on which the mother plant is living is, the more costly its maternal care will be and the more rigorous resource allocation is to be expected.

Numerous authors (e.g. Baker 1972) argued that there is a close tie between seed size and physical environment, and that seed size influences the probability of successful germination and seedling survival (e.g. Werner 1977, 1979). Seed size and number are frequently considered as apparent alternatives in the strategy of reproduction (e.g. Harper 1977). According to Smith (1975), a compromise seed size conferring a maximized inclusive fitness is larger in harsh environments than in more mesic ones (see also Solbrig 1980).

Tab. 1. Various forms of reproduction by seed and origin of seed components

Reproduction	Breeding system	Origin of progeny	Embryo	Endosperm	Seed coat
sexual	allogamy	biparental*	♀ + ♂	♀ + ♂	maternal
sexual	autogamy	uniparental**	♀ + ♂	♀ + ♂	maternal
asexual	autonomous agamospermy	uniparental	♀	♀	maternal
asexual	pseudogamy	uniparental	♀	♀ + ♂	maternal
asexual/ sexual	facultative agamospermy	uni- or biparental	♀ or ♀ + ♂	♀ or ♀ + ♂	maternal

*.** The terms “biparental” and “uniparental” refer to cases where gametes are contributed by two different individuals and a single individual, respectively.

Tab. 2. Dry biomass in some seeds from alpine and subnival vegetation belt in the Swiss Alps; mean values of five samples. Unpublished data of M. Schütz

Family	Taxon	Dry weight (g)/100 seeds
Fabaceae	<i>Trifolium badium</i>	0.090 ± 0.002
	<i>Trifolium Thalii</i>	0.102 ± 0.004
	<i>Trifolium nivale</i>	0.122 ± 0.004
	<i>Trifolium alpinum</i>	0.456 ± 0.010
	<i>Lotus alpinus</i>	0.118 ± 0.004
	<i>Oxytropis campestris</i>	0.216 ± 0.006
	<i>Oxytropis Jacquinii</i>	0.314 ± 0.004
	<i>Anthyllis alpestris</i>	0.327 ± 0.008
Caryophyllaceae	<i>Sagina Linnaei</i>	0.004 ± 0.000
	<i>Moehringia ciliata</i>	0.040 ± 0.000
	<i>Cerastium latifolium</i>	0.062 ± 0.004
	<i>Gypsophila repens</i>	0.070 ± 0.004
	<i>Silene Willdenowii</i> (= <i>S. glareosa</i>)	0.083 ± 0.008
Asteraceae	<i>Achillea atrata</i>	0.032 ± 0.004
	<i>Chrysanthemum alpinum</i>	0.041 ± 0.002
	<i>Hieracium intybaceum</i>	0.048 ± 0.006
	<i>Hieracium alpinum</i>	0.060 ± 0.010
	<i>Taraxacum alpinum</i>	0.064 ± 0.006
	<i>Doronicum Clusii</i>	0.076 ± 0.006
	<i>Leontodon hyoserioides</i>	0.138 ± 0.004
	<i>Cirsium spinosissimum</i>	0.234 ± 0.020

Alpine ecosystems are well-known for their low-nutrient budget and exceedingly harsh life conditions (Billings 1974, Bliss 1962, 1980, Landolt 1983, Urbanska 1984, 1985, 1986, Urbanska, in press). As revealed by our studies, the seeds of plants inhabiting the alpine and subnival vegetation belts generally have rather limited biomass (Table 2). These values are, however, relative, as seeds in closely related taxa inhabiting lower altitudes tend to increase in size along an altitudinal gradient (Landolt 1967). Seed size in alpine plants may vary from one taxon to another within a given genus or even within a single individual; for instance, the largest legume seeds found in the material from our research area were those of *Trifolium alpinum* (2.5 mm) whereas *T. badium* had the smallest (1.6 mm). A pronounced variation in seed size even within a single fruit was observed in, e.g., *Lotus alpinus* (Urbanska unpubl., Weilenmann 1980). It should be added that biomass and size of seeds produced by various taxa inhabiting a given alpine site frequent do not correlate, so that seed size cannot be classified by habitat alone.

The trade-off between individual seed size and seed number in alpine plants cannot be assessed unequivocally, either. Independent of seed size, large fluctuations occur in the seed output per individual, within and between populations and also from year to year (e.g. Fossati 1976, 1980, Schütz 1983 and unpubl., Urbanska 1985, 1986, Urbanska, in press). The unpredictable environmental conditions above timberline seem to defy reproductive strategies based on seed number.

The ultimate environmental control of seed production may be exemplified by *Cirsium spinosissimum*, currently studied in our research program. This pan-Alpine en-

demic species is very successful in scree and talus slopes at high altitudes, both upon siliceous as well as on calcareous substrates. Leafy flowering shoots of *C. spinosissimum*, unusually tall for a high-altitude plant, bear numerous capitules assembled in a head-like group. Prickly leaves and involucre protect the plants and their reproductive structures rather effectively from cattle and sheep, an occasional grazing by ibex apparently being of no consequence. The energetic cost of producing anti-herbivore structures is supposed to result in less competitive plants or in a lower seed output (Solbrig 1980); the reproduction by seed in *C. spinosissimum* seems to confirm this assumption at first sight, for the number of developed achenes per capitule is generally low. It should be stressed, however, that seed output in *C. spinosissimum* may also be nil if the weather conditions are unfavourable, as witnessed by the present authors in, e.g., 1984.

It seems that the environmental control of seed production may operate indirectly via resources the mother plant is supplied with and/or directly via meteorological conditions during the seed formation period. As far as the areas above timberline are concerned, the latter factor appears to be of particular importance.

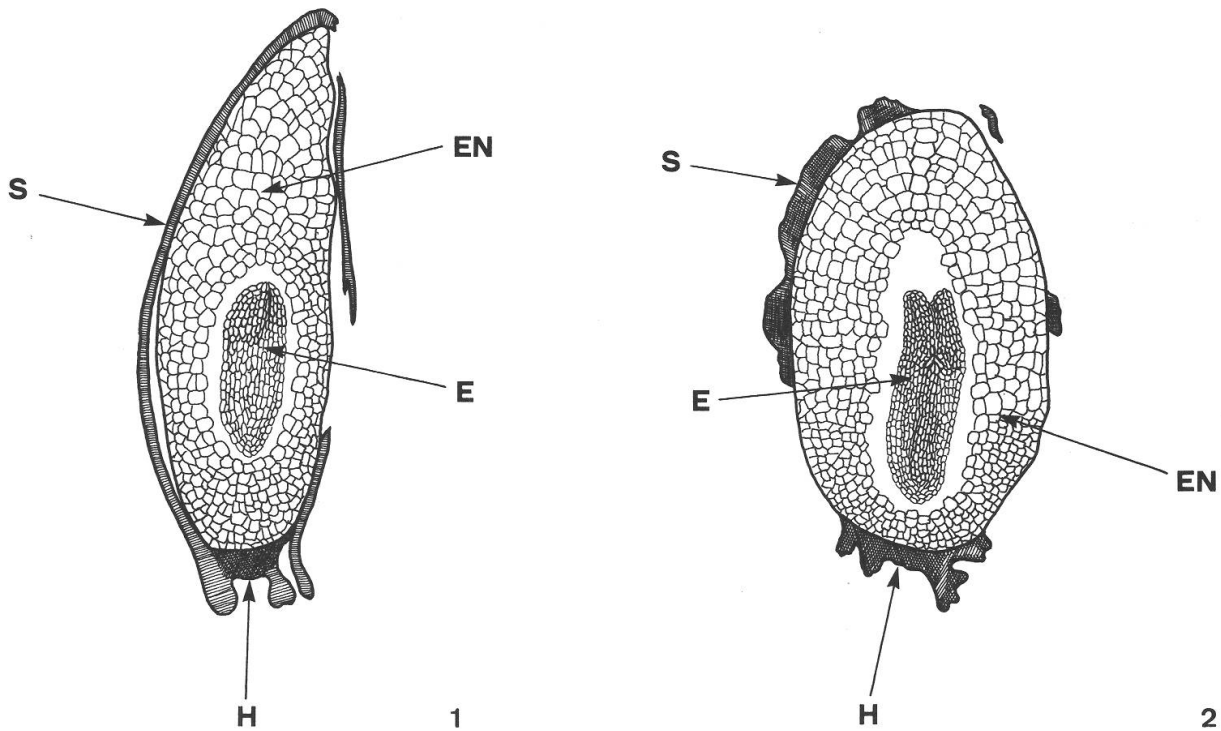
Seed dormancy and germination in alpine plants from Switzerland

Seed dormancy has been defined by some authors (e.g. Amen 1968) as a state in which viable seeds fail to germinate under conditions favourable for vegetative growth. Harper (1957) distinguished between "seeds that are born dormant, those which acquire dormancy and those which have dormancy thrust upon them"; later, he proposed to distinguish between innate, induced, and enforced dormancy and considered the two latter phenomena as opportunistic (Harper 1977).

Seed dormancy and germination has been the subject of very numerous reviews, both their physiology and ecological aspects being discussed in detail. The aim of the present paper is not to offer lengthy comments on all possible aspects and mechanisms but to focus rather on the behaviour of some alpine plants from Switzerland studied by our group.

Innate dormancy refers to the inability of seeds to germinate under favourable conditions immediately after removal from the mother plant. It may be caused, among other factors, by an incomplete development of the embryo. This category is represented in our material, by e.g., *Ranunculus Grenierianus*. In seeds of *R. Grenierianus* Fossati (1976) observed a multicellular but not differentiated embryo occupying only about $\frac{1}{10}$ of the total seed volume and surrounded by well-developed endosperm. Weilenmann (1980, 1981) found no differences in this seed material after five years of dry storage; on the other hand, the embryo in seeds of *R. Grenierianus* harvested in the same alpine area in another year was completely differentiated, albeit small, and occupied about $\frac{1}{4}$ of the total seed volume. Germination percentages were negligible in both series, in spite of the developmental differences.

Differentiated but small embryos are representative of the genus *Gentiana*, but were also found in other families, e.g., *Campanula barbata*, *Soldanella pusilla*, and *Pulsatilla alpina* (Figs. 1–2). An intermediate situation is represented by *Ligusticum Mutellina* where an exceedingly small embryo (about $\frac{1}{20}$ of the total seeds volume) had rather well-defined primordia of cotyledons (Weilenmann 1980). Innate dormancy due to an incomplete development of the embryo may sometimes be broken by pretreatment of seeds with gibberellin (Dickenmann 1982, Müller 1977); in some cases, however, better results were obtained when the gibberellin treatment was combined with scarification



Figs. 1–2. Seed anatomy in some alpine plants. 1. *Campanula barbata*. 2. *Gentiana nivalis*. E=embryo; EN=endosperm; S=seed coat; H=hilum. About 60 \times . Redrawn from Fossati (1976).

(Fossati 1976, 1980, Schütz unpubl.). It should be noted that these treatments are not always effective (Weilenmann 1980, 1981). The post-maturation period in seeds with underdeveloped embryos may range from a few months (e.g. *Soldanella pusilla*, Weilenmann 1980, 1981) to one year or more.

Another well-known cause of innate dormancy is physical restriction of water or gas access due to the structure of the seed coat (Harper 1977). This kind of dormancy can be at least partially broken by scarification and occurs rather frequently in taxa inhabiting sites above timberline in the Swiss Alps (Fossati 1976, 1980, Urbanska et al. 1979, Weilenmann 1980, 1981, Zuur-Isler 1981, 1982, Schütz 1983 and unpubl.); it was also reported from other alpine areas, e.g., the Rocky Mts (e.g. Pelton 1956, Amen 1966). As far as our material is concerned, scarification proved so far to be effective in 45 out of 113 taxa studied.

Induced dormancy is supposed to appear as a result of some experience the seeds had after release from the parent (Harper 1977). In plants from high altitude sites, induced dormancy is rather difficult to assess, and further studies are indispensable. A rather good example is *Gypsophila repens*. Three months old, dry-stored seeds of this taxon germinated exceedingly well under controlled laboratory conditions (Fig. 3); on the other hand, seeds about nine months old from the same harvest, also dry-stored and then sown in the field in early summer, germinated only in four per cent of the cases although other taxa responded well to favourable environmental conditions. After having passed the whole growing season and the following winter in the alpine soil, seeds of *G. repens* germinated well and gave rise to vigorous seedlings (Schütz unpubl.).

Biscutella levigata represents a rather complex case where both induced and enforced dormancy seem to influence the behaviour of seeds. Three months old seeds of

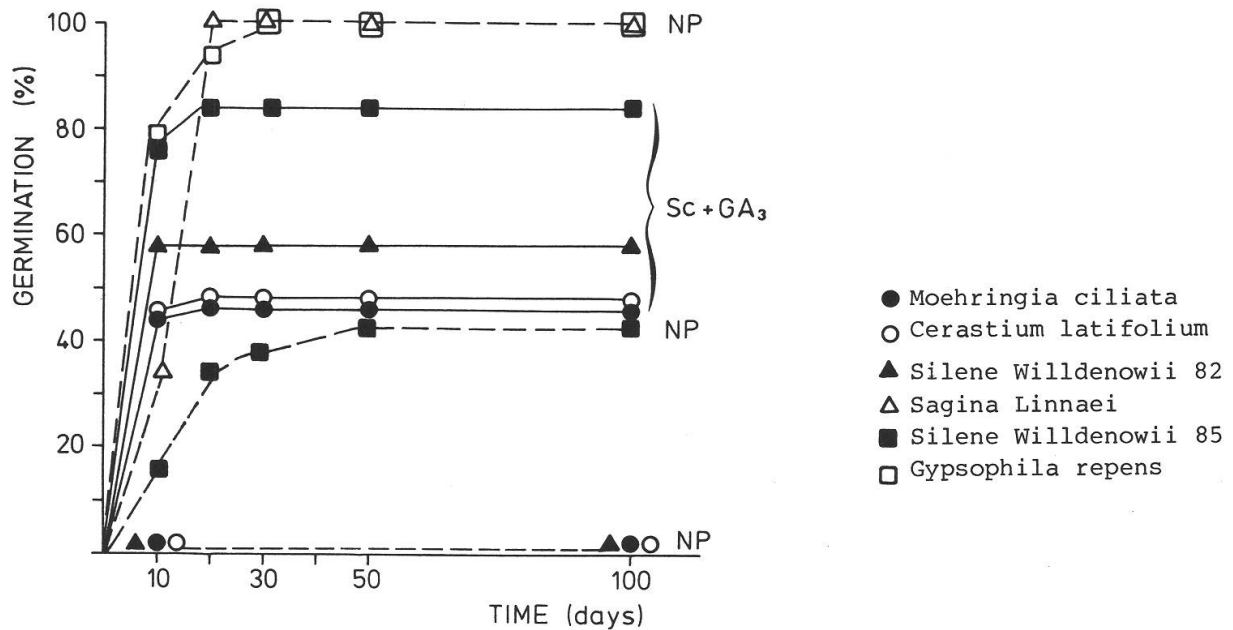


Fig. 3. Germinating behaviour of some alpine taxa of the Caryophyllaceae. NP=no seed pre-treatment; Sc + GA₃=mechanical scarification combined with gibberellin treatment. Except for data on *Sagina Linnaei* (Fossati 1980), results of Schütz (1983 and unpubl.).

this taxon, dry-stored prior to the laboratory trials, germinated rather rapidly and well (Weilenmann 1980, 1981). Germination of freshly harvested seeds was still better; on the other hand, seeds sown in the field soon after the harvest in early fall did not germinate until the following summer, but then germination was gradual, and seedlings continued to emerge throughout four consecutive growing seasons (Gasser 1986). Nine months old, dry-stored seeds sown in the field in early summer germinated only in 4% of the cases and germination improved only after the seeds had remained in the soil throughout the growing season and the following winter (Schütz unpubl.).

Seed dormancy is sometimes variously interpreted. For instance, Hyde (1954) argued that the seed coat-influenced dormancy in the Leguminosae is induced and regulated by the hilum; on the other hand, our experimental studies that include the hilum excision strongly suggest an innate dormancy *sensu* Harper (1977) in alpine legumes (Fossati 1976, 1980, Urbanska et al. 1979, Weilenmann 1980, 1981, Schütz 1983 and unpubl.).

Enforced dormancy depends on the maintenance of an unfavourable environmental situation, e.g., physical stress (Angevine and Chabot 1979). It seems to be a rather general feature in alpine plants at the end of the growing season. In our research area, virtually no seedlings were observed in autumn, and seedling emergence was mostly noted within the first ten days after the snow had melted in early summer (Fossati 1976, 1980, Dickenmann 1982, Zuur-Isler 1981, 1982, Schütz 1983 and unpubl., Schütz und Urbanska 1984). It should be stressed, however, that enforced dormancy in alpine plants may frequently obscure other dormancy mechanisms and certainly does not represent the only aspect of behaviour in plants inhabiting high altitude sites. Billings (1974) argued that most seeds in alpine locations in fact have no dormancy and the elapsed year or more between seed production and germination is environmentally imposed. In our material, seeds of 49 taxa germinated well under labora-

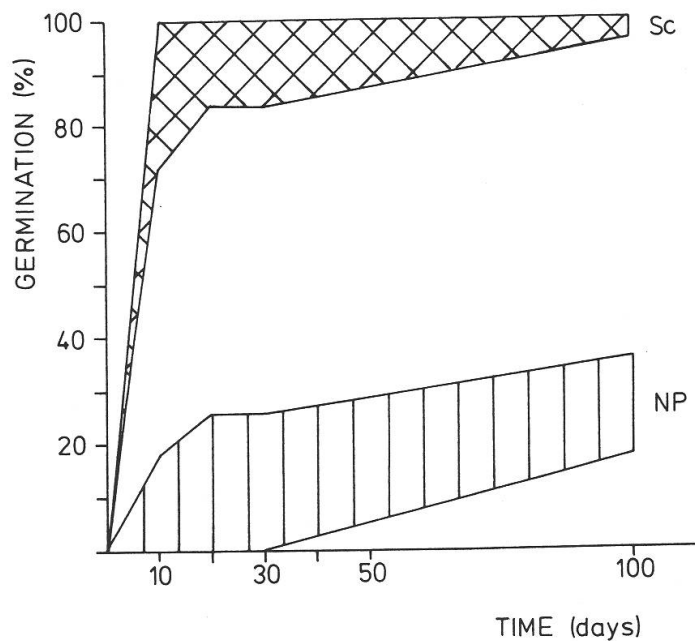


Fig. 4. Pattern of germinating behaviour in most alpine legumes. NP=no seed pretreatment; Sc=mechanical scarification.

tory conditions three months or later after harvest and subsequent storage, no pretreatment being required; the enforced dormancy concept applies to the behaviour of these taxa in their natural sites. However, in numerous alpine taxa germination under laboratory conditions is very poor or nil and it is rather difficult to explain this behaviour in terms of enforced dormancy.

As demonstrated by our studies, germination in alpine plants is exceedingly varied; no consistent patterns emerge from results obtained so far, in spite of rather ample material studied. Germinating behaviour of seeds in a given taxon may vary from year to year, from site to site, from one population sector to another, and also within a single individual. Germinating behaviour within a given plant family most frequently does not follow a single pattern either, as exemplified by the Caryophyllaceae (Fig. 3). Alpine legumes are, to some extent, comparable to each other (Fig. 4), but even within this group there are exceptions: some seeds samples of *Oxytropis campestris*, *O. Jacquinii*, and *Lotus alpinus* germinated quite well without scarification, contrary to the usual pattern observed in the Leguminosae studied (Weilenmann 1980, 1981, Schütz 1983 and unpubl.). It might be supposed that superficial abrasions of the seed coat were sufficient for stimulating germination in this material, but further studies are required.

For illustrating a particularly pronounced diversity in germinating behaviour and dormancy-breaking pretreatment requirements, some grasses and graminoids frequently occurring in our study area have been selected. In *Nardus stricta*, for example, germination percentages in non-pretreated seeds were nil to 16%; removal of glumes improved the germination only in two per cent (Fossati 1980). Seeds of *Sesleria coerulea* germinated in various percentages (22–74%), but removal of glumes considerably improved germination (86%, Fossati 1980). Non-pretreated seeds of *Agrostis rupestris* germinated still better than those of *Sesleria coerulea* (80%), and removal of

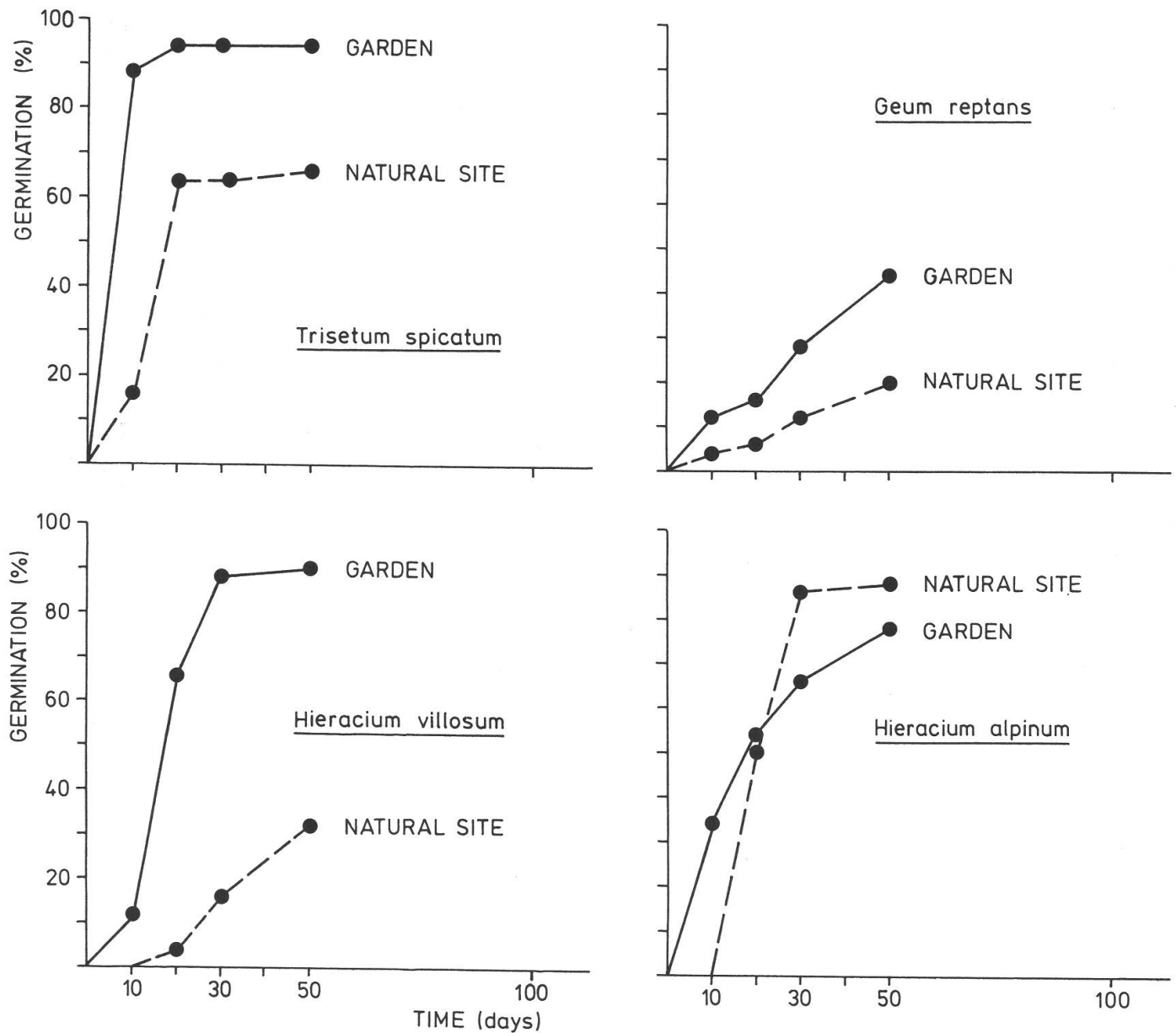


Fig. 5. Germinating behaviour in four alpine taxa: seeds grown in experimental garden (400 m a. s. l.) and collected in original populations (about 2500 m a. s. l.). Data refer to non-pretreated seeds.

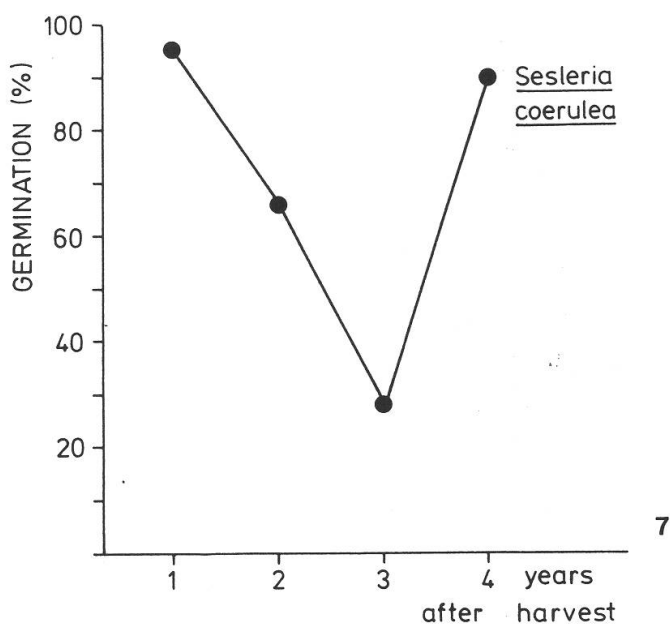
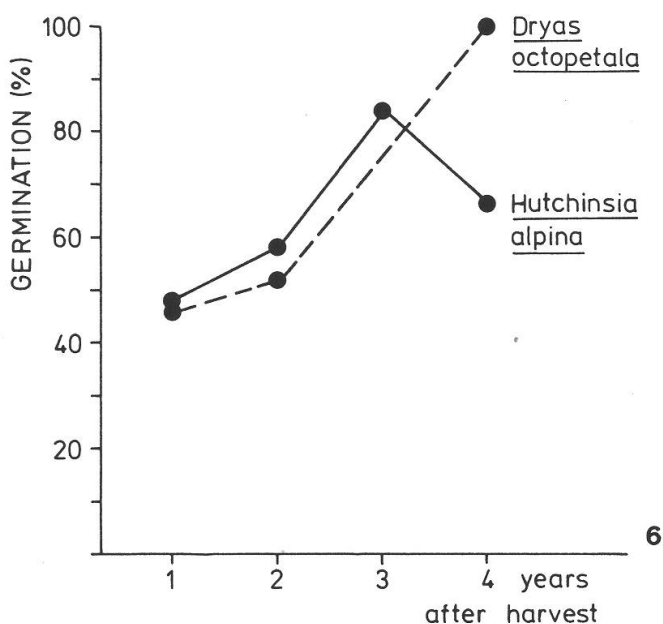
glumes further increased germination percentages (Schütz 1983). In *Trisetum distichophyllum* removal of glumes combined with gibberellin pretreatment increased germination percentages from 22 to 92 per cent, but removal of glumes only or the gibberellin pretreatment only were not very effective (Schütz unpubl.). *Helictotrichon versicolor* seeds did not germinate at all or germinated rather poorly without pretreatment when they were three months old; removal of glumes improved germination to some extent (Fossati 1980, Schütz unpubl.), but the most important factor in this case seems to be the age of the seeds: in recent experiments germination in seven years old seeds of *H. versicolor* approached 100% (Schütz unpubl., in Urbanska 1986).

Seeds of *Carex parviflora* were completely dormant, but precise scarification of the radicle area resulted in exceedingly good germination (98%, Weilenmann 1980, 1981).

In *C. firma* three to six months old seeds germinated in 28% without pretreatment; germination percentages increased to 42% after removal of the utricule, scarification of the radicle area resulted in 52% of germinating seeds, but the best results were obtained after chemical scarification with H_2SO_4 , the corresponding percentage being 66% (Weilenmann 1980, 1981). Curiously enough, the same high germination percentage was obtained in non-pretreated but two years old seeds that had been dry-stored prior to the laboratory trials (Fossati 1980). In *Kobresia myosuroides* the complete dormancy proved as yet unbreakable and further treatments are planned (Elmer unpubl.). Seeds of *Luzula spadiccea* harvested in 1982 exhibited complete dormancy, but those produced in 1983 germinated for 80% without any pretreatment (Schütz 1983 and unpubl.); on the other hand, germination in *L. multiflora* was variable in seeds from a single harvest, the corresponding percentages ranging from 60 to 100% (Fossati 1980).

A further interesting aspect of variation in germinating behaviour in alpine plants emerged in recent studies of the junior author. Well-developed plants of four alpine taxa were brought from their natural sites to the experimental garden of the Geobotanical Department in Zürich and remained in a cold frame over the winter. Seeds harvested in the garden and those produced in the original populations next summer were tested for their germination after dry storage of a few months. In three taxa studied, germination in garden-grown seeds was better than in samples collected above timberline (Fig. 5). Conditions under which seeds are produced apparently sometimes influence not only the seed output but also germination.

Seeds in most alpine plants remain viable for at least a few years. Germination rates and/or percentages decrease sometimes with seed age; however, in numerous plants older seeds germinate well and some taxa manifest an improved germination with increasing seed age (Fig. 6); a cyclic germination pattern may also occur (Fig. 7). Our results suggest that the seed bank in soils above timberline consists of numerous seed generations, and seedlings emerging in a given growing season may well represent various age classes.



Figs. 6–7. Tendencies in germinating behaviour of some alpine taxa. 6. *Hutchinsia alpina*. 7. *Sesleria coerulea*. Data refer to non-pretreated seeds. After Fossati (1980).

Seed dormancy is generally considered a strategy of escape from unfavourable environmental conditions (e.g. Amen 1966) and an alternative to dispersal. An prolonged period of life spent as a buried and dormant seed may increase individual fitness in hazardous conditions. Intermittent germination over a longer period of time can thus be of survival and success value to alpine populations, especially to those living near the limit of growth in the Alps. In this perspective, behaviour of high altitude plants, reflecting the unpredictability of life conditions above timberline, supports the opinions of Harper (1977) that age takes on a new significance for organisms that have long-lived seeds.

Establishment and safe sites above timberline

Reproduction by seed is a high-risk strategy not only because of hazards involved in seed production and dispersal; the establishment phase, when the life-form of the plant changes from a cryptobiotic seed to a physiologically autonomous individual, is equally critical for survival.

The establishment period has sometimes been defined as the time from germination to a the production of the first pair of true leaves (Solbrig 1980). An established seedling is expected to have its photosynthetic surface expanded beyond that of the cotyledons and to have its radicle immersed in the soil, so that uptake of water and mineral nutrients is possible. At this stage, site exploitation is beginning. Early developmental phases are very important in the life cycle of plants, physical and/or biotic stresses greatly influencing the dynamics of seedling populations. Essential requirements at the establishment phase comprise thus a) availability of resources indispensable for successful development, and b) protection from environmental hazards. These basic requirements have been included into the concept of safe site developed mostly by Harper and his collaborators.

Safe site has been defined as a set of habitat conditions that favour germination and seedling establishment (Harper 1977, Harper et al. 1970, Cook 1979); more precisely, it refers to the immediate environment of the seed, i.e., soil microtopography, moisture status, light conditions, and temperature. Safe sites are specific for a given taxon (Harper et al. 1961); their availability is supposed to determine largely abundance and species diversity in a given habitat (Harper et al. 1965, Harper and Benton 1966, Sheldon 1974). For that reason they are considered important regulators of plant population dynamics (Harper 1977).

The concept of safe site is generally applicable. However, it should be remembered that the taxon-specific and habitat-specific safe sites have to fit into the general ecological frame of life conditions characteristic of a given ecosystem. This point is rather important because a given stress (e.g., nutrient deficiency) may be naturally associated with some environments but in others it represents an isolated hazard. Safe sites are supposed – per definition – not only to provide elements necessary for establishment but also to exclude risks; they should therefore be defined by hierarchy of importance of hazards characteristic of a given ecosystem.

We propose now to consider summarily the life conditions occurring above timberline. For more detailed information, the reader is referred to, e.g., Billings (1974), Billings and Mooney (1968), Bliss (1971, 1980), Landolt (1983); more ample literature is available on the subject. It should be emphasized that subnival and alpine en-

vironments are entirely different from those of the subalpine vegetation belt and assessments made for the latter areas are hardly valid for the former.

Alpine ecosystems are known for their low heat budget resulting in a short growing season, cold winters and chilly summers with extreme temperature fluctuations. Unlike the situation in the subalpine belt, the physical environment dominates the vegetation, modifications of the microclimate by plants being generally minimal and very local. Much of the alpine landscape is characterized by scattered plants that are often separated by patches of raw soil, talus or rock. The patterning in alpine vegetation is largely due to local moisture gradients, not only the actual soil moisture content but also wind action playing an essential rôle.

Numerous authors argued that major sources of seedling mortality are water stress (e.g. Cook 1979, 1980, Mack 1976, Solbrig 1980, Sharitz and McCormick 1973) and herbivore damage (e.g. Solbrig 1980). As far as the areas above timberline are concerned, summer and winter drought and also frost action represent some of the most important hazards; the latter factor may operate directly upon plants or indirectly via affected stabilization of soil (cryoturbation). Overgrazing is locally important but presumably not as extensive as below timberline; the growth pattern of numerous alpine plants (e.g. flat, small rosettes) often has a protective value.

It has long been recognized that alpine soils are rather poorly developed and generally have a low-nutrient budget, some nutrients being limiting. Also in this respect, alpine and subnival habitats strongly differ from most of the subalpine environments where soil development is usually advanced and soil nutrient content is often rather high. It should be noted, however, that tundra plants living in low-nutrient environment presumably are well adapted to low nutrient availability and have been se-

Tab. 3. Seedling mortality (%) in contrasting habitats of alpine vegetation belt. Calculated from experimental data of Fossati (1980). S/F = summer/fall

Habitat	Soil surface	First year S/F	First winter	Second year S/F
Acidic silicate:				
snow-bed	vegetation-covered	18.7	57.6	0.0
	bare (denuded)	45.9	10.0	47.6
S-facing slope	vegetation-covered	0.0	0.0	0.0
	denuded	72.7	11.1	24.4
wind-exposed hummock	vegetation-covered	0.0	0.0	0.6
	denuded	20.0	38.6	36.0
Dolomite:				
snow-bed	vegetation-covered	30.2	15.0	9.1
	denuded	32.8	6.6	6.5
S-facing slope	vegetation-covered	20.6	0.0	23.6
	denuded	22.8	0.0	4.7
wind-exposed hummock	vegetation-covered	33.3	0.0	10.0
	denuded	17.1	4.1	0.4

Silicate plots: seeds of 9 taxa harvested on silicate, 100 seeds/taxon/plot.

Dolomite plots: seeds of 11 taxa harvested on dolomite, 100 seeds/taxon/plot.

lected for maintenance of high physiological efficiency under such conditions rather than for a large growth response to nutrient availability (Shaver and Chapin 1980). Not only various physiological features, but also some life history strategies demonstrate that functioning of alpine plant populations is not impaired by nutrient limitations and other adverse conditions occurring above timberline (Urbanska 1985, 1986).

As far as the establishment phase in high altitude plants is concerned, data on seedling population dynamics are scarce. Two reports from our research area deserve a brief mention. Experimental data of Fossati (1980) suggest that protection by standing crop and plant litter may enhance the survival of seedlings in sun- and wind-exposed sites on acidic silicate, whereas data from comparable habitats on dolomite show much more variations (Table 3). Seedling losses observed in summer and early fall by Gasser (1986) in natural populations of *Biscutella levigata* on dolomite were generally similar to those reported by Fossati from roughly comparable experimental plots (18.1 vs. 20.6% in the first season, 23.9 vs. 23.6% in the second), but winter losses were strikingly different (Tables 3–4). It seems that small differences in microenvironmental parameters may indeed be decisive for the fate of seedlings, and the importance of safe sites of plants reproducing by seed in extreme alpine areas is primary.

Further studies are required for gaining a better insight into patterns and processes accompanying the establishment in high altitude taxa; however, successful establishment cannot be assessed by the accumulation of aboveground biomass alone, as the first year of life in many alpine plants may be mostly devoted to root-system establishment (Urbanska 1985, 1986, Schütz 1983 and unpubl.).

For future purposes it seems useful to define in a general way the safe sites above timberline (Table 5). Our aim is to distinguish life conditions and major hazard characteristics in the alpine and subnival vegetation belts from those occurring in subalpine areas. Safe sites will have to be further assessed in relation to a given taxon as well as a given alpine habitat, the substrate being particularly important. Some of the features specified as site conditions obviously overlap with those listed as hazards from which safe sites are expected to protect, but it cannot be avoided, as the two factor groups are

Tab. 4. Seedling mortality (%) in natural populations of *Biscutella levigata* in various habitats of alpine vegetation belt. Unpublished data of M. Gasser

Habitat	Soil surface	First year S/F	First winter	Second year S/F
Dolomite:				
scree slope	bare	8.9	18.8	24.1
intermediary scree/tundra	medium vegetation cover	18.1	13.6	23.9
developed tundra	dense vegetation	virtually no seedlings		virtually no seedlings
Serpentine:				
tundra	sparse vegetation cover	18.5	11.1	39.1
tundra	intermediate vegetation cover	24.0	28.9	18.7
tundra	dense vegetation cover	13.5	22.6	23.0

Tab. 5. Safe sites above timberline

Site features	Major environmental hazards from which safe site should protect
soil surface stabilized, at least temporarily	needle ice formation
soil texture suitable for radicle penetration	frost heaving
sufficient soil moisture	wind
sufficient light	extreme fluctuation of soil surface temperature
nutrients (may be low or limiting)	overgrazing

closely interrelated. It goes without saying that the concept proposed is valid for native alpine plants only, taxa from lowland and those of foreign origin having different ecological requirements.

Revegetation research above timberline

Revegetation research in Europe refers mostly to subalpine and lower situated areas, studies above timberline being exceedingly scarce. Apart from assessments of various commercial practices (e.g. Schiechl 1978), available reports deal most frequently with evaluation of damages resulting from artificially made and maintained ski runs (e.g. Cernusca 1977, Grabherr 1978). In some of these publications, suggestions are offered for management of ski runs on which commercial seed mixtures were sown with unsatisfactory results.

Investigations focusing on successional stages and/or soil dynamics in high alpine disturbances (e.g. Mosimann 1983) are also mostly concerned with ski runs sown with lowland seed or left untreated. Of special interest in this respect is the current study of Meisterhans (1982, and in preparation) dealing with machine-graded ski runs in our alpine research area near Davos (E. Switzerland).

Some authors admit that the seed material from low altitudes used in commercial revegetation trials above timberline is not adapted to alpine environments, but they argue that alpine seeds are not available on the market. The argument that economic constraints involved in providing material from high altitudes are too large, has been generally accepted by enterprises carrying out construction of ski-lifts and ski runs, little attention having been paid so far to the potential of high altitude plants for revegetation above timberline.

To the best of our knowledge, the Geobotanical Department of SFIT Zürich is the only European institution carrying out revegetation research above timberline with use of native plants in seeding and/or planting. Our field trials, rather limited to date, are based on results obtained in studies on behaviour of high-alpine plants; both the selection of material and its treatment prior to the revegetation experiments in the wild follow patterns observed in natural populations and laboratory/experimental garden. In some plots, safe site conditions are simulated by use of biodegradable materials. Our preliminary results are rather encouraging (Hefti unpubl., Schütz unpubl., Urbanska 1986).

Recently an interesting revegetation study in which native plants were used was reported from the German Alps (Markert 1985); however, the trials were carried out in

an approximate altitudinal bracket of 1700–1900 m (a.s.l.) and therefore do not relate precisely to the extreme areas above timberline.

Attempts to revegetate ski runs in the Swiss Alps started in the early seventies; actual scientific investigations began some years later. Contrary to this situation, high altitude revegetation research in North America has been carried out since 1938, when the native plant material was used experimentally in the Rocky Mts National park area (Harrington 1946). Studies representing diverse fields of science and technology yielded a great amount of data, the exchange of information and experience being greatly stimulated by the bi-annual High Altitude Revegetation Workshops (HAR). For more information, the reader is referred to the proceedings of these meetings, traditionally published by the University of Colorado at Fort Collins; the references given in the present paper are necessarily limited to a few selected topics.

Much attention in high altitude revegetation research in North America has been given to specific conditions and management requirements of alpine tundra and alpine disturbances (e.g. Bliss 1980, Brown and Johnston 1979, 1980, Brown et al. 1978, Burns 1980). Various studies reveal that numerous taxa adapted to alpine environments may represent a valuable source of seed and/or vegetative material for revegetation (e.g. Brown et al. 1984, Etra et al. 1984, Hassel 1980). Cultivation of plants assessed as suitable for revegetation at high altitudes was also investigated (e.g., Hassel 1980, Riley et al. 1984). Some authors (e.g., Cuany 1979) argue that cultivars specifically adapted to high altitudes should be developed and made available for revegetation.

In spite of the great progress made by the high altitude revegetation research in North America, documented studies on revegetation above timberline are still rather few. This may be at least partly due to the fact that high altitudes in, e.g., the Rocky Mts frequently correspond to the subalpine vegetation belt.

It should also be noted that high altitude disturbances in North America seem to result more frequently from mining operations and/or high altitude road construction than from development of infrastructure in winter resorts; the specific environmental problems related to this exploitation of high altitude ecosystems are taken into consideration in numerous studies (e.g. Johnston et al. 1975).

Concluding remarks

The evolutionary importance of sexual reproduction in plants is well-known, and so is the biological importance of reproduction by seed in general. For this reason our comments are confined to the aspects that are of relevance for revegetation research above timberline.

Reproduction by seed in plants above timberline is risk-exposed but effective. Most alpine seeds remain viable for at least several years; dormancy occurs frequently but is by no means absolute; in many taxa, gradual emergence of seedlings and low recruitment rates correspond to the slow population turnover in developed stands. Establishment in high-alpine plants cannot be assessed by accumulation of aerial biomass alone, development of root system being frequently more important for survival and exploitation of the low-nutrient environment than an extensive photosynthetic surface.

Life history strategies evolved by plants adapted to subnival and alpine ecosystems are partly reflected in their safe site requirements, generally different from those observed in taxa inhabiting subalpine areas and/or low altitudes.

The potential represented by alpine plants for revegetation of high-alpine disturbances deserves to be investigated in detail. Further development of research dealing with revegetation above timberline offers exciting perspectives and is urgently needed in Europe; exchange of unbiased opinions and neutral scientific information would be most desirable.

Economical aspects certainly are not negligible when revegetation of any disturbance above timberline is being planned; on the other hand, it may prove more economical to commit more funds in initial phases of revegetation, particularly if there is a threat that the entire procedure has to be repeated when the results are not satisfactory.

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Zusammenfassung

Die Arbeit befaßt sich mit verschiedenen Aspekten der Fortpflanzung durch Samen alpiner Pflanzen und ihrer Bedeutung für die Wiederbegrünungsforschung oberhalb der Waldgrenze.

Samen werden als bedeutende Investition der Mutterpflanze betrachtet. Ihre Bildung wird stark durch die Umwelt beeinflusst, entweder indirekt durch die Ressourcen, die der Mutterpflanze zur Verfügung stehen, oder/und direkt durch die klimatischen Bedingungen während der Samenentwicklung. Die Keimruhe von Samen alpiner Pflanzen kann angeboren (innate), induziert (induced) oder erzwungen (enforced) sein. Die erzwungene Keimruhe, die gegen Ende der Vegetationsperiode zu beobachten ist, überlagert häufig die anderen Keimruhetypen. Angeborene Keimruhe wird bei alpinen Pflanzen oft durch die Ausbildung der Samenschale beeinflusst; diese Arten reagieren immer stark positiv auf Skarifikation.

Die Etablierung ist eine weitere risikoreiche Phase im Lebenszyklus alpiner Pflanzen. Geschützte Stellen (safe sites) sind dabei von entscheidender Bedeutung. Nach Meinung der Autoren sind die geschützten Stellen nicht nur art- bzw. standortspezifisch, sondern auch ökosystem-spezifisch. Es wurde deshalb ein Konzept von geschützten Stellen vorgeschlagen, das für Gebiete oberhalb der Waldgrenze allgemein gültig ist. Unterschiede zwischen Vegetationsstufen, die unter- bzw. oberhalb der Waldgrenze liegen, werden betont. Alpine Ökosysteme haben oft einen beschränkten Nährstoffhaushalt, einheimische Pflanzen sind jedoch daran angepaßt; ein übermäßig großer Nährstoffgehalt im Boden wird demzufolge an alpinen geschützten Stellen nicht erwartet, da andere Faktoren wichtiger sind. Das vorgeschlagene Konzept der geschützten Stellen gilt deshalb nur für alpine Pflanzen.

Es wird betont, daß die Erforschung von einheimischen alpinen Pflanzen im Hinblick auf ihre Verwendung zur biologischen Erosionsbekämpfung in den Schweizer Alpen besonders wichtig ist.

References

- Amen R. 1966. The extent and role of dormancy in alpine plants. *Quart. Rev. Biol.* 41: 271–281.
- Amen R. 1966. A model of seed dormancy. *Bot. Rev.* 34: 1–31.
- Angevine M. W. and Chabot B. F. 1979. Seed germination syndromes in higher plants. In: Solbrig O. T., Jain S., Johnson G. B. and Raven P. H. (eds.): *Topics in plant population biology*, p. 118–206.
- Baker H. 1972. Seed weight in relation to environmental conditions in California. *Ecology* 53: 997–1010.
- Billings, D. W. 1974. Arctic and alpine vegetation: plant adaptations to cold summer climates. In: Ives J. D. and Barry R. G. (eds.): *Arctic and alpine environments*, p. 403–443.
- Billings D. W. and Mooney H. A. 1968. The ecology of arctic and alpine plants. *Biol. Rev.* 43: 481–529.
- Bliss L. C. 1962. Adaptations of arctic and alpine plants to environmental conditions. *Arctic* 15: 117–144.
- Bliss L. C. 1971. Arctic and alpine life cycles. *Ann. Rev. Ecol. Syst.* 2: 405–438.
- Bliss L. C. 1980. Physiology and life cycles of arctic-alpine plants. *Proc. 4th HAR Workshop, Fort Collins*, p. 65–78.
- Brown R.A. and Johnston R. S. 1979. Revegetation of disturbed alpine rangelands. In: Johnson D. A. (eds.): *Special management needs of alpine ecosystems*, p. 78–94.
- Brown R. W. and Johnston R. S. 1980. An assessment of revegetation techniques for alpine disturbances. *Proc. 4th HAR Workshop, Fort Collins*, p. 126–146.
- Brown R. W., Johnston R. S. and Chambers J. C. 1984. Responses of seed native grasses to repeated fertilizer application on acidic mine spoils. *Proc. 6th HAR Workshop, Fort Collins*, p. 200–214.
- Brown R. W., Johnston R. S. and Johnson D. A. 1978. Rehabilitation of alpine tundra disturbances. *J. Soil Water Conserv.* 33: 154–160.
- Burns S. F. 1980. Alpine soil factors in disturbance and revegetation. *Proc. 4th HAR Workshop, Fort Collins*, p. 210–227.
- Cernusca A. 1977. Schipisten gefährden die Gebirgslandschaft. *Umschau* 77: 109–112.
- Cook R. E. 1979. Patterns of juvenile mortality and recruitment in plants. In: Solbrig O. T., Jain S., Johnson G. B. and Raven P. (eds.): *Topics in plant population biology*, p. 207–231.
- Cook R. E. 1980. The biology of seeds in soil. In: Solbrig O. T. (ed.): *Demography and evolution in plant populations*. *Bot. Monogr.* 15: 107–129.
- Cuany R. L. 1974. Plant breeding and its role in supplying new plant material. *Proc. 1st HAR Workshop, Fort Collins*, p. 44–54.
- Dickenmann R. 1982. Genetisch-ökologische Untersuchungen an *Ranunculus montanus* Willd. s. l. aus der alpinen Stufe von Davos (Graubünden). *Veröff. Geobot. Inst. ETH Zürich* 78.
- Etra J., Cuany R. L. and Thor G. L. 1984. Persistence and performance of grass and legume strains at subalpine test plots in Colorado. *Proc. 6th HAR Workshop, Fort Collins*, p. 59–77.
- Fossati A. 1976. Die Keimung von Hochgebirgspflanzen. *Diploma Thesis Geobot. Inst. ETH Zürich*.
- Fossati A. 1980. Keimverhalten und frühe Entwicklungsphasen einiger Alpenpflanzen. *Veröff. Geobot. Inst. ETH Zürich* 73.
- Gasser M. 1986. Genetic-ecological investigations in *Biscutella levigata* L. *Veröff. Geobot. Inst. ETH Zürich* 85.
- Grabherr G. 1978. Schädigungen der natürlichen Vegetation über die Waldgrenze durch die Anlage von Skipisten und deren Fähigkeit zur Regeneration. *Begrünungsmaßnahmen im Gebirge. Tagungsber. Akad. Natursch. Landschaftspfl.* 2.
- Guillaume M. 1980. Alpine revegetation research at the Climax molybdenum mine. *Proc. 4th HAR Workshop, Fort Collins*, p. 185–203.
- Johnston R. S., Brown R. W. and Cravens J. 1975. Acid mine rehabilitation problems at high elevations. *Proc. Watershed Managem. Symp. Amer. Soc. Civil Engin. New York*, p. 66–79.

- Harper J. L. 1957. Biological flora of the British Isles, *Ranunculus acris* L., *R. repens* L., *R. bulbosus* L. J. Ecol. 45: 289–342.
- Harper J. L. 1977. Population biology of plants. Academic Press London.
- Harper J. L. and Benton R. A. 1966. The behaviour of seeds in soil. II. The germination of seeds on the surface of a water supplying substrate. J. Ecol. 54: 151–166.
- Harper J. L., Clatworthy J. N., McNaughton J. H. and Sagar G. R. 1961. The evolution of closely related species living in the same area. Evolution 15: 209–227.
- Harper J. L., Lovell P. H. and Moore K. G. 1970. The shapes and sizes of seeds. Ann. Rev. Ecol. Syst. 1: 327–356.
- Harper J. L., Williams J. I. and Sagar G. R. 1965. The behaviour of seeds in soil. I. The heterogeneity of soil surfaces and its role in determining the establishment of plants from seeds. J. Ecol. 53: 273–286.
- Harrington H. D. 1946. Results of a seeding experiment at high altitudes in the Rocky Mts National Park. Ecology 27: 375–377.
- Hassel W. G. 1980. Latest advances in plant material development at the Meeker Environmental Plant Center. Proc. 4th HAR Workshop, Fort Collins, p. 153–172.
- Hyde E. O. C. 1954. The function of the hilum in some Papilionaceae in relation to the ripening of the seed and the permeability of the testa. Ann. Bot. N. S. 18: 241–256.
- Landolt E. 1967. Gebirgs- und Tieflandpflanzensippen von Blütenpflanzen im Bereich der Schweizer Alpen. Bot. Jb. 86: 463–480.
- Landolt E. 1983. Probleme der Höhenstufen in den Alpen. Bot. Helv. 93: 255–268.
- Mack R. 1976. Survivorship of *Cerastium atrovirens* at Averffraw, Anglesey, J. Ecol. 64: 309–312.
- Markert P. 1985. Wiederansiedlung standortgerechter Vegetation an Hanganrissen in den Hochlagen, dargestellt am Modell Kleinwalsertal. Self-published, Schwanstetten.
- Meisterhans E. 1982. Entwicklungsmöglichkeiten für Vegetation und Boden auf Skipistenplanierungen. Fachbeitr. Schweiz. MAB-Inform. 10: 13–26.
- Mosimann T. 1983. Landschaftsökologischer Einfluß von Anlagen für den Massenskisport. Mat. Physiogeogr. Basel 3: 1–72.
- Müller G. 1977. Action de l'acide gibbérélique sur la germination des gentianes de la section *Cyclostigma*. Bull. Soc. Neuchât. Sci Nat. 100: 121–126.
- Pelton J. 1956. A study of seed dormancy in eighteen species of high altitude Colorado plants. Butler Univ. Bot. Stud. 13: 74–84.
- Riley R. H., Fisher A. G. and Brick M. A. 1984. Dryland seed production of revegetation species. Proc. 6th HAR Workshop, Fort Collins, p. 161–169.
- Schiechtel H. M. 1978. Probleme der ingenieurbioologischen Begrünungsverfahren im Gebirge. Ber. Akad. Naturschutz Landschaftspfl. 2: 8–16.
- Schütz M. 1983. Keimverhalten und frühe Lebensphasen alpiner Pflanzen von Silikat- und Kalkschuttstandorten. Diploma Thesis Geobot. Inst. ETH Zürich.
- Schütz M. and Urbanska K. M. 1984. Germinating behaviour and growth potential in *Taraxacum alpinum* (2n=32) from the Swiss Alps. Ber. Geobot. Inst. ETH 51: 118–131.
- Sharitz R. R. and McCormick J. F. 1973. Population dynamics of two competing annual plant species. Ecology 54: 723–740.
- Shaver G. R. and Chapin F. S. 1980. Response to fertilization by various plant growth forms in Alaskan tundra: nutrient accumulation and growth. Ecology 61: 662–675.
- Sheldon J. C. 1974. The behaviour of seeds in soil. III. The influence of seed morphology and the behaviour of seedlings on the establishment of plants from surface lying seeds. J. Ecol. 62: 47–66.
- Smith C. C. 1975. The coevolution of seeds and seed predators. In: Gilbert L. E. and Raven P. H. (ed.): Co-evolution of animals and plants, p. 51–77.
- Solbrig O. T. 1980. Demography and natural selection. In: Solbrig O. T. (eds.): Demography and evolution in plant populations, Bot. Monogr. 15: 1–20.
- Urbanska K. M. 1984. Plant reproductive strategies. In: Grant F. W. (ed.). Plant Biosystematics, p. 211–228.

- Urbanska K. M. 1985. Some life history strategies and population structure in asexually reproducing plants. *Bot. Helv.* 95: 81–97.
- Urbanska K. M. 1986. High altitude revegetation research in Switzerland – problems and perspectives. *Veröff. Geobot. Inst. ETH Zürich* 87.
- Urbanska K. M. Behaviour of alpine plants and high altitude revegetation research. Proc. 7th HAR Workshop, Fort Collins, in press.
- Urbanska K. M., Schwank O. and Fossati A. 1979. Variation within *Lotus corniculatus* L. s. l. from Switzerland. II. Reproductive behaviour of *L. alpinus* (DC) Schleicher. *Ber. Geobot. Inst. ETH* 46: 62–85.
- Weilenmann K. 1980. Bedeutung von Keim- und Jungpflanzenphase für alpine Taxa verschiedener Standorte. Diploma Thesis Geobot. Inst. ETH Zürich.
- Weilenmann K. 1981. Bedeutung von Keim- und Jungpflanzenphase für alpine Taxa verschiedener Standorte. *Ber. Geobot. Inst. ETH* 48: 68–119.
- Werner P. A. 1977. Ecology of plant populations in successional environments. *Syst. Bot* 1: 246–268.
- Werner P. A. 1979. Niche differentiation and coexistence in plants: the role of seeds and seedlings. In: Solbrig O. T., Jain S., Johnson G. B. and Raven P. H. (eds.): *Topics in plant population biology*, p. 287–310.
- Zuur-Isler D. 1981. Zum Keimverhalten von alpinen Pflanzen und Serpentinboden. Diploma Thesis Geobot. Inst. ETH Zürich.
- Zuur-Isler D. 1982. Germinating behaviour and early life phases of some species from alpine serpentine soils. *Ber. Geobot. Inst. ETH* 49: 76–107.