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Revegetation trials above timberline - an exercise in experimental population ecology

Wiederbegrünungsversuche oberhalb der Waldgrenze -
eine Übung in experimenteller Populationsökologie

by

Krystyna M. URBANSKA, Martin SCHÜTZ and Max GASSER

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1. INTRODUCTION

Revegetation research is very important to the biological erosion control. As far as high-altitude sites are concerned, revegetation represents a great challenge on account of harsh and generally unpredictable life conditions as well as the short growing period. For this reason scientific trials above the timberline are essential to establishment of a reliable basis for a subsequent larger-scale revegetation work (URBANSKA 1986a,b, URBANSKA 1988, URBANSKA and SCHÜTZ 1986).

It has been demonstrated that native species are superior to introduced taxa in revegetation of alpine disturbances (see e.g. BROWN et al. 1978, CHAMBERS et al. 1987, SCHÜTZ 1988, URBANSKA 1986a,b, URBANSKA 1988, URBANSKA and SCHÜTZ 1986, URBANSKA et al. 1987). However, population dynamics processes operating in new ecological situations and diverse life history strategies in alpine plants still are far from being fully understood.

One goal of the revegetation research is to develop a concept of native, self-supporting and maintenance-free plant cover in disturbed sites. In this respect, scientific revegetation trials screening potentially suitable plant material can be considered as application-oriented studies. It should be remembered, however, that revegetation research forms an essential part of the ecosystem reconstitution science and therefore represents fundamental studies too: the field data on behaviour and development of experimental populations constitute information pertinent to a correct assessment of the ecosystem functioning.

Scientific revegetation trials above the timberline represent thus an important exercise in experimental population ecology. The purpose of the present paper is to illustrate this aspect using as examples selected experimental populations of native alpine plants included in the research programme of our group. We propose to outline some patterns emerging from our studies rather than to discuss in detail all the results; for more information, the reader is referred to the papers published previously by various members of our team (e.g. FOSSATI 1980, GASSER 1986, URBANSKA and SCHÜTZ 1986, URBANSKA et al. 1987, SCHÜTZ 1988)

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The manuscript profited from constructive criticism of Prof. Dr. E. Landolt. We thank to many persons who greatly helped with establishment of the clonal module populations above the timberline. The biologically degradable matting was partly obtained free of charge from Tricon AG, Zürich; this help is gratefully acknowledged.

2. ECOLOGICAL AND BIOLOGICAL CHARACTERISTICS OF THE SPECIES DISCUSSED

Trisetum distichophyllum, *T. spicatum*, *Anthyllis alpestris* and *Biscutella levigata* chosen for the present paper are rather broadly distributed in the Alps (HESS et al. 1967-1972, LANDOLT 1984). Within the alpine vegetation belt they most frequent form part of stationary communities ("Dauergesellschaften"); they are also sometimes observed in early seral communities (LANDOLT, pers. comm.). The ecological characteristics given below are valid for the area of Davos.

Trisetum distichophyllum inhabits mobile scree slopes and boulder fields, occasionally also rocky crevices up to 3000 m a.s.l. *T. spicatum* occurs in stabilized scree slopes, moraines, exposed rocky ridges up to 3100 m a.s.l. *Anthyllis alpestris* grows in alpine pastures and loose patches of low alpine grassland, in rocky soils up to 2800 m a.s.l. *Biscutella levigata* occurs in scree slopes and patches of the low alpine grassland, in rocky soils up to 2600 m a.s.l.

Our research is carried out in the alpine/subnival vegetation belt in surroundings of Davos, Grisons, NE Swiss Alps (for the classification of the altitudinal belts, see LANDOLT 1983). Within this area *Trisetum distichophyllum* has a distinct preference for calciferous substrata, but several populations were also found on acidic silicate (SCHIBLER 1937, URBANSKA unpubl.). On the other hand, *T. spicatum* occurs mostly on silicate; the rare colonies growing on limestone or dolomite (SCHIBLER 1937) usually inhabit sites with well-developed soil where a direct influence of the mother-rock is buffered by a humus layer (URBANSKA unpubl.). *Anthyllis alpestris* occurs mostly on limestone and dolomite, less frequently on serpentine (SCHIBLER 1937, GASSER 1986). *Biscutella levigata* grows most frequently on dolomite and serpentine but is rare on acidic silicate (SCHIBLER 1937, GASSER 1986).

As far as the **life form** is concerned, the four species selected represent, respectively, grasses and forbs. *T. spicatum* and *A. alpestris* are hemi-

cryptophytes, *T. distichophyllum* and *B. levigata* at least partly geophytes which enables them to grow in non-stabilized soils. Each taxon is characterized by different patterns of growth and reproduction which strongly influence the structure of particular populations.

Trisetum distichophyllum is characterized by a strong clonal growth: single tillers of this grass are loosely interconnected by slender aboveground stolons, frequently covered by the mobile scree. Clones of *T. distichophyllum* are often extensive and it is possible that some populations consist of only few large genets. Reproduction by seed and fragmentation of clones contribute to the development of populations (URBANSKA unpubl.).

Trisetum spicatum forms small tussocks by means of intravaginal tiller growth (URBANSKA et al. 1987). Populations of this species occupy a rather limited space; they are distinctly mosaic-patterned, and even the smallest colony scrutinized so far comprises at least a dozen individuals (URBANSKA unpubl.); the genets are easily identifiable because of the compact growth. *T. spicatum* reproduces by seed; vegetative reproduction by fragmentation of clones is theoretically possible but not likely to occur in natural sites. The seed dispersal radius is so far unknown.

Anthyllis alpestris is a legume with a taproot usually supporting several leaf rosettes. Alpine populations of this species consist of well-defined individuals scattered over large areas. Population size is variable, but a given colony most frequently includes very numerous genets; some of them may represent sibling or half-sibling groups (GASSER unpubl.). *A. alpestris* reproduces by seed.

Biscutella levigata (*Cruciferae*) manifests a strong clonal growth: new ramets and ramet groups are issued from unusual root buds and form a loose net. Both the actual clone area and the number of interconnected ramets are exceedingly difficult to assess in the field (GASSER 1983, 1986). The patchy populations of *B. levigata* vary in size and their structure is strongly influenced by site conditions and altitude; however, numerous genets are included in most cases. Since the seed dispersal radius is often very limited, at least some genets within a given colony represent family groups of siblings or half-siblings (GASSER 1983, 1986, SCHÜTZ 1988). Sexual reproduction in *B. levigata* is accompanied by vegetative reproduction resulting from fragmentation of clones.

The populations further described in the present paper all originated from dolomite (ca. 2500-2700 m a.s.l.); the trial plots were established on dolomite, too.

3. GERMINATING BEHAVIOUR

It is generally recognized that knowledge of the seed germination characteristics is important for establishing the desired plant community in disturbed sites (CHAMBERS et al. 1987), and for a general success of revegetation by seeding. Our research programme follows this line of thinking and the germinating behaviour of the species used in revegetation trials above timberline is also studied in laboratory conditions.

All the data on germinating behaviour presented here are based on tests carried out in a climatized chamber for 100 days. Detailed descriptions of trials are given e.g. by FOSSATI (1980) or SCHÜTZ (1988).

The seeds were considered germinated when the radicle penetrated the seed coat. This definition is rather widely accepted (see e.g. EVENARI 1956, FOSSATI 1980, CHAMBERS et al. 1987, SCHÜTZ 1988). However, it is satisfactory only in assessment of laboratory tests carried out on blotting paper or on soil surface. In the field conditions or in laboratory trials carried out with buried seeds, the seedlings recorded may represent but some part of the actually germinated seeds because some seedlings are not yet sufficiently developed to appear above the soil surface or some seeds perished just after the germination (SARUKHAN and HARPER 1973). For this reason the term "seedling emergence" is better suited to description of the field trials (see also HARPER 1977).

The four species dealt with in the present paper represent various types of germinating behaviour. The principal differences observed in laboratory trials relate to the **presence or absence of seed dormancy** as well as the **type of dormancy** which in turn influenced the behaviour of seeds (Figs. 1, 2). On the other hand, the meteorological conditions during the seed formation period apparently play an important role in all four species, as suggested by differences in germination noted among seed populations originating from various harvests (see also URBANSKA and SCHÜTZ 1986).

Seeds of *Trisetum distichophyllum* manifest a strong innate dormancy apparently related to an inactive embryo; the dormancy can be successfully broken by the pretreatment with gibberellin (Fig. 1, see also SCHÜTZ 1988). The most pronounced dormancy occurs in young seeds and clearly diminishes with age; on the other hand, the seed germinability remains generally unchanged at least within the first 27 months after harvest (Fig. 2).

Trisetum spicatum was not yet fully evaluated, further trials being still in progress. The results obtained so far suggest, however, that germinating behaviour of this species may be comparable to that of *T. distichophyllum*. For

instant, not pretreated six-month-old seeds of *T. distichophyllum* germinated in 68%, whereas the seeds of *T. spicatum* representing the same age-class and originating from two different natural populations germinated in 52% and 64%, respectively. Curiously enough, plants of *T. spicatum* transplanted from these populations into an experimental garden in Zürich produced seeds which at the age of six months germinated better than those harvested in the wild (URBANSKA and SCHÜTZ 1986, SCHÜTZ 1988).

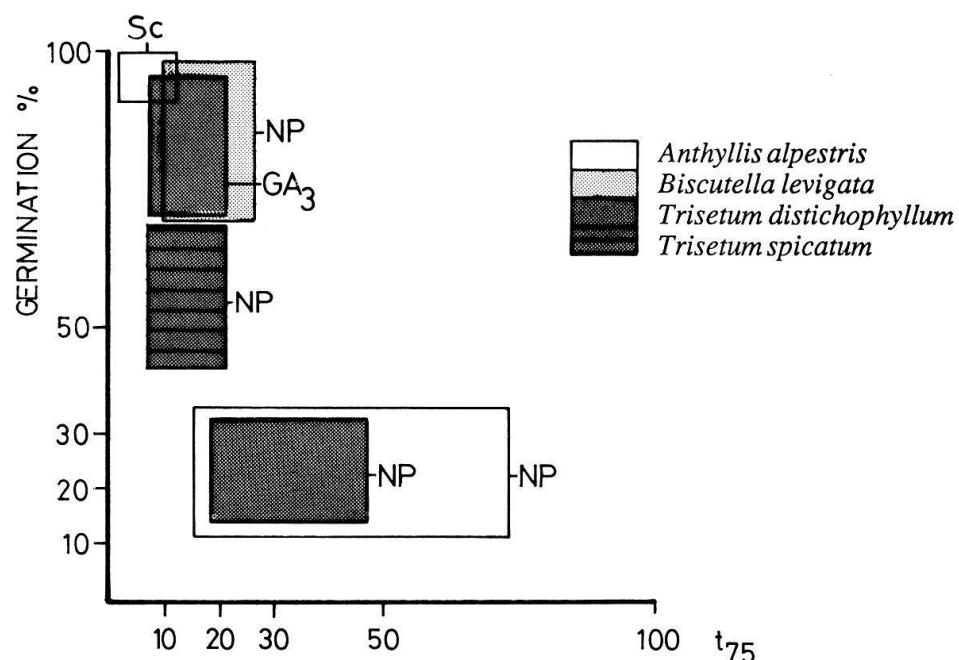


Fig. 1. Germinating behaviour of the four species discussed. t_{75} = time required for 75% of the final germination percentage to be reached; NP = no seed pretreatment; Sc = mechanical scarification; GA₃ = seed pretreatment with gibberellin. Based on data of FOSSATI (1980), WEILENMANN (1980), GASSER (1986) and SCHÜTZ (1988 and unpubl.).

Keimverhalten der vier untersuchten Arten. t_{75} = benötigte Zeit, bis 75% der Endkeimungsrate erreicht wird; NP = keine Samenvorbehandlung; Sc = mechanische Skarifikation; GA₃ = Samenvorbehandlung mit Gibberellin. Daten von FOSSATI (1980), WEILENMANN (1980), GASSER (1986) und SCHÜTZ (1988 und unveröff.).

Germinating behaviour of *Anthyllis alpestris* is strongly influenced by innate dormancy due to the hard seed coat, and young seeds respond exceedingly well to mechanical scarification (Figs. 1, 2, see also FOSSATI 1980, SCHÜTZ 1988). However, the seed germinability decreases after about three years (Fig. 2).

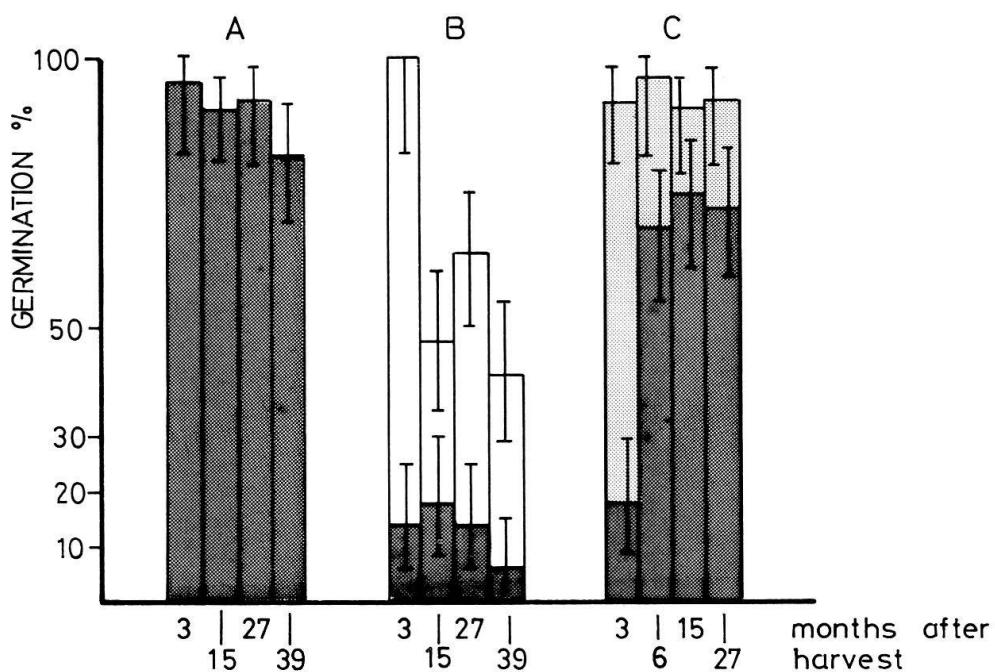


Fig. 2. Germinating behaviour with increasing age of seeds. A = *Biscutella levigata*; B = *Anthyllis alpestris*; C = *Trisetum distichophyllum*. Confidence intervals indicated.
Keimverhalten mit zunehmendem Samenalter. A = Biscutella levigata; B = Anthyllis alpestris; C = Trisetum distichophyllum. Angabe der Vertrauensintervalle.

- no seed pretreatment - *keine Samenvorbehandlung*
- mechanical scarification - *mechanische Skarifikation*
- ▨ seed pretreatment with gibberellin - *Samenvorbehandlung mit Gibberellin*

No innate seed dormancy occurs in *Biscutella levigata*. The seeds with pericarp removed germinate more rapidly and better than those still confined in the fruit (WEILENMANN 1980, 1981, GASSER 1983, 1986). The germinability of seeds does not seem to be perceptibly affected by their increasing age at least during the first three years after harvest (Fig. 2).

4. SINGLE-RAMET CLONING (SRC) EXPERIMENTS

Single-ramet cloning represents a useful technique because

- an individual potential for recovery after extensive damage can be studied in family groups
- the material necessary for revegetation by planting can be provided rapidly

and without too much damage to natural populations (URBANSKA 1986a,b, URBANSKA 1988, URBANSKA et al. 1987)

- some taxa respond to this type of cloning with an intensified and rapid reproduction, and the experimental populations may soon be reinforced by seeds or propagules.

The single-ramet cloning was carried out for the first time in alpine grasses (URBANSKA 1986, URBANSKA et al. 1987, HEFTI-HOLENSTEIN in prep.). The term "single-tiller cloning" used in those studies has been replaced now by "single-ramet cloning" (SRC) since not only grasses but other life forms have been included in our programme (see e.g. TSCHURR 1988).

The ramets of a given donor plant were separated from each other and singly planted in ROOTRAINER compartments. The series cloned were kept for several weeks in greenhouse where the survival of initial ramets and development of clonal modules was studied. The whole procedure is described in detail in some previous papers (e.g. URBANSKA et al. 1987, TSCHURR 1987, 1988).

The response to cloning observed in the four species discussed here was rather diversified (Tab. 1, Fig. 3). The differences in survival of initial ramets and development of clonal modules may be partly influenced by the timing of the SRC experiments: *Trisetum distichophyllum* and *T. spicatum* were cloned in summer, and *Biscutella levigata* in spring, whereas cloning of *Anthyllis alpestris* was carried out partly in winter and partly in spring. On the other hand, the behaviour of the ramets cloned is apparently related, too, to the diverse growth strategies of the species studied.

Tab. 1. Survival of initial ramets and development of clonal modules in the SRC experiments. Observation period of 4 weeks.

Überleben der Anfangsramets und Entwicklung der klonalen Module nach den SRC-Klonierungen. 4-wöchige Beobachtungsperiode.

Species	initial ramets (IR)	dead initial ramets	new ramets (NR)	NR/IR	dead new ramets	total
<i>Trisetum spicatum</i>	100	4	44	0.44	0	140
<i>T. distichophyllum</i>	145	36	36	0.25	0	145
<i>Anthyllis alpestris</i>	140	3	39	0.28	0	176
<i>Biscutella levigata</i>	64	3	13	0.20	0	74

From the third week on, development of the clonal modules clearly progressed (Fig. 3). The best performance was observed in *Trisetum spicatum* followed by

Anthyllis alpestris ; growth in *Biscutella levigata* proceeded less rapidly, whereas *Trisetum distichophyllum* grew well but apparently was handicapped by the pronounced initial losses.

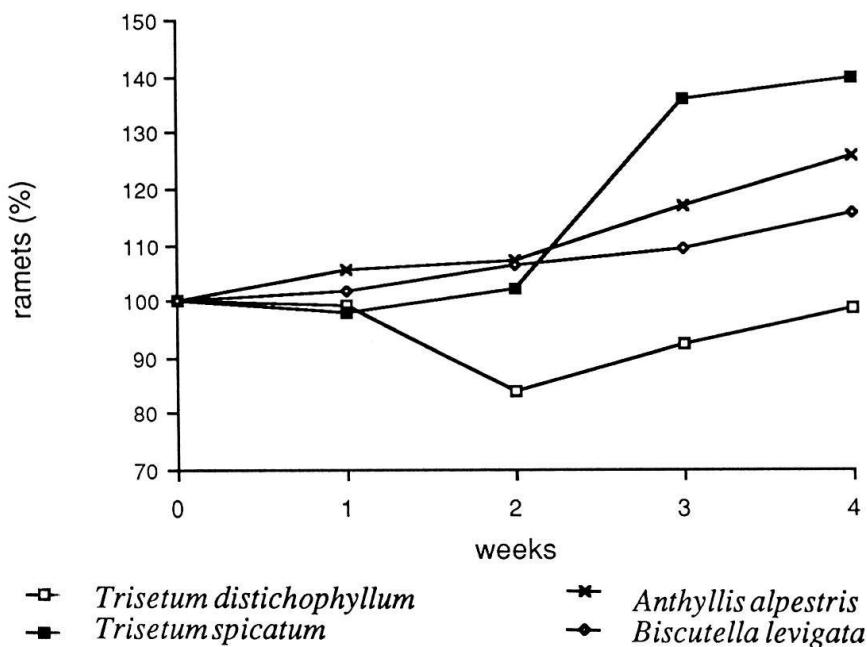


Fig. 3. Development of clonal modules within the first four weeks after the SRC experiments. Partly after URBANSKA et al. (1987).

Entwicklung der klonalen Module während der ersten 4 Wochen nach den SRC-Klonierungen. Teilweise nach URBANSKA et al. (1987).

Of a particular interest was an early onset of flowering observed in *Anthyllis alpestris* : up to 30 % of the clonal modules developed flowers within six weeks after cloning. Of the four species discussed here *A. alpestris* was the only one which reached rapidly the reproductive phase.

5. REVEGETATION TRIALS

5.1. ESTABLISHMENT OF EXPERIMENTAL POPULATIONS

Since some important population parameters can be determined initially, scientific revegetation trials offer numerous possibilities. The choice of a given population type may be decisive to its subsequent development and functioning in the field conditions.

In our trials a special attention was given to the **stage-variants** sensu RABOTNOV (1978), and also to the **neighbourhood type** (Tab. 2, see also URBANSKA 1988). On the one hand, populations consisting exclusively of seeds were chosen (SCHÜTZ 1988); on the other hand, populations including only clonal modules of several to numerous ramets each were established (URANSKA et al. 1987, HEFTI-HOLENSTEIN in prep., GASSER unpubl.). Last but not least, mixed populations consisting both of clonal modules and seeds were included in the trials (GASSER unpubl.).

The chronological age of given seed populations was uniform: the seeds were harvested in the autumn preceding the field trials. All the seeds used originated from natural populations. The seeds for a given experimental population were arbitrarily selected from a larger sample harvested in a single natural colony; they represented various genotypes but siblings and half-siblings born from the same mother were frequent.

As far as the clonal modules are concerned, the chronological age of the donor plants could not have been determined and it is conceivable that they represented various generations. The family groups resulting from cloning of *Anthyllis alpestris* and *Biscutella levigata* corresponded to numerous genets, whereas the clonal modules of *Trisetum spicatum* originated from fewer donors. The modules of *T. distichophyllum* represented only two genotypes. In the mixed populations, clonal modules and seeds clearly corresponded to different generations.

Tab. 2. Stage-variant status of experimental populations.
Lebensphasenbedingte Varianten der Versuchspopulationen.

Species	Seeds only	Clonal modules only	Clonal modules and seeds
<i>Trisetum distichophyllum</i>	yes	yes	no
<i>Trisetum spicatum</i>	yes	yes	no
<i>Anthyllis alpestris</i>	yes	yes	yes
<i>Biscutella levigata</i>	yes	yes	yes

Both single-species and mixed-species neighbourhoods were established in the revegetation trials. The seeds broadcasted by hand represented either a mixture of various alpine taxa or corresponded to one species only (SCHÜTZ 1988). The

populations of clonal modules were planted by hand according to a precise design (URBANSKA et al. 1987, HEFTI-HOLENSTEIN in prep., GASSER unpubl.); the resulting plant groups formed either pure stands of a given species or mixtures of several taxa. The seeds sown in some mixed populations were always introduced into single-species neighbourhoods.

The initial density of experimental populations and also the population area were varied. The seed populations with mixed-species neighbourhoods included 100 seeds of a given taxon per 1 m²; on the other hand, singlespecies neighbourhoods consisted of 100 seeds distributed over an exceedingly limited area of only 0.08 m². The populations of clonal modules had a medium density of 50 modules per 1 m². In the mixed populations, clonal modules were similarly distributed, but the seeds sown into selected neighbourhoods remained within very limited sectors (about 0.05 m²).

5.2. SIMULATION OF SAFE SITE CONDITIONS

As seedlings and/or young plants are particularly exposed to environmental hazards, the establishment phase represents a crucial stage in population dynamics. It also demonstrates well that biology and ecology of populations cannot be separated. The concept of safe site, developed first by HARPER and his collaborators (e.g. HARPER 1977, HARPER et al. 1970) and further elaborated by COOK (1979, 1980), plays a very important role in understanding this interface.

HARPER and his group defined safe site as an immediate environment of seed favourable to germination and seedling establishment, and protecting the germinated seed from environmental hazards. They argued that safe sites are specific to a given taxon and a given habitat (HARPER et al. 1961), and that the availability of numerous, diverse safe sites is a prerequisite for development of a species-rich vegetation (see HARPER 1977, HARPER et al. 1965, HARPER and BENTON 1966, SHELDON 1974).

The concept of safe site was further developed by two of the present authors (URBANSKA and SCHÜTZ 1986). Considering safe sites as not only habitat-, but also ecosystem-specific, we proposed that they should be defined by some characteristic features and the **hierarchy** of hazards naturally associated with a given environment. Some features of safe sites above the timberline (Tab. 3) and in particular nutrients which may be low or limiting apply to native species only; on the other hand, the hierarchy of major environmental hazards from which

safe sites in the alpine belt should protect, determines successful establishment of native and introduced species alike (see also e.g. BILLINGS and MOONEY 1968, BLISS 1971, LANDOLT 1984).

Tab. 3. Safe sites above the timberline. After URBANSKA and SCHÜTZ (1986).
Schutzstellen oberhalb der Waldgrenze. Nach URBANSKA und SCHÜTZ (1986).

Site features	Major environmental hazards from which safe sites should protect
soil surface stabilized, at least temporarily soil surface suitable for radicle penetration sufficient soil moisture sufficient light nutrients (may be low or limiting)	1/ needle ice formation 2/ frost heaving 3/ wind 4/ extreme fluctuations of soil surface temperature 5/ overgrazing

In our trials safe site conditions were simulated with the CURLEX matting. It is a three-dimensional structure of non-resinous wood fiber with a fine polyethylene net forming the top layer. The wood fibers decompose in the usual way, whereas the photodegradation of the non-stabilized polyethylene follows under the influence of the UV energy (LOCK and FRANK 1973, LOCK et al. 1973).

The biologically degradable matting not only helped to eliminate the major environmental hazards, but also favourably influenced most of the features expected of safe sites above timberline (Tab. 3): the stabilization of the soil surface and a rather balanced soil moisture content was an immediate effect of the application. On the other hand, alteration of the uppermost soil layer texture and some changes in the nutrient content were brought about gradually by the degradation of the wood fiber, nearly completed within three years (SCHÜTZ 1988). The light conditions under the matting were obviously changed, too. Safe site conditions were simulated in all the series where revegetation by planting was studied; as far as the seeding experiments are concerned, some plots were left unprotected.

5.3. DEVELOPMENT OF POPULATIONS

5.3.1. Seedling emergence and recruitment

The development of seed populations followed diverse patterns and was apparently influenced by various types of seed dormancy, seed pretreatment, and timing of the seeding trials.

Trisetum distichophyllum established in the autumn series manifested the seedling emergence of 39% after the first winter (Fig. 4); however, no new seedlings were seen in the second growing period. The genet recruitment was rather good (32%, Fig. 4) but plants developed slowly. No flowering occurred within the first two years after seeding. The behaviour of *T. distichophyllum* was classified by SCHÜTZ (1988) as the LTT type. The data presented above have to be completed yet by early summer seeding trials.

It seems that *T. spicatum* behaves similarly to *T. distichophyllum*; the preliminary observations must be verified in further studies.

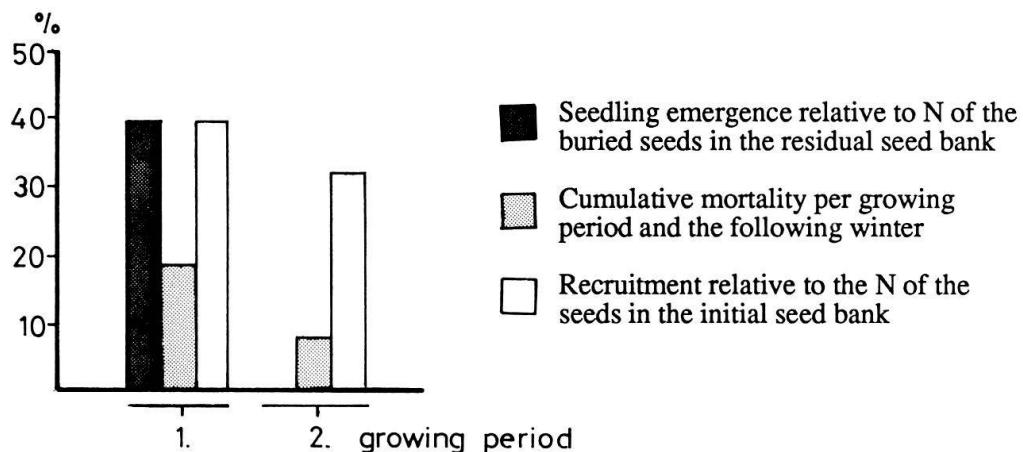


Fig. 4. Seedling emergence, mortality and genet recruitment in seed populations of *Trisetum distichophyllum* established in the autumn. Reworked data of SCHÜTZ (1988). *Keimlingsaufkommen, Sterblichkeit und Rekrutierung der Genets in Samenpopulationen von Trisetum distichophyllum. Aussaat im Herbst. Nach SCHÜTZ (1988) verändert.*

Seed populations of *Anthyllis alpestris* represented two behavioural types. The seedling emergence in populations consisting exclusively of scarified seeds and established in early summer was exceedingly fast and corresponded to 50%

(Fig. 5a); however, no more seedlings appeared in the second growing period. The seedlings and very young plants suffered mortality during the first and the second winter, so that the recruitment was moderate (23%, Fig. 5a). From the third summer on, however, no more losses occurred; the recruited genets developed very well and some of them produced flowers and seeds in the fourth year of their life.

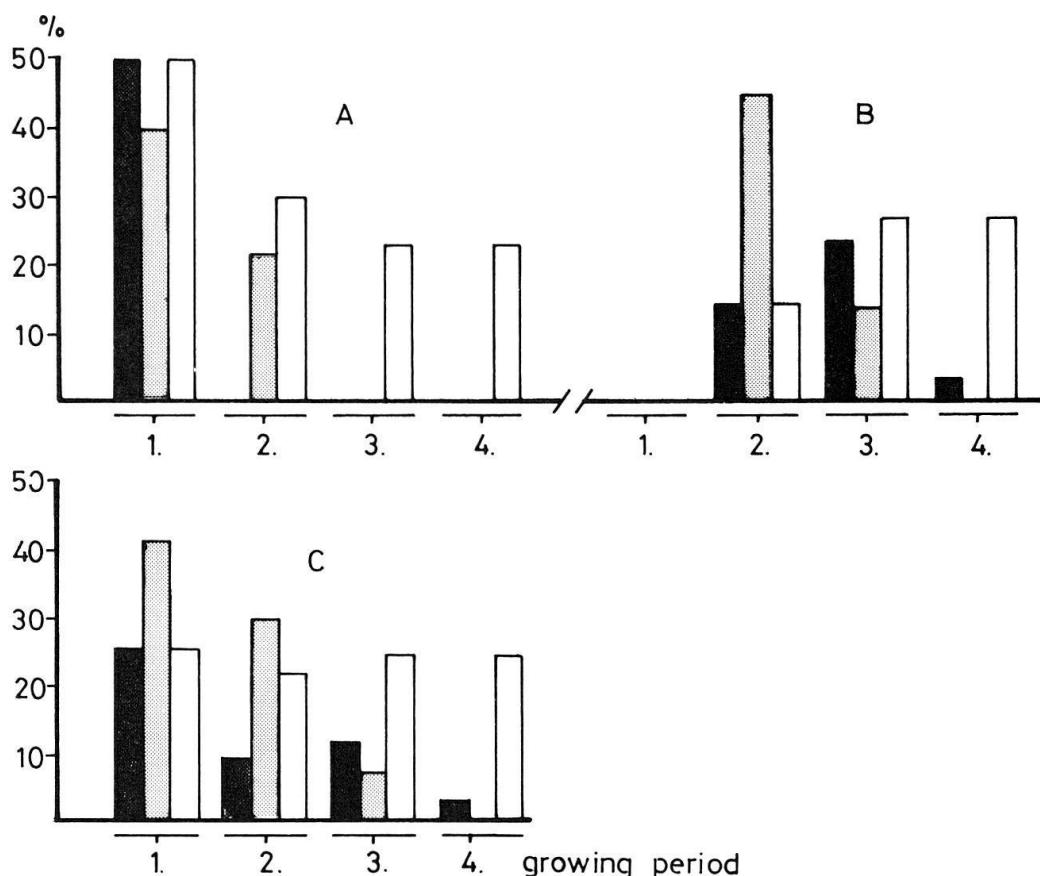


Fig. 5. Seedling emergence, mortality and genet recruitment in seed populations of *Anthyllis alpestris*. 5a. Scarified seeds; 5b. Non-scarified seeds. 5c. Scarified and non-scarified seeds 1:1. Reworked data of SCHÜTZ (1988). For detailed explanations, see Fig. 4.
Keimplingsaufkommen, Sterblichkeit und Rekrutierung der Genets in Samenpopulationen von Anthyllis alpestris. 5a. Skarifizierte Samen; 5b. Nicht skarifizierte Samen; 5c. Skarifizierte und nicht skarifizierte Samen 1:1. Nach SCHÜTZ (1988) verändert. Weitere Erklärungen, siehe Fig. 4.

The populations of *A. alpestris* consisting exclusively of non-scarified seeds produced first seedling cohorts only after the first winter (Fig. 5b); further

cohorts emerged in two subsequent growing periods. Seedling emergence was followed by some losses (Fig. 5b). From the end of the third year on, an apparent stabilization of the recruited genets was reached, but new seedlings were exceptionally rare. No flowering occurred so far.

The development of seed populations comprising scarified and non-scarified seeds in proportion 1 : 1 was of a particular interest (Fig. 5c). The rather well-balanced gains and losses of genets suggest that this kind of populations may be the best adapted to particular field situations.

The behaviour of scarified seed populations of *A. alpestris* was classified by SCHÜTZ (1988) as the L_s type; on the other hand, non-scarified seed populations were assigned to the BS type typically represented by *Biscutella levigata* (Fig.6).

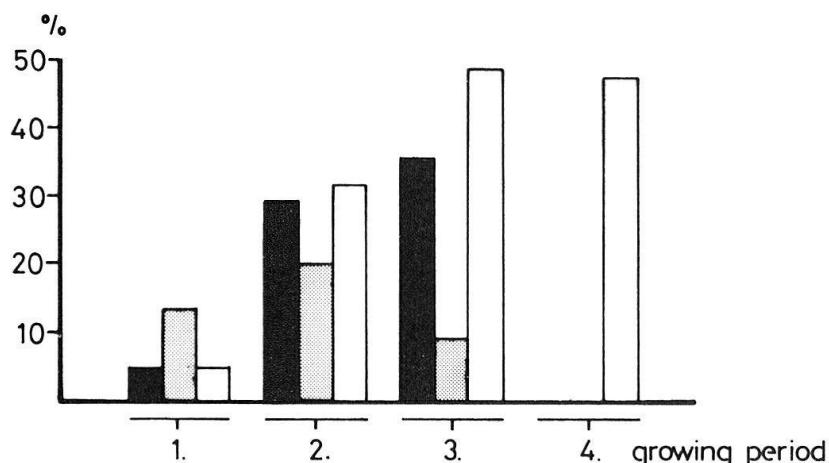


Fig. 6. Seedling emergence, mortality and genet recruitment in seed populations of *Biscutella levigata*. Reworked data of SCHÜTZ (1988). For detailed explanations, see Fig.4.

Keimlingsaufkommen, Sterblichkeit und Rekrutierung der Genets in Samenpopulationen von Biscutella levigata. Nach SCHÜTZ (1988) verändert. Weitere Erklärungen, siehe Fig.4.

The seedling emergence in populations of *Biscutella levigata* established in early summer was very limited (4%) in the growing period following the seeding trials. The seedlings emerged mostly after the winter break, immediately after the snow has melted. After the first winter in the field, seedling emergence was on average 29%, whereas it corresponded to 35% after the second winter. After the third winter, no more new seedlings emerged. The highest mortality in

seedlings and young plants corresponded to 20% and occurred in the second growing period /winter (Fig. 6). From the third summer on, the populations apparently became stabilized.

Some recruited genets of *Biscutella levigata* flowered and produced seed already in the third year of their life; seedling cohorts clearly representing a new generation were observed in the following summer (SCHÜTZ 1988).

5.3.2. Behaviour of clonal modules

The varied development of clonal modules was at least partially due to the fact that they represented various classes of relative age, and were established in various series. However, some behavioural tendencies appear to be influenced by the very growth strategies of a given species.

Survival and growth. *Trisetum distichophyllum* and *T. spicatum* invariably manifested the 100% survival in all series by the end of their third summer in the field (HEFTI-HOLENSTEIN in prep.). About seven weeks after planting in early summer, *T. distichophyllum* did not show any appreciable growth whereas *T. spicatum* was very vigorous. The clonal modules planted in autumn remained dormant throughout the last weeks of September and their further development was observed after the winter snow has melted in summer. The clone expansion during the second summer was more pronounced in *T. distichophyllum* than in *T. spicatum*.

Anthyllis alpestris established in early summer survived in 100% by the end of the first growing period, but the populations experienced some losses during the second summer and the survival by the end of the second growing period was 90.6%. In the autumn series, the survival after the first winter in the field corresponded to 63.3% and remained unchanged by the end of the first growing period. The clonal modules were vital in both series, but the production of new ramets was limited.

Biscutella levigata was planted so far only in early summer 1987 and the series included only 17 modules. By the end of the first summer 8 modules were apparently dead; however, these observations have yet to be verified as *B. levigata* often shows a transient dormancy (GASSER 1983). The general vitality of the active clonal modules was rather low and they did not produce any new ramets to date.

Flowering. Of the four species involved in the planting trials, only *Biscutella levigata* did not flower so far, either in greenhouse or in the field. On the other

hand, both the onset of flowering as well as the actual percentage of the clonal modules that reached the generative phase were quite varied among various series of the same taxon, and also among particular species.

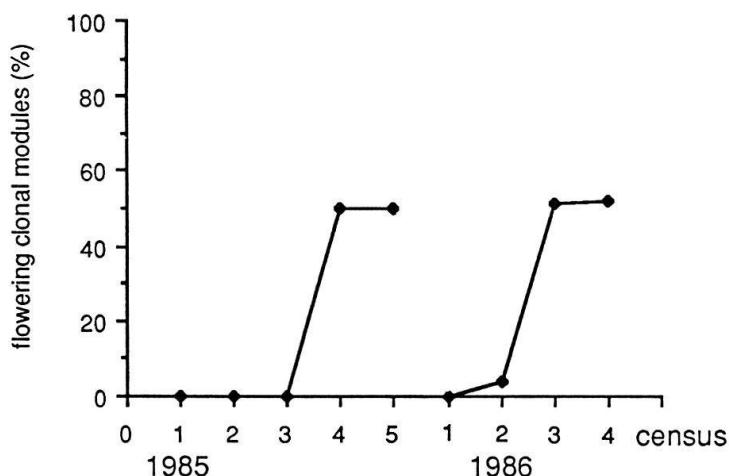


Fig. 7. *Trisetum spicatum*: flowering in experimental populations of clonal modules planted on dolomite in early summer 1985. After URBANSKA et al. (1987).

Trisetum spicatum: Blütenbildung in experimentellen Populationen von klonalen Modulen auf Dolomit. Gepflanzt im Frühsommer 1985. Nach URBANSKA et al. (1987).

Trisetum distichophyllum and *T. spicatum* did not flower before planting. *T. distichophyllum* established in early summer series developed flowers only in its second growing period above the timberline and the number of flowering modules was negligible (HEFTI-HOLENSTEIN unpubl.). *T. spicatum* established in early summer series 1985 flowered very well after planting; the flowering modules corresponded to 50% and this percentage did not change appreciably in the second summer (Fig. 7). On the other hand, much less culms were produced in the third summer but the clonal growth clearly improved in the same time (URBANSKA 1988, HEFTI-HOLENSTEIN in prep.). The series planted in autumn 1985 flowered only in 25% during their first summer, whereas those established in early summer 1986 did not yet produce any flowers.

Anthyllis alpestris flowered already during the greenhouse trials and flowers were removed before planting. The modules established in early summer did not produce any new flowers during the weeks following the planting. On the other hand, they performed exceedingly well during the second summer (77.1%), and the onset of flowering was rapid (Fig. 8). The modules planted in autumn

flowered after their first winter too, but the percentage of the flowering plants was lower than that in the early summer series (39.3%, Fig. 8).

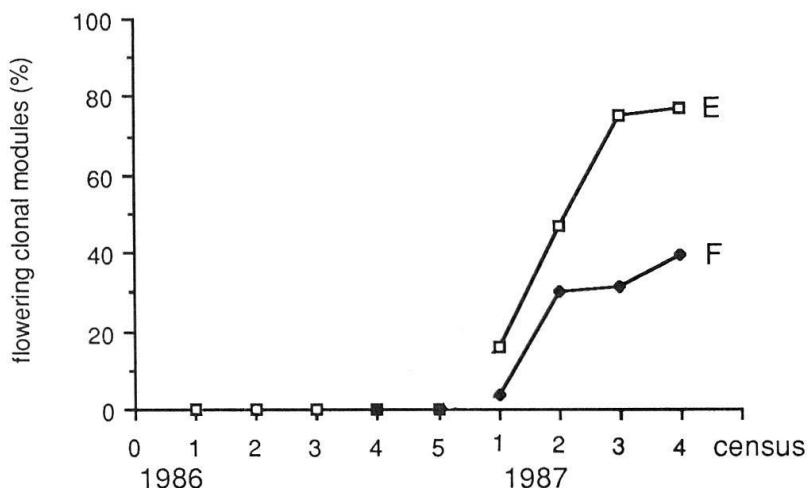


Fig. 8. *Anthyllis alpestris*: flowering of clonal modules in mixed populations established in 1986. E = early summer series; F = autumn series.

Anthyllis alpestris: Blütenbildung in gemischten Populationen von klonalen Modulen. Gepflanzt 1986. E = Frühsommerserien; F = Herbstserien.

5.3.3. Spontaneous immigration of plants from the neighbouring vegetation

Development of experimental populations in the field was accompanied by a spontaneous establishment of species not included in the trials but forming part of the neighbouring vegetation. Since it is not very likely that the plants observed might have originated from seeds or propagules buried in the soil within the trial plots, they are regarded as immigrants.

The immigrant populations developed from various types of the founder units (Tab. 4), not only fruits/seeds but also specialized vegetative propagules being involved.

On the whole, seven species were determined to date; in addition, seedlings and young plants of the *Compositae* family were observed but not identified so far. The population development of *Plantago atrata* and other species which immigrated into planted plots remains yet to be fully assessed (HEFTI-HOLENSTEIN in prep., GASSER unpubl.). In the present paper we propose to consider the behaviour of the six species which immigrated into the plots sown.

The global assessment (Tab. 5) is enlarged by comments of the stage-variant structure of populations.

Tab. 4. Founder unit types in the immigrant populations. S = plots sown; P = plots planted.
Verbreitungseinheiten der eingewanderten Populationen. S = angesäte Flächen; P = angepflanzte Flächen.

Taxon	Founder unit	Experimental plot
<i>Poa alpina</i>	propagule-derived tiller or tiller group	S
<i>Polygonum viviparum</i>	bulbil, active or dormant	S
<i>Moehringia ciliata</i>	seed	S
<i>Arabis pumila</i>	fruit	S
<i>Hutchinsia alpina</i>	fruit	S, P
<i>Sedum atratum</i>	seed	S, P
<i>Plantago atrata</i>	seed	P
<i>Compositae</i>	achene	P

The species discussed occurred in various combinations in the diverse trial plots except for the unprotected ski run plot where no immigration was observed (SCHÜTZ 1988). The population development of the immigrant species was clearly related to their multifarious life history strategies; it was also influenced by site conditions in a given plot. A high genet turnover was found in the biennial *Sedum atratum*: seedlings and young plants grew fast and numerous genets flowered in the second year of their life giving rise to numerous seeds. The individuals which flowered were dead by the end of the growing period, but seedling cohorts clearly representing the new generation were seen; the numbers of individuals per plot remained thus relatively stable (Tab. 5). In *Hutchinsia alpina*, seedlings and young genets developed rapidly too, and some individuals were reproducing in the second year of their life. Since the life-span of *H. alpina* comprises more than two years in our research area, genets occurring in a given plot and corresponding to various stage-variants viz. seedlings, young plants, non-reproducing and reproducing adults, obviously represented various generations by the end of the fourth growing period (Tab. 5). The drastic difference in the population size observed between protected and unprotected plots apparently reflects the establishment requirements of *H. alpina*.

Tab. 5. Immigrant populations in the plots seeded in early summer 1984. No immigrant species found in the unprotected ski run plot. Reworked data of SCHÜTZ (1988).
Populationen eingewandelter Arten auf den im Frühsommer 1984 angesäten Flächen. Keine Einwanderung auf der ungeschützten Skipistenfläche. Nach SCHÜTZ (1988) verändert.

Taxon	scree unprotected			scree CURLEX			ski run CURLEX		
	1985	1986	1987	1985	1986	1987	1985	1986	1987
<i>Poa alpina</i>	0	0	0	0	0	0	9	10	41
<i>Polygonum viviparum</i>	0	0	0	1	1	1	0	0	0
<i>Moehringia ciliata</i>	8	8	14	28	34	23	0	0	0
<i>Arabis pumila</i>	0	0	0	0	0	0	6	6	9
<i>Hutchinsia alpina</i>	2	2	2	16	24	28	8	13	15
<i>Sedum atratum</i>	0	0	0	0	0	0	20	18	23
Total N of individuals	10	10	16	45	59	52	43	47	88

Moehringia ciliata and *Arabis pumila* did not reproduce so far. Both taxa became established rather soon, but the population size of *A. pumila* remained small; on the other hand, *M. ciliata* formed rather small populations in unprotected plots but performed very well in the plot covered by the matting. Of the two taxa which reproduce vegetatively by specialized propagules, *Polygonum viviparum* was represented only by a single founder individual (Tab. 5). Since the development of organs proceeds very slowly in this species and plants invest mostly into underground structures (HARTMANN 1957, URBANSKA 1985), a more substantial development of populations would probably require a repeated immigration of propagules. By contrast with the behaviour of *P. viviparum*, the performance of viviparous *Poa alpina* was remarkable: the few founder units developed very fast and some of them reached the reproductive phase in the second year after having been noticed in the plot. The small tussocks produced culms bearing numerous daughter-plantlets and the pronounced increase in the population size was undoubtedly due to the establishment of the subsequent propagule generations (Tab. 5).

6. DISCUSSION

Despite experimental limitations, the results of our study are important both from theoretical and practical point of view. The implications for revegetation of alpine disturbances, and the behaviour of clonal module populations will be

discussed in other papers; we propose thus to consider here some aspects related to reproduction by seed and population ecology of alpine plants.

The temporal patterns of seedling emergence in the field trials were undoubtedly influenced by various types of seed dormancy. Seed populations of the species studied proved to consist of several sub-groups that had varying germination capabilities apparently related to microenvironmental conditions. The distribution of seedling emergence over several growing periods is common in populations of wild species (HARPER 1977) and frequently occurs in alpine plants (AMEN 1966, FOSSATI 1980, WEILENMANN 1981, ZUUR-ISLER 1982, SCHÜTZ 1988); it is also often observed in aggressive pioneer species inhabiting other ecosystems (see e.g. BARNHILL et al. 1983). It seems that the differences observed in the present study were in addition determined by some finely-balanced mechanisms. *Trisetum distichophyllum* produced a seedling population only in one growing period and the residual seed bank remained inactive throughout the following summer. In the non-scarified seed populations of *Anthyllis alpestris* and *Biscutella levigata* seedlings consistently emerged during three subsequent summers, but differences in the time of emergence of the first cohort and the annual variation in the cohort size were distinct. Further studies will show whether the residual seed bank of these populations is still active or the seeds have lost their ability to germinate. On the other hand, it is virtually certain that the scarified seeds of *Anthyllis alpestris* have not survived their first winter in the alpine soil as their life-span is rather short (SCHÜTZ 1988).

The spatial patterns of seedling emergence were different in different plots: the seedling populations were patchy in larger plots, whereas a rather regular distribution occurred in small plots. If we consider the availability of safe sites as the factor determining the seedling emergence (HARPER 1977), it might be assumed that the differences observed are influenced not only by the size of the plots sown but also by the neighbourhood type. The species discussed constituted but a small part of the mixed-species neighbourhoods in larger plots and thus were probably distributed at random while being sown; however, it is possible that they would not find access to all adjacent safe sites anyway since other species claimed them. By contrast, all germination sites would be available to a given seed population forming a single-species neighbourhood. It would be desirable to study dynamics of seed populations established in various neighbourhood types and at various sowing densities because germination sites in the alpine belt may be mostly non-specific of a given taxon, but available to seeds with similar characteristics. It is possible that the only taxon-specific

germination sites in the alpine or subnival belt occur on extreme substrata inhabited only by exceedingly well-adapted plants. The results obtained in the elegant study of HARPER and SAGAR (1953) on three *Ranunculus* from English Midlands grassland may not be confirmed in more extreme environments. It is conceivable that the availability of germination sites above the timberline is primarily determined by the extent of ecophysiological specialization and not microdifferences in seed morphology.

The genet mortality occurred mostly in seedlings and young plants. The losses observed appear to follow in this respect the power function equation established by HETT (1971) for sugar maple and implying a declining probability of death as seedlings age (compare also DEEVEY 1947). The losses suffered by our experimental populations at early developmental stages indicate that the sites sufficiently safe for a successful recruitment decidedly are less numerous than the germination sites. The low genet turnover observed in the plots where safe site conditions were simulated clearly demonstrated this aspect. Previous experimental studies show that the conditions favourable to seed germination of alpine plants are not necessarily favourable to the seedling development (see e.g. DICKENMANN 1982, ZUUR-ISLER 1982, SCHÜTZ 1986, 1988). Since the fate of a seedling ultimately depends on its successful recruitment, a more precise meaning should be given to the "safe site" term. We propose to discriminate between "germination site" and "safe site", the latter being defined by a successful seedling establishment.

An apparent stabilization of populations of *Anthyllis alpestris* and *Biscutella levigata* coincided both with the flower development in some genets, and a scarce or non-existent recruitment of further seedlings from the initial seed bank. This aspect was particularly striking in *Biscutella levigata* where new seedling clusters emerging in the fourth growing period positively represented a new generation of seeds produced *in situ*. The rather early onset of reproduction by seed in the experimental populations indicate that at least some perennial species inhabiting high-altitude sites are able to reach the reproductive phase within a few years despite a relatively small aboveground biomass. This result does not support the often repeated, generalized view that alpine plants need a very long time to reach their reproductive maturity and frequently remain at non-reproducing stage for ten years or more (BLISS 1971, REISIGL and KELLER 1987). Contrary to another long-standing belief that sexual reproduction above the timberline is largely replaced by vegetative propagation (e.g. BILLINGS and MOONEY 1968, BLISS 1971, GRIME 1979), our studies demonstrate that the clonal growth is obviously important in alpine plants but they can and do

reproduce by seed, sexually and asexually (FOSSATI 1976, 1980, WEILENMANN 1980, 1981, ZUUR- ISLER 1981, 1982, GASSER 1983, 1986, SCHÜTZ 1983, 1988, SCHÜTZ and URBANSKA 1984, URBANSKA et al. 1979, URBANSKA 1986a,b, URBANSKA and SCHÜTZ 1986). The present results and, in particular, the spontaneous immigration of various species into our experimental plots constitute a further supporting evidence in this respect. The species presented in this paper exemplify well the great diversity of life history strategies of the numerous high-altitude plants inhabiting our research area. Of about 350-400 species known within the altitude bracket of our research area, already SCHIBLER (1937) listed 227 within the subnival belt from 2600 m a.s.l. upwards; in spite of the decrease in number of life forms, the life history strategies remain diversified, very complex patterns being recognizable in growth, clonal development, reproduction etc. We cannot thus share the generalized belief of some authors who argued that the number of species and also the number of life history strategies decrease as one moves towards more rigorous environments (MULLER 1952, MACMAHON 1981, CHAMBERS et al. 1988). It is likely that alpine ecosystems in various parts of the world differ from each other in some relevant features and there are hazards in oversimplifying. Generalizations help to organize data, but they fail to recognize complexity and thus may result in interpretative difficulties (MURRAY 1987).

SUMMARY

The paper deals with various aspects of experimental population ecology and biology of four alpine species. The multifarious differences in life history strategies occurring between these taxa relate to e.g. presence or absence of seed dormancy, type of dormancy, temporal and spatial patterns of seedling emergence in the field, growth type, reproductive age. Development of populations of other alpine taxa spontaneously established in the trial plots reflect diverse life strategies too.

It is suggested that germination sites in high-alpine areas may be mostly non-specific of a given taxon but available to seeds with similar characteristics, the only taxon-specific germination sites occurring on extreme alpine substrata. The authors propose to discriminate between "germination sites" and "safe sites" as not all sites safe for germination are sufficiently safe for a successful recruitment.

Contrary to some generalized views, the study demonstrates that many alpine species can and do reproduce by seed, and that some high-altitude plants are able to reach the reproductive maturity within only few years from their birth.

The authors conclude that the concept of paucity of adapted species and decrease in number of life history strategies, suggested by some authors for more extreme ecosystems, apparently does not apply to the alpine/subnival vegetation belt of NE Swiss Alps.

ZUSAMMENFASSUNG

Die Arbeit befasst sich mit verschiedenen Aspekten der experimentellen Populationsökologie und -biologie von vier verschiedenen Arten. Sehr unterschiedliche, komplexe Lebensstrategien dieser Arten beziehen sich beispielsweise auf ausgeprägte bzw. fehlende Keimruhe, Keimruhetypen, diverse zeitliche und räumliche Muster des Keimlingsaufkommens im Felde, Wachstumstypen und Fortpflanzungsalter. Die Entwicklung der Populationen von anderen alpinen Arten, die spontan in die Versuchsfächen oberhalb der Waldgrenze eingewandert sind, spiegelt ebenfalls diverse Lebensstrategien wider.

Es wird vermutet, dass Keimungsstellen in alpinen Hochlagen meist nicht spezifisch für eine Pflanzenart, sondern für Samen mit vergleichbaren Merkmalen verfügbar sind und dass die einzigen taxon-spezifischen Keimungsstellen an extremen alpinen Standorten zu finden sind. Die Autoren schlagen vor, dass ein klarer Unterschied zwischen "Keimungsstellen" und "Schutzstellen" gemacht wird, sichern doch nicht alle Keimungsstellen eine erfolgreiche Rekrutierung von Keimlingen.

Im Gegensatz zu einigen verbreiteten Ansichten zeigt die Arbeit, dass viele alpine Arten sich erfolgreich durch Samen fortpflanzen und mindestens einige ausdauernde Hochgebirgspflanzen fähig sind, ihre Fortpflanzungsreife in nur wenigen Jahren nach der Keimung zu erreichen.

Die Autoren vertreten die Meinung, dass das für extreme Ökosysteme manchmal als repräsentativ betrachtete Konzept von der Armut der angepassten Arten und der Verminderung der Anzahl von Lebensstrategien, für die alpine/subnivale Vegetationsstufe der nordöstlichen Schweizer Alpen nicht anwendbar ist.

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