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Germinating behaviour and early life phases of some species from alpine serpentine soils

(Keimverhalten und frühe Lebensphasen einiger Arten von alpinen Serpentinböden)

by

Doris ZUUR-ISLER

Contents

1. Introduction

The characteristic features of plants growing on serpentine substratum have long held the interest of botanists. The weathering of serpentine rocks results in soils poor in nutrients, unfavourable for plant growth. The particular climate factors associated with the alpine vegetation belt also generate extreme ecological conditions. Alpine plants growing in serpentine soils are therefore subject to particularly difficult conditions; it may be expected that these plants exhibit adaptations already in the germination phase and other early stages of their life.

The present study deals with germination and early developmental phases in some plants from alpine serpentine soil. Three aspects were particularly taken into consideration:

1. Germinating behaviour under controlled laboratory conditions.
2. Germination and development of young plants on the parent serpentine soil under controlled conditions in the greenhouse.
3. Germination and development of young plants on serpentine soil in the field.

To date, the germinating behaviour of alpine plants and first stages of their development are not very well known. LüDI (1932) was among the first in Switzerland to study this problem. Extensive studies on alpine species from acidic silicate and carbonate soils have been carried out recently at the Geobotanical Institute by FOSSATI (1976, 1977, 1980) and WEILENMANN (1980, 1981). The present study, employing similar methods but involving plants from serpentine soils, brings about a further contribution to the general knowledge of plant life strategies within the alpine vegetation belt.

Acknowledgements

The present study was carried out at the Geobotanical Institute SFIT Zurich, under the supervision of Prof. Dr. E. LANDOLT and Prof. Dr. K. URBANSKA. I gratefully acknowledge the help of Prof. Dr. K. URBANSKA who revised the text and supported me with constructive criticism. R. GRAF made copies of the photos and E. SCHäFFER, A. HEGI and H.P. ACKERMANN helped in the laboratory and the greenhouse. A. HONEGGER typed the manuscript. Thanks are also due to all my colleagues for their assistance in the field. A cordial thank is addressed to my husband B. ZUUR who helped to translate into English.

2. Material and methods

Seeds from 21 alpine species (Table 2) were harvested in September and October 1980, in a south slope of Totalphorn (2200 m a.s.l.) in the serpentine area of Davos, Grisons, E Switzerland. The geology of the area was studied by PETERS (1963), the floristic investigations were previously carried out by CAFLISCH (1974) and EGGER (1974, in preparation).

Ripe seeds, taken directly from the plants, were dried on paper at room temperature for several days prior to storage in glass bottles at 4^{o} C. Some of those seeds were later embedded in paraffin for studies on seed anatomy in microtome sections.

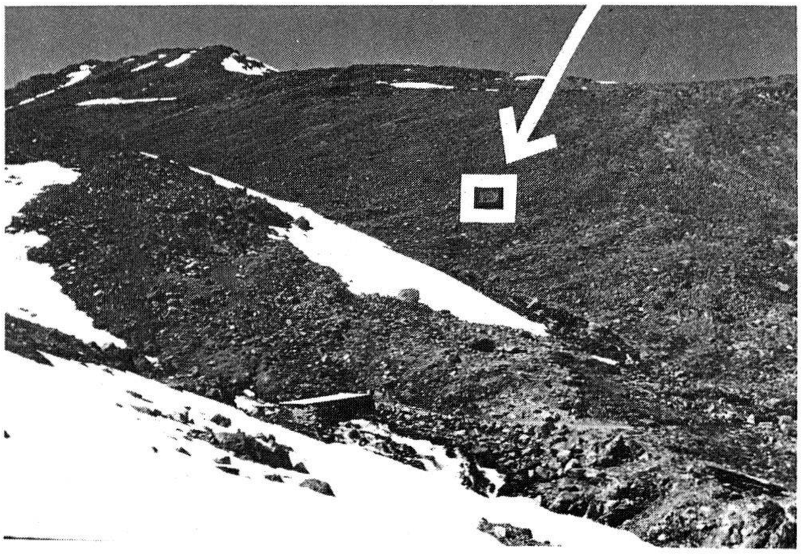


Fig. 1. Study area in south slope of Totalphorn; arrow refers to the experimental plot.

Untersuchungsgebiet im Südhang des Totalphorns; Pfeil bezeichnet die Versuchsfläche.

Laboratory experiments. Fifty seeds of each of the 21 species were sown onto wet blotting paper in Petri dishes and incubated under a temperature regime of 20^{o}C (Day, 13 hrs) and 10^{o}C (Night, 11 hrs) at a relative air humidity of 80 %. The samples were scored for germination three times a week within the 100 day period, germination being defined as the stage when the radicle had penetrated the pericarp. A first trial involved not pretreated seeds of all collected species. The seeds of species which germinated poorly or not at all were pretreated in the second trial. The following techniques were used (FOSSATI 1980):

- *Mechanical scarification*: The pericarp was scratched with glass-paper or, alternatively, with a razor-blade.
- *Chemical scarification*: The seeds were treated with concentrated sulphuric acid. Depending on seed size, the treatment varied from one to five minutes. Subsequently, the seeds were rinsed with tap paper.
- *Gibberelline treatment*: The seeds were soaked in a $5x10^{-3}$ M aqueous solution of gibberellic acid for six days. The solution was renewed once.
- *Stratification*: The seeds were stored in water at 4^{o} C for 14 days.

In the second trial, control samples of non-treated seeds were incubated in parallel to pretreated series.

Studies in the greenhouse. 100 seeds per species were sown in trays (50x35x6 cm) filled with the parent serpentine soil, and maintained under greenhouse conditions for 160 days from mid March on. The number of seedlings and young plants were counted three times a week.

For comparison purposes, some seedlings from this experiment were transfered onto garden soil and kept under the same conditions.

Field observations. An experimental plot was established on the same slope of the Totalphorn where the seeds for investigation were collected (Fig. 1). Within the plot, existing vegetation was removed, and the soil was stabilized by burying wire netting in four rows perpendicular to the slope at a depth of 20 cm. A one meter high wire fence offered protection against grazing mammals. 100 seeds per species were sown in early October, 1980 (Table 1, Fig. 2). The plot was examined six times between mid June and mid September 1981, the number of seedlings and young plants as well as the number of leaves in growing individuals being counted.

Table 1. Arrangement of species sown (on 5th/6th October 1980) within the experimental plot.

Plan der Aussaat (vom 5./6. Oktober 1980) in der Versuchsfläche.

<table>
<tr><td colspan="2">Gentiana kochiana</td><td colspan="2">Carex ericetorum</td><td colspan="2">Senecio doronicum</td><td colspan="2">Lotus alpinus*</td><td colspan="2">Thesium alpinum</td><td colspan="2">Leontodon hyoseroides</td></tr>
<tr><td>Silene willd.</td><td colspan="2">Viola calc.</td><td colspan="2">Cerastium latifolium</td><td>Dryas octop.</td><td colspan="2">Silene acaulis</td><td colspan="2">Carex semperv.</td><td colspan="2">Gentiana campestris</td></tr>
<tr><td colspan="2">Daphne striata</td><td colspan="4">Anthoxanthum alpinum</td><td colspan="2">Minuartia verna</td><td colspan="2">Anthyllis alpestris</td><td colspan="2">Homogyne alpina</td></tr>
<tr><td colspan="2">Biscutella levigata*</td><td colspan="2">Bartsia alpina</td><td colspan="2">Carduus defloratus</td><td colspan="2">Antennaria dioeca*</td><td colspan="2">Solidago alpestris</td><td colspan="2">Biscutella levigata*</td></tr>
</table>

* not used in the present study

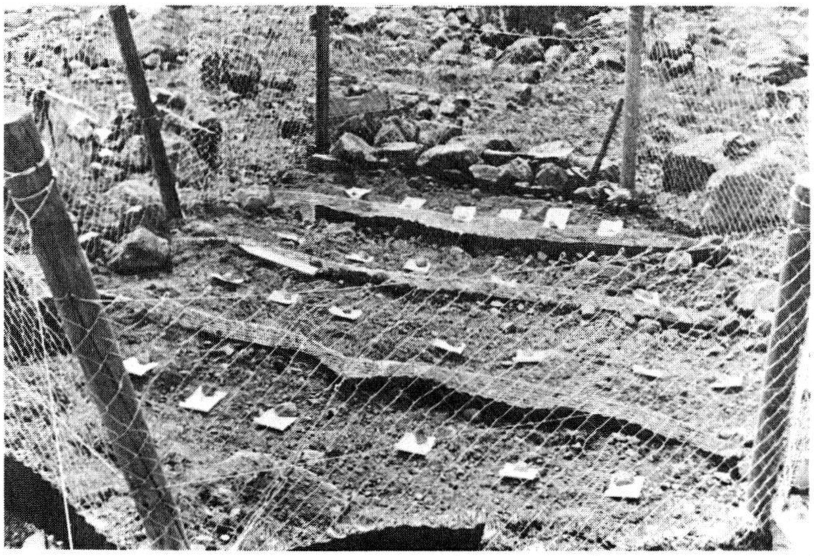


Fig. 2. Arrangement of the experimental plot: each piece of paper marks the place of one sown species (see table 1).

Anordnung der Versuchsfläche: jedes Stück Papier bezeichnet den Ort einer ausgesäten Art (s. Tab. 1).

3. Results

3.1. *Germination trials with non-treated seeds*

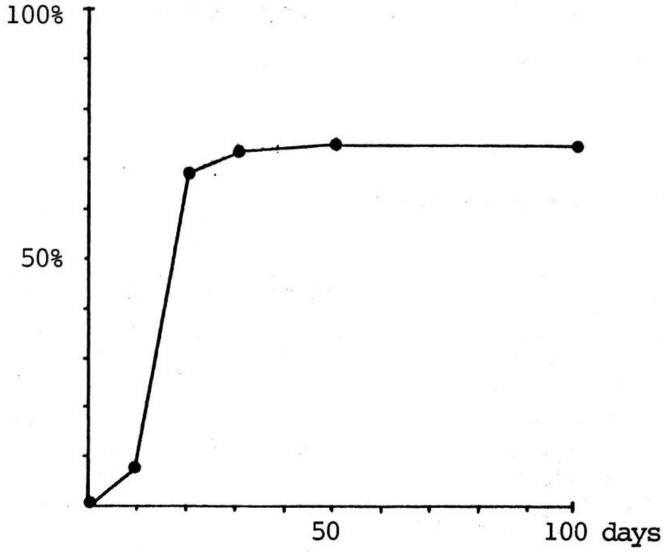
The material investigated was assigned to four groups, respectively comprising species with good, moderate and poor germinations as well as those with no germination (Table 2). As the classification criterion, the percentage of seeds germinated on 100th day of experiment was accepted. The diagrams are correspondingly marked.

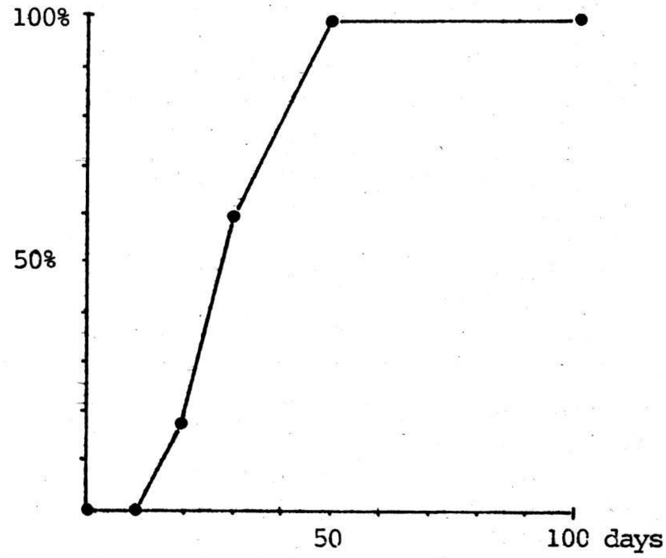
Table 2. Germinating behaviour of non-treated seeds.
Keimverhalten von unbehandelten Samen.

Species	Family	% of seeds germinated 10	30	100 days
Species with good germination (more than 70%):				
Soldanella alpina	*Primulaceae*	0	60	100
Solidago alpestris	*Compositae*	52	94	96
Carduus defloratus	*Compositae*	22	78	86
Senecio doronicum	*Compositae*	8	72	74
Species with moderate germination (30-50%):				
Leontodon hyoseroides	*Compositae*	6	36	48
Silene willdenowii	*Caryophyllaceae*	16	32	46
Silene acaulis	*Caryophyllaceae*	24	28	40
Dryas octopetala	*Rosaceae*	0	28	38
Carex ericetorum	*Cyperaceae*	0	0	32
Species with poor germination (2-15%):				
Anthoxanthum alpinum	*Graminae*	0	0	14
Anthyllis alpestris	*Papilionaceae*	0	0	12
**Daphne striata*	*Thymelaceae*	0	2	10
Homogyne alpina	*Compositae*	0	2	8
**Minuartia verna*	*Caryophyllaceae*	2	6	6
**Bartsia alpina*	*Scrophulariaceae*	0	2	2
**Carex sempervirens*	*Cyperaceae*	0	0	2
Species with no germination:				
**Thesium alpinum*	*Santalaceae*	0	0	0
**Cerastium latifolium*	*Caryophyllaceae*	0	0	0
**Viola calcarata*	*Violaceae*	0	0	0
Gentiana kochiana	*Gentianaceae*	0	0	0
**Gentiana cempestris*	*Gentianaceae*	0	0	0

* seeds pretreated in the second trial

Species with good germination. In four species, more than 70% of the seeds sown germinated. Most of the germination in these species occurred during the first month of the trial; it usually started four or five days after the beginning of incubation, the majority of seeds germinating between the 20th and 30th day (e.g. *Senecio doronicum*, Fig. 3). The germination of *Soldanella alpina* started somewhat later than the others, but then all the fifty seeds germinated within the next 35 days. (Fig. 4).

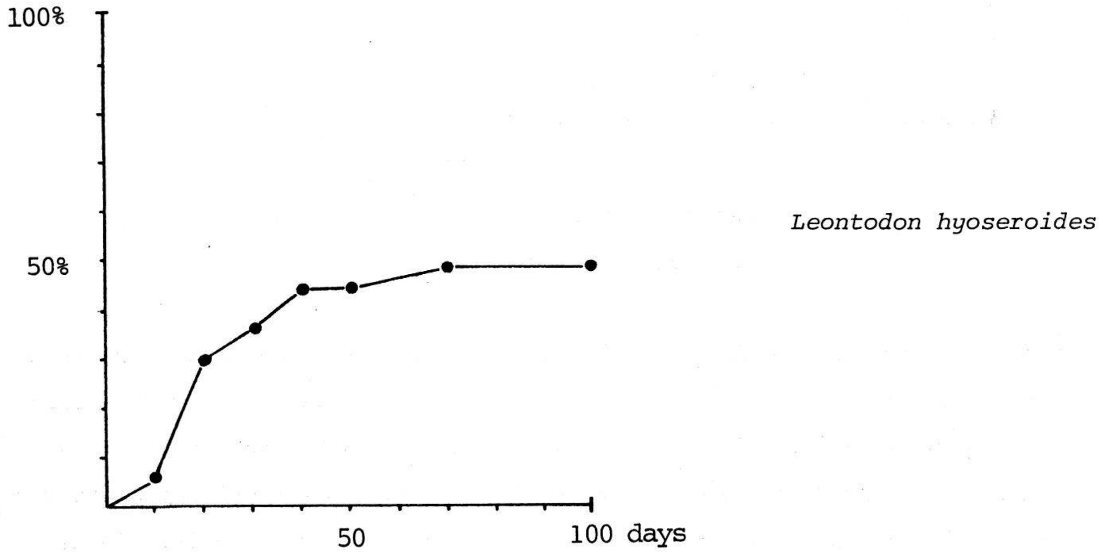


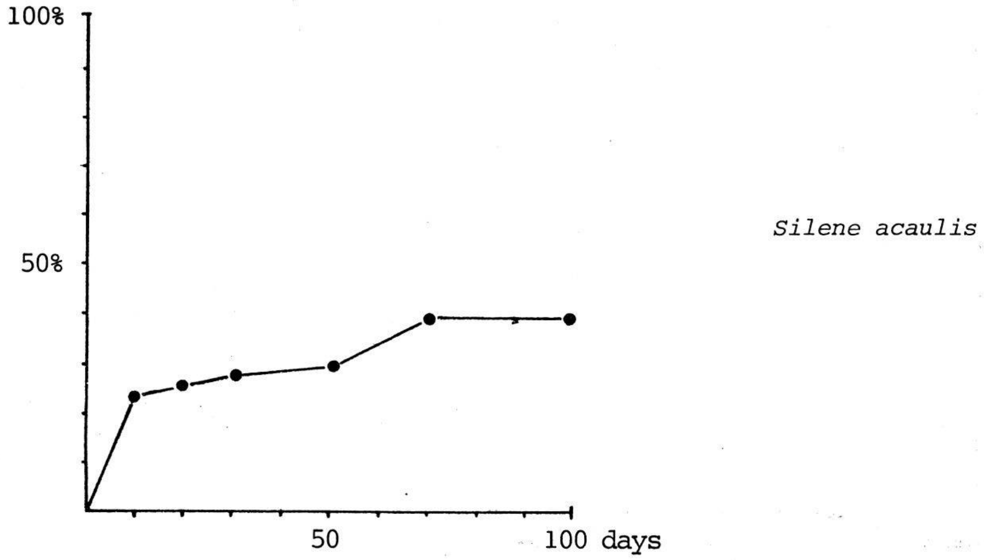


Figs 3-4. Germinating behaviour of *Senecio doronicum* and *Soldanella alpina*.

Keimverhalten von Senecio doronicum und Soldanella alpina.

Species with moderate germination. Five species germinated in 30%-50%. In *Leontodon hyoseroides*, most of germination occurred very early and only very few seeds germinated after fifty days (Fig. 5). The germinating behaviour of *Dryas octopetala* and *Silene willdenowii* followed a similar pattern. The germination in *Silene acaulis* was comparable, although 10% of the seeds germinated only in the ninth week (Fig. 6). Compared to these species, *Daphne striata* germinated somewhat later and *Carex ericetorum* (Fig. 7) considerably later.





Figs 5-6. Germinating behaviour of *Leontodon hyoseroides* and *Silene acaulis*.

Keimverhalten von Leontodon hyoseroides und Silene acaulis.

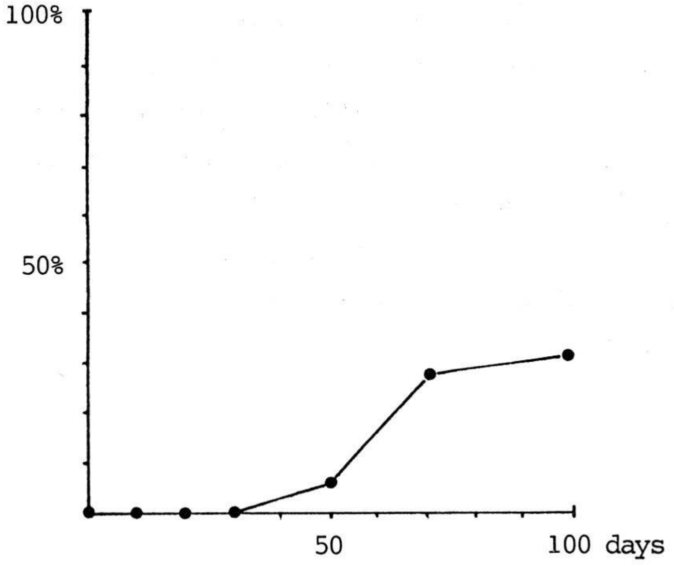


Fig. 7. Germinating behaviour of *Carex ericetorum*.
Keimverhalten von Carex ericetorum.

Species with poor germination. In seven species, only a low percentage of seeds germinated. Just one seed each of *Bartsia alpina* and *Carex sempervirens* germinated, on the 12th and 40th day, respectively. Three seeds of *Minuartia verna* germinated very early, but no more germination was observed afterwards (Fig. 8). The germination in *Homogyne alpina, Daphne*

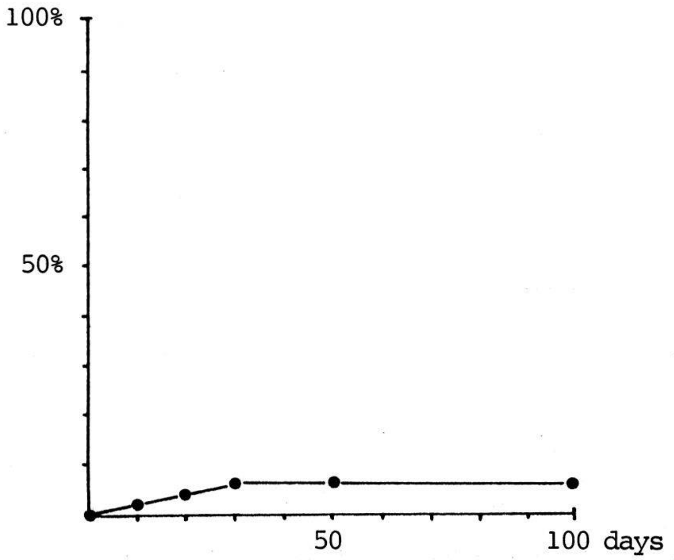


Fig. 8. Germinating behaviour of *Minuartia verna*.
Keimverhalten von Minuartia verna.

striata, Anthoxanthum alpinum and *Anthyllis alpestris* was somewhat delay-ed, especially in the latter two species (Fig. 9).

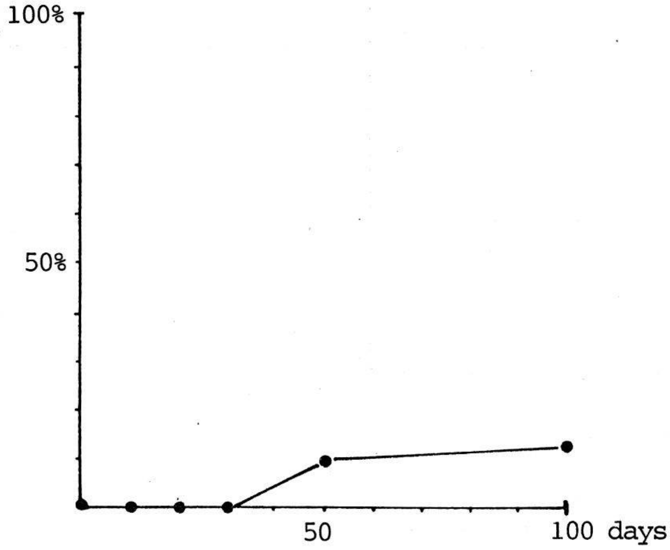


Fig. 9. Germinating behaviour of *Anthyllis alpestris*.
Keimverhalten von Anthyllis alpestris.

Species with no germination. The seeds of *Thesium alpinum, Cerastium latifolium, Viola calcarata, Gentiana kochiana* and *Gentiana campestris* failed to germinate.

3.2. *Germination trials with pretreated seeds*

The trials with pretreated seeds were carried out with the eight species that manifested none or very poor germination (10% or less in non-treated material, Table 2). It was not possible to carry out these trials with *Homogyne alpina,* owing to an insufficiency of collected seeds. *Gentiana kochiana* was not studied, for its germinating behaviour was thoroughly investigated before (FOSSATI 1980). The pretreatments generally resulted in an improved germination (Table 3).

Table 3. Germinating behaviour of pretreated seeds.

Keimverhalten der behandelten Samen.

Treatment	C	One factor: SCr	SCg	GA	SA	Two or three factors: GA+SCr	ST+SCr	ST+SCr+GA
Symbol								
Species								
Carex sempervirens	+	++						
Thesium alpinum	-	-		++	-	+	+	++
Cerastium latifolium	-		+++	+	-	++		
Minuartia verna	++		+++	++	++	++		
Viola calcarata	+	++		++	+	+++		
Daphne striata	-	++		++	+++	+++		
Gentiana campestris	-			+++				
Bartsia alpina	-			+++				

C : Control (no treatment)
SCr: Scarification with razor-blade
SCg: Scarification with glass-paper
GA : Treatment with gibberellic acid
SA : Chemical scarification with sulphuric acid
ST : Wet stratification at 4° C
- : no germination
+ : germination less than 10%
++ : germination between 10% and 50%
+++: germination more than 50%

Carex sempervirens. - (Fig. 10). Mechanical scarification resulted in an improved germination (14%), whereas the control series germinated only in 4%. All germinated seeds developed into seedlings.

Thesium alpinum. - (Fig. 11). Treatment with gibberellin generated a germination of 10%, whereas mechanical scarification combined with stratification led to a germination of 8%. A combination of these three factors was the most successful (germination of 18%). Mechanical and chemical scarification as well as mechanical scarification combined with the gibberellin treatment failed to stimulate the germination. No germination was observed in the control series. The control sample was covered by a fungus growth, whereas pretreated series and especially the stratified sample suffered much less from this infection.

Cerastium latifolium. - (Fig. 12). Mechanical scarification with glass-paper was very successful, with numerous seeds germinating after five

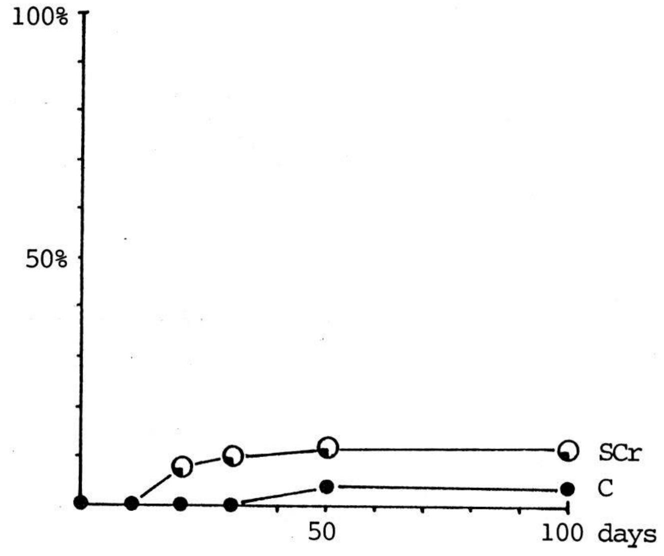


Fig. 10. Germinating behaviour of *Carex sempervirens* after mechanical scarification.

Keimverhalten von Carex sempervirens nach mechanischer Skarifikation.

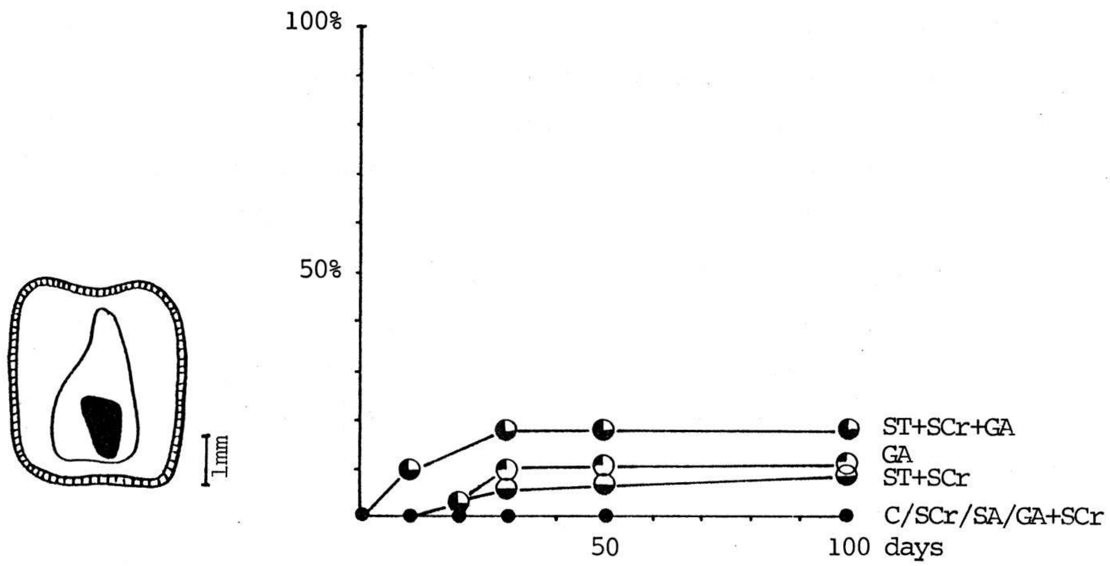


Fig. 11. Germinating behaviour of *Thesium alpinum* after various pretreatments. Left: Seed anatomy.

Keimverhalten von Thesium alpinum nach verschiedenen Vorbehandlungen. Links: Samenanatomie.

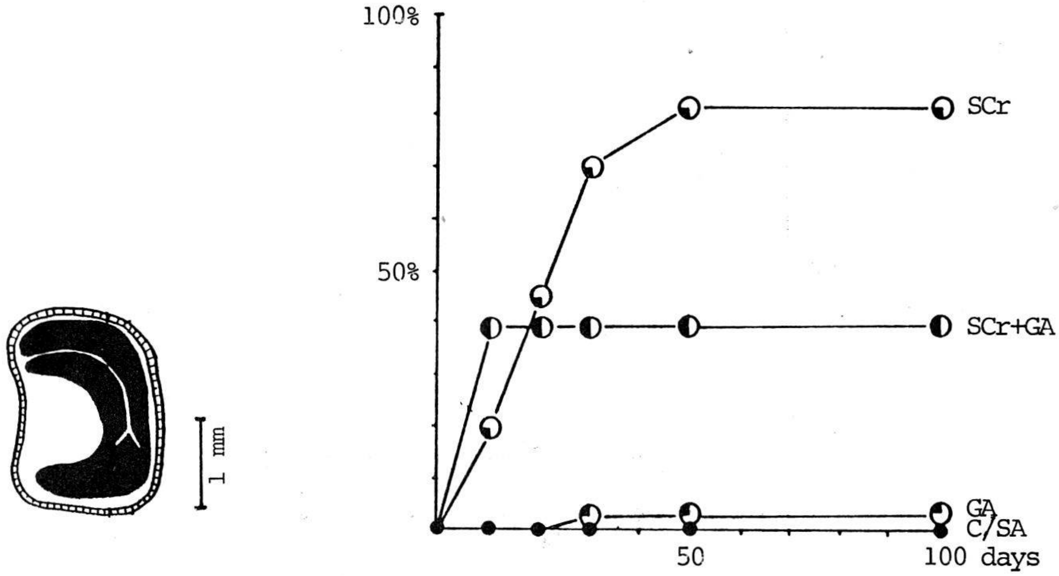


Fig. 12. Germinating behaviour of *Cerastium latifolium* after various pre-treatments. Left: Seed anatomy.

Keimverhalten von Cerastium latifolium nach verschiedenen Vorbehandlungen. Links: Samenanatomie.

days. 84% of seeds germinated by the end of the experiment most of them developing into healthy seedlings. The combination of a mechanical scarification and the gibberellin treatment stimulated germination (40%), but only few of seeds germinated developed into seedlings; this sample was infected by a fungus. No seeds germinated after the chemical scarification but the treatment may have been too long, as the embryos were mostly aborted. Non-treated seeds of this species did not germinate.

Minuartia verna. - (Fig. 13). All the applied treatments improved the germination. The most successful in this respect was the mechanical scarification (66%), but only two of the seeds germinated developed into seedlings. On the other hand, the gibberellin treatment resulted in 40% germination, all germinated seeds giving rise to vigorous seedlings. In the control series, 12% of seeds germinated.

Viola calcarata. - (Fig. 14). Except for chemical scarification that was apparently unfavourable, all treatments improved the germination. Mechanical scarification resulted in germination of 32%, the gibberellin treatment worked slightly better (46%), and the best results were obtained by

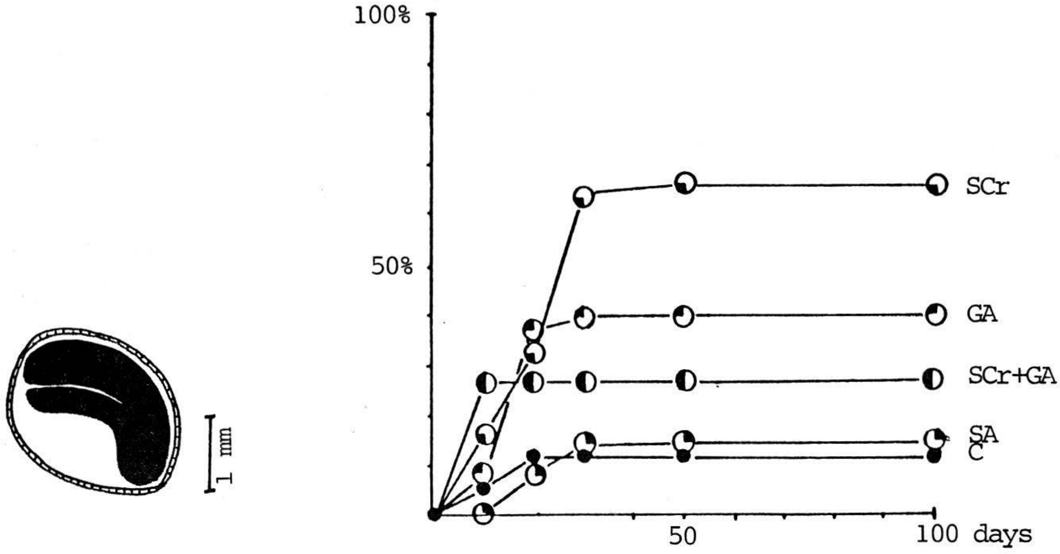


Fig. 13. Germinating behaviour of *Minuartia verna* after various pretreatments. Left: Seed anatomy.

Keimverhalten von Minuartia verna nach verschiedenen Vorbehandlungen. Links: Samenanatomie.

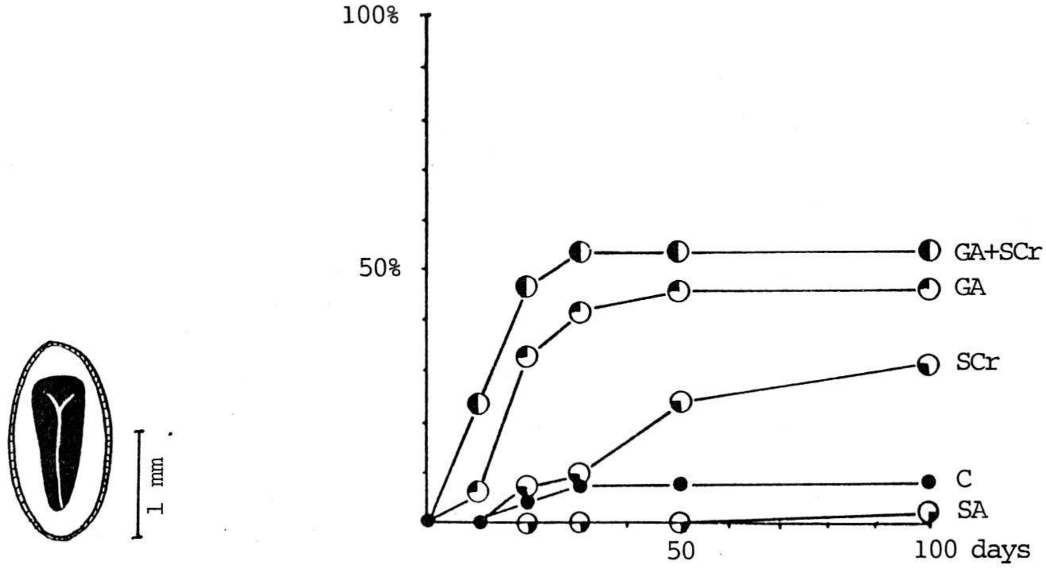


Fig. 14. Germinating behaviour of *Viola calcarata* after various pretreatments. Left: Seed anatomy.

Keimverhalten von Viola calcarata nach verschiedenen Vorbehandlungen. Links: Samen Anatomie.

the combination of the two factors (54%). Only 8% of seeds germinated in the control series. All seeds germinated developed into healthy seedlings. The seeds with the combined treatment were heavily covered by fungus growth, but the germination or subsequent seedling development appeared to be unaffected.

Daphne striata. -(Fig. 15). Mechanical scarification led to a germination of 38%; the gibberellin treatment had virtually the same effect (40%) and a combination of these factors was even more successful (50%). However, the latter test involved a trial of only ten seeds. Maximum germination was generated by chemical scarification (58%), with most of the germination occurring between the 50th and the 70th day. The chemical scarification also resulted in a marked reduction in fungus growth (Fig. 16). In the first trial with non-treated material, 10% of the seeds germinated, but seeds in the control of the second trial failed to germinate.

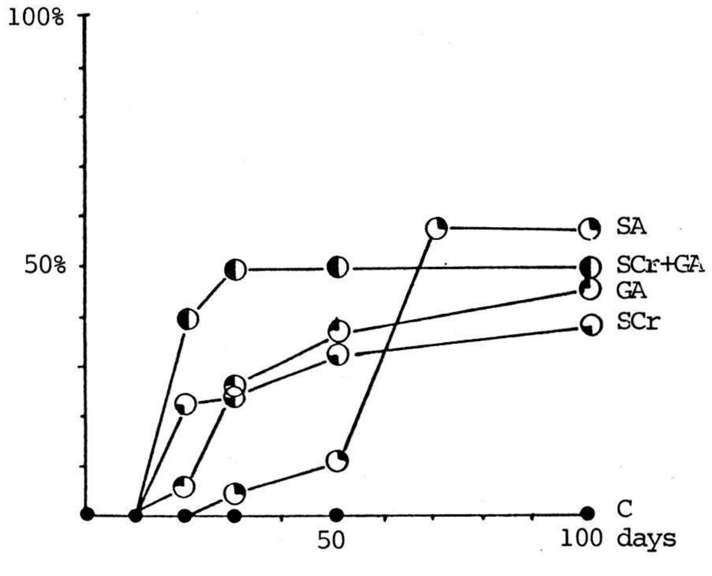


Fig. 15. Germinating behaviour of *Daphne striata* after various pretreatments.

Keimverhalten von Daphne striata nach verschiedenen Vorvehandlungen.

Gentiana campestris. - (Fig. 17). Treatment with gibberellin led to a germination of 96%, all seeds germinated developing into healthy seedlings. No control seeds germinated.

Bartsia alpina. - (Fig. 18). Gibberellin treatment had a marked effect on the germination - 76% compared to zero in the control. All the seeds germinated developed rapidly but then died about two weeks later.

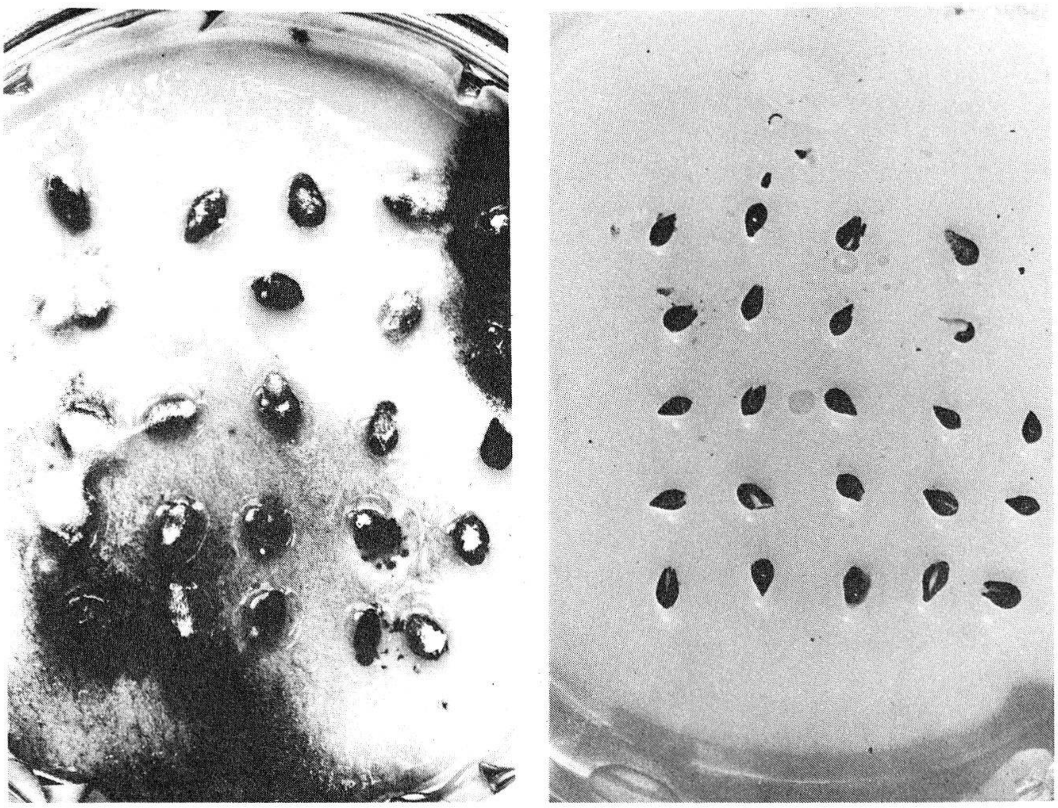


Fig. 16. Seed samples of *Daphne striata:* Left - non-treated sample infected with fungus; right - no fungus growth in the sample pretreated with sulphuric acid.

Samenserien von Daphne striata: Links - unbehandelte Serie, mit Pilzinfektion bedeckt; rechts - keine Pilzinfektion in der mit Schwefelsäure behandelten Serie.

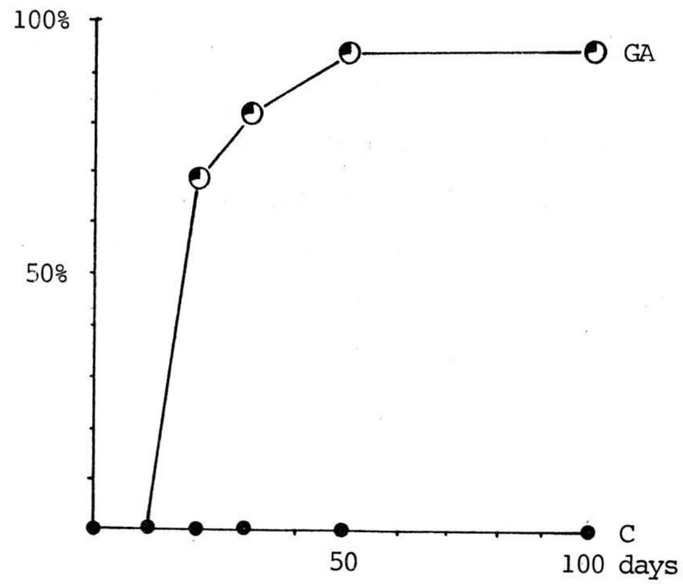


Fig. 17. Germinating behaviour of *Gentiana campestris* after various pre-treatments.

Keimverhalten von Gentiana campestris nach verschiedenen Vorbehandlungen.

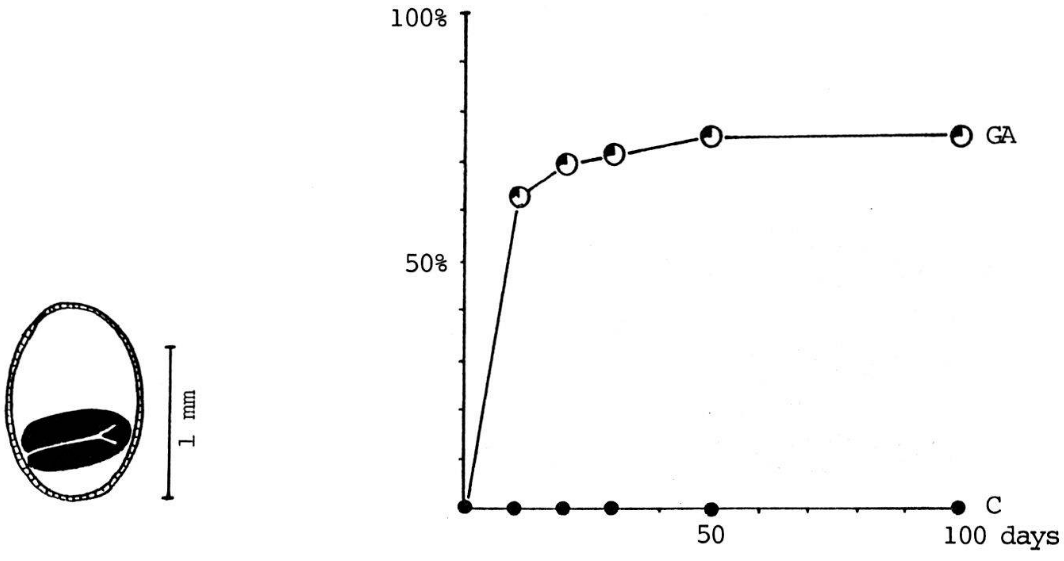


Fig. 18. Germinating behaviour of *Bartsia alpina* after various pretreatments. Left: Seed anatomy.

Keimverhalten von Bartsia alpina nach verschiedenen Vorbehandlungen. Links: Samenanatomie.

3.3. *Experiments in the greenhouse*

Seeds of the 21 species were sown on serpentine soil in the greenhouse. In ten species no germination occurred, whereas seeds of five species germinated very poorly (1%-4%). In five further species, germination below 30% was observed and only one species germinated in 60% (Table 4). Subsequent development of the young plants was generally poor, but this may be attributed to the insufficient care (irregular watering) these plants received.

Table 4. Germination and development of the species sown on serpentine soil in the greenhouse.

Keimung und Entwicklung der Arten, ausgesät auf Serpentinerde im Gewächshaus.

Species	Germination	Development
Carex ericetorum	0	-
Carex sempervirens	0	-
Thesium alpinum	0	-
Cerastium latifolium	0	-
Dryas octopetala	0	-
Soldanella alpine	0	-
Gentiana kochiana	0	-
Gentiana campestris	0	-
Bartsia alpina	0	-
Homogyne alpina	0	-
Anthoxanthum alpinum	+	0
Silene acaulis	+	+
Minuartia verna	+	+
Daphne striata	+	+
Leontodon hyoseroides	+	0
Silene willdenowii	++	++
Anthyllis alpestris	++	++
Viola calcarata	++	+
Carduus defloratus	++	+
Senecio doronicum	++	0
Solidago alpestris	+++	+

Germination: 0 : 0%
+ : 1%-4%
++ : 5%-30%
+++: more than 30%

Development: 0 : no development
+ : 1 - 8 leaves
++ : many leaves

Despite the best germination, the seedlings of *Solidago alpestris* and *Senecio doronicum* exhibited a slow and stunted growth and most of them died. On the other hand, the seeds of *Anthyllis alpestris* and *Silene willdenowii*, respectively, germinated only in 10% and 20%, but their seedlings developed rapidly. Young plants of *Silene willdenowii* grew to a height of up to 30 cm (natural height in the field is ca 25 cm); two individuals flowered on the 100th and 110th day, respectively (Fig. 19).

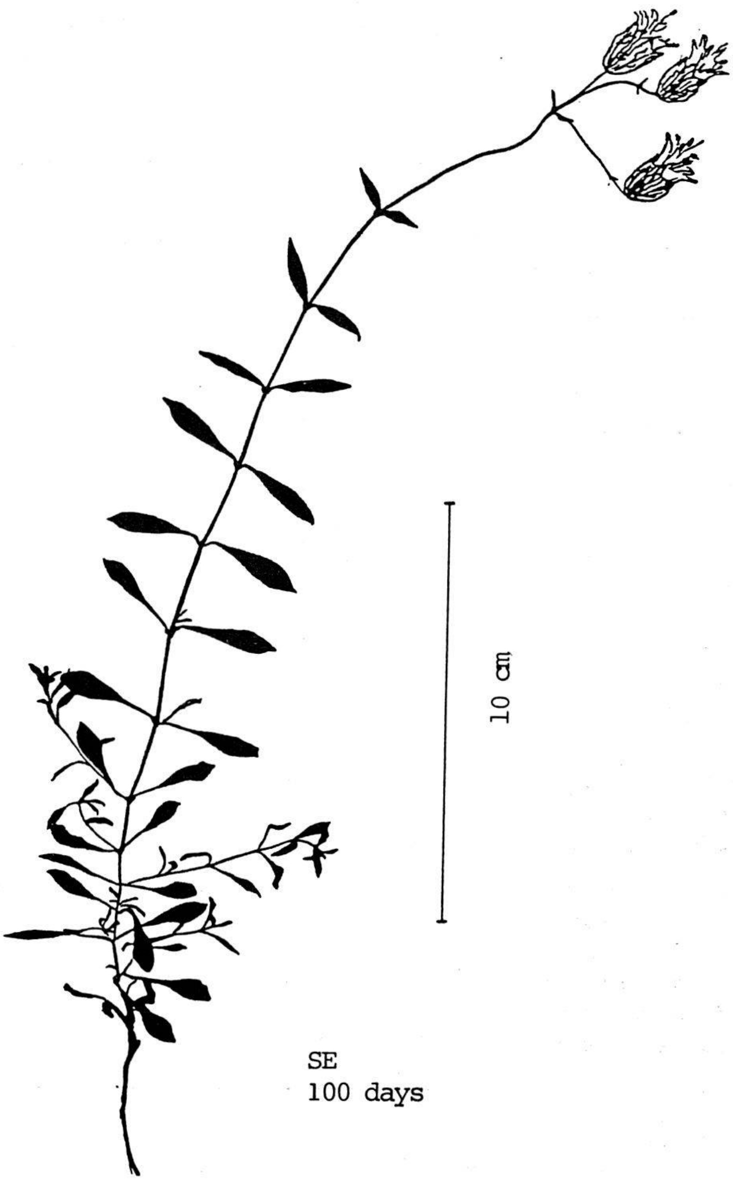


Fig. 19. *Silene willdenowii* in the greenhouse: Development on serpentine soil (SE).

Silene willdenowii im Gewächshaus: Entwicklung auf Serpentinerde (SE).

The seedlings of *Viola calcarata, Carduus defloratus, Silene willdenowii, Daphne striata, Senecio doronicum* and *Solidago alpestris* were planted, for comparison purposes, in a garden soil. Most of these seedlings grew under the same conditions much faster and better on garden soil than on alpine serpentine soil (e.g. *Viola calcarata*, Fig. 20). An interesting exception was *Silene willdenowii* which grew on serpentine soil much more rapidly than on garden soil (Fig. 21, Fig. 19).

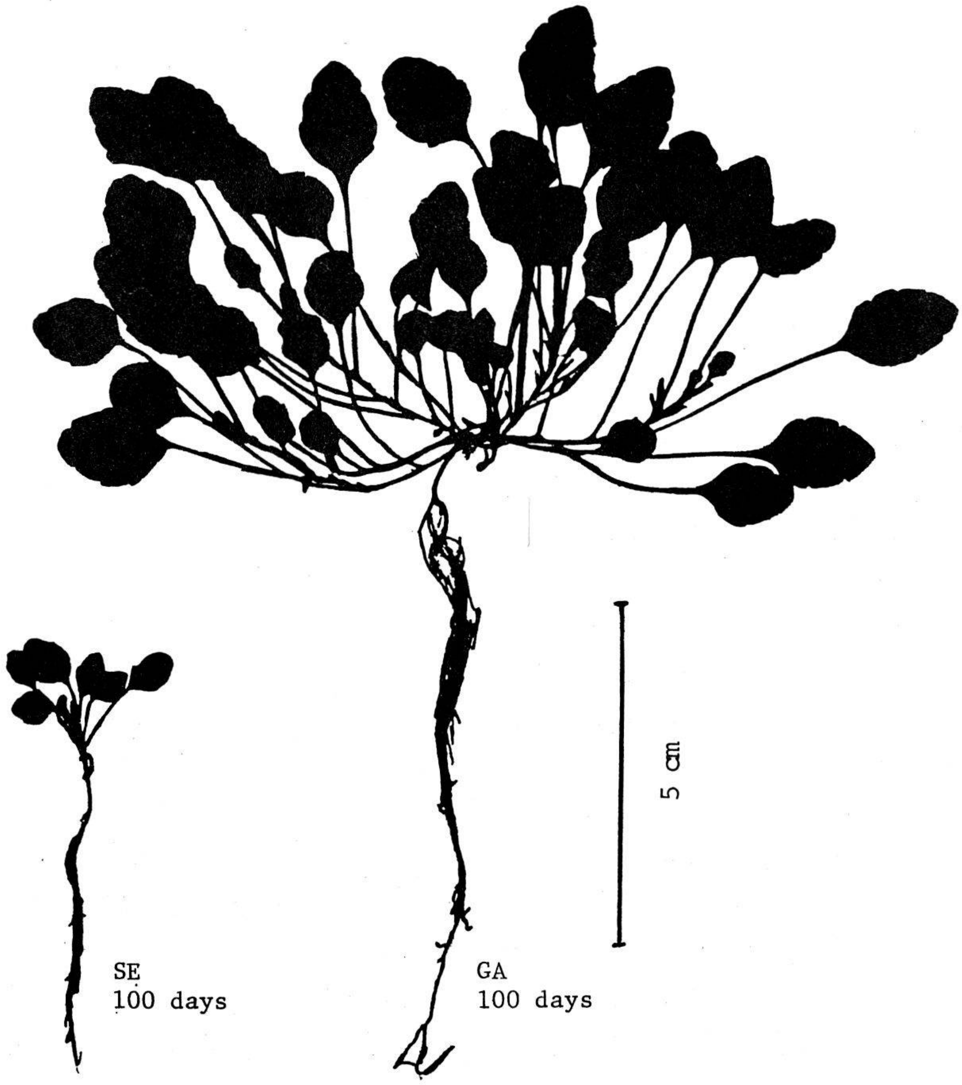


Fig. 20. *Viola calcarata* in the greenhouse: Development on serpentine (SE) and garden soil (GA).

Viola calcarata im Gewächshaus: Entwicklung auf Serpentin- (SE) und Gartenerde (GA).

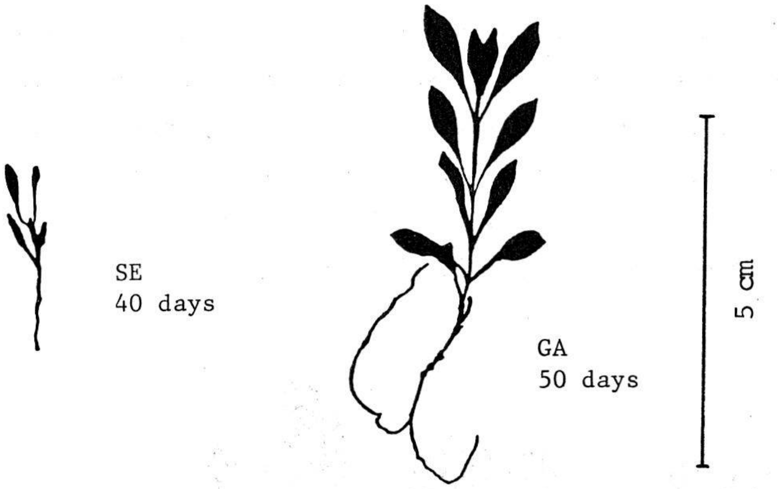


Fig. 21. *Silene willdenowii* in the greenhouse: Development on serpentine (SE) and garden soil (GA).

Silene willdenowii im Gewächshaus: Entwicklung auf Serpentin- (SE) und Gartenerde (GA).

3.4. *Field experiments*

Of the seeds of 20 species sown in the experimental plot, those of eight species failed to germinate. Seeds of five species germinated poorly (less than 10%) and those of seven species in more than 10% (Table 5). The number of seedlings in *Senecio doronicum* found during the control within the plot was rather variable. It is possible that seeds germinated and died between observations, leading to an underestimation of the actual germination and mortality. However, in other species studied the number of seedlings remained more or less constant (*Daphne striata, Silene acaulis, Silene willdenowii, Minuartia verna, Lotus alpinus, Solidago alpestris*) or was gradually increasing (*Anthoxanthum alpinum, Viola calcarata, Carduus defloratus, Homogyne alpina, Leontodon hyoseroides*).

Mortality of seedlings in field appeared to be rather low although it snowed twice during the observation period. At the last control of the plot the young plants of *Leontodon hyoseroides* were the most abundant whereas those of *Carduus defloratus* grew most vigorously.

Table 5. Germination and development on the experimental plot in the field.

Keimung und Entwicklung auf der Versuchsfläche im Feld.

	Number of seedlings/young plants, and average number of leaves in brackets, C = Cotyledones					
Dates of control	14.6.81	29.6.81	14.7.81	4.8.81	17.8.81	7.9.81
Species with no germination:						
Carex sempervirens						
Carex ericetorum						
Thesium alpinum						
Cerastium latifolium						
Dryas octopetala						
Gentiana kochiana						
Bartsia alpina						
Species with germination less than 10%:*						
Daphne striata			2(C)	2(C)	2(C)	
Minuartia verna			3(C)	2(C+2)	4(C+4)	2(C+4)
Anthyllis alpestris			4(C+2)	1(C+1)	1(C+1)	2(C+1)
Silene willdenowii			4(C)	4(C+2)	3(C+2)	3(C+3)
Silene acaulis	9(C)	5(C)	9(C+2)	7(C+4)	8(C+6)	8(C+6)
Species with germination over 10%:*						
Homogyne alpina	9(C)	7(C)	9(C)	9(C+1)	15(C+1)	15(C+1)
Viola calcarata		1(1)	13(C)	14(C+1)	17(C+3)	15(C+4)
Anthoxanthum alpinum	1(C)	4(C)	21(C+1)	27(C+1)	25(C+6)	24(C+6)
Solidago alpestris	35(C)	31(C)	28(C+2)	30(C+2)	31(C+2)	31(C+2)
Senecio doronicum	42(C)	53(C)	49(C+1)	38(C+5)	27(C+5)	31(C+6)
Carduus defloratus		22(C)	37(C+1)	41(C+2)	43(C+3)	38(C+3)
Leontodon hyoseroides	7(C)	18(C+1)	25(C+1)	38(C+2)	42(C+2)	42(C+2)

* data from the last control (September 7, 1981)

4. Discussion

The flora of the alpine vegetation belt consists of species whose life strategies are very variable. The present study shows that this variability may appear already in germination phase, even in plants growing on the same substratum.

In trials under controlled conditions, germination of non-treated seeds was nil in five species; in twelve further species, less than half of the seeds germinated within the trial period of 100 days. In three species a good germination of more than 70% was observed and seeds of one species germinated in 100%. The percentages observed could be influenced by pronounced differences in seed dormancy. However, largely depending on the year of harvest and the arbitrary choice of seeds for investigation, they do not represent constant, reproducible values and should be considered only as tendencies. Seed dormancy is an efficient strategy distributing the risk of germination and satisfactory development over a broad period - only some seeds contribute to the population turnover at a given time, the rest remaining as a seed bank in the soil. Seeds of alpine species usually retain their viability for some years (see e.g. WEILENMANN 1981). Some authors suppose that the seed dormancy of species dominating in some alpine communities may contribute to their success (AMEN 1966).

The spontaneous germination of the *Compositae* was a germination feature observed in the present study: four of the five *Compositae* studied germinated rapidly without any pretreatment. Similar tendencies were previously observed by LÜDI (1932) and FOSSATI (1976, 1980); a frequent absence of dormancy in the *Compositae* was noted as well by PELTON (1954). Such behaviour can be attributed to the seed morphology of the species investigated, the embryos being completely differentiated and fully grown. The only exception in the group of *Compositae* studied was *Homogyne alpina* with a very poor germination of only 8%; our observations corroborated the previous data of LÜDI (1932) who characterized this species as germinating slowly and incompletely. WEILENMANN (1980) observed a similar behaviour in non-treated seeds of *Homogyne alpina*, whereas gibberellin treatment and mechanical scarification improved the germination to 100%. The results of WEILENMANN (1980) suggest that the structure of the pericarp of the inactivity of the fully differentiated and grown embryo may be responsible for the poor germination of non-treated seeds in this species.

Germinating behaviour of *Carex* spp. was very variable. Considerable differences were seen between the present results and those of previous studies, sometimes within the same species. For example, the observed germination of *Carex sempervirens* was only 8%. Curiously enough, this taxon was considered by LüDI (1932) to be a rapidly and very well germinating species. On the other hand, FOSSATI (1976, 1980) observed no germination in his material. The seeds of *Carex sempervirens* studied by LüDI (1932) originated from carbonate soils in the Central Alps; FOSSATI (1976, 1980) used material from silicate soils near Davos, whereas the seeds for the present study were harvested on serpentine soils within the same area; the varying germination percentages could therefore reflect an ecotypic differentiation possibly influenced by different substrata and leading to the development of edaphic races. Mechanical scarification of the seeds of *Carex sempervirens* from serpentine soils led to a slight improvement of the germination. In this respect, the present results differ from unsuccessful pretreatment of the material from acidic silicate soils (FOSSATI 1976, 1980). On the other hand, scarification precisely located near the radicula favourably influenced germination of *Carex firma* and *Carex parviflora* (WEILENMANN 1980). Other species of the genus *Carex* show further variation in the germinating behaviour and their responses to various pretreatments. For instance, *Carex ericetorum* studied in the present investigation germinated better after stratification (BOGENRIEDER 1974) and the germination of *Carex albonigra* originating from the Rocky Mountains was improved by scarification (AMEN and BONDE 1964). The great variability in the germinating behaviour within the genus *Carex* was attributed to various mechanisms of seed dormancy. It was also supposed that the aneuploidy and vegetative reproduction frequently occurring in this genus promote genetic diversity and may influence a subsequent differentiation (AMEN and BONDE 1964).

Seed dormancy in *Thesium alpinum* was very pronounced. None of the treatments applied improved the germination significantly, the most effective being a stratification combined with scarification and gibberellin treatment (18%). Neither a chemical nor a mechanical scarification was successful and treatment with gibberellin resulted only in a slow and sparse germination. No data on germinating behaviour in *Thesium alpinum* could be found in the literature. Some clues to the behaviour may be found in the seed anatomy: although morphologically differentiated, the embryo was small and it may be assumed that it was at least partly responsible for the dormancy. The thick and suberinized pericarp could also restrict germination - it was probably not sufficiently cut by the scarification treatment.

Non-treated seeds of *Cerastium latifolium* did not germinate, but mechanical scarification succeeded in breaking the dormancy. The closely related taxon *Cerastium alpinum* was observed by SöYRINKI (1938/39) to germinate fast without any treatment (90% within two days). Therefore, our data bring about a further example of the variability of germinating behaviour to be found within a given genus.

The non-treated seeds of *Viola calcarata* germinated very poorly. Seed dormancy within this genus was previously noted in *Viola epipsila* and *V. biflora* (SöYRINKI 1938/39). In the present study, the germination of *V. calcarata* was stimulated by mechanical scarification and by the gibberellin treatment. Results of our anatomical study suggest that seed dormancy in *V. calcarata* may be influenced by the thickness of the pericarp and/or the incomplete development of the embryo.

Non-treated seeds of *Minuartia verna* germinated as well only in a low percentage, the germination being much improved by the scarification and gibberellin treatments. Seeds exposed to short-day conditions (30 minutes light per day) also germinated much better than non-treated material (FOSSATI 1976). A variety of treatments being successful in improving germination in *Minuartia verna* and also in *Viola calcarata*, it is apparent that very complex factors influence the seed dormancy of these species.

The seeds of *Daphne striata* germinated very slowly and poorly without pretreatment; all the applied treatments stimulated the germination, the chemical scarification by sulphuric acid being particularly successful. PELTON (1956) observed in *Androsace septentrionalis* and *Thlaspi arvense* an increased germination after scarification with sulphuric acid and compared this behaviour to natural scarification by soil bacteria. Sulphuric acid may also have an indirect influence on germination in *Daphne striata*. The four series, viz. no treatment, mechanical scarification, treatment with gibberellin and chemical scarification with sulphuric acid resulted not only in successively increasing germination, but also reduced the fungus growth; the acid treatment killing the fungus may indidirectly improve the germination, otherwise hampered by the fungus infection. This aspect should be investigated in the future. On the other hand, it should be noted that seeds of *Daphne striata* are often dispersed by animals (MüLLER 1977). It is conceivable that these seeds are scarified in a natural way during the passage through animal digestive tracts. An indirect influence of digestive fluids has been suggested by LAMPREY et al. (1974) and HALEGY (1974), cited after SIMPSON (1977), in *Prosopis juliflora* where an intensive seed predation by bruchid beetles is known. The seed dispersion in this species depends on vertebrates that eat the fruit; many seeds pass then the digestive tract unharmed and are free from the beetles that have been killed by the digestive fluids. The successful germination of various seeds collected from animal faeces has been reported previously by MüLLER (1977). In view of these data research on the effectiveness of a chemical scarification by hydrochloric acid would be of interest.

The seeds of *Gentiana campestris* reacted to the gibberellin treatment with a rapid germination, conforming to the well-known pattern of germinating behaviour within this genus (KALLIO and PIIROINEN 1959, MüLLER 1977, FOSSATI 1976, 1980). The gibberellin may lead initially to embryo growth and then stimulate the actual germination (FOSSATI 1980).

Bartsia alpina also responded well to the gibberellin treatment; our observations corroborate thus the results previously obtained by KALLIO and PIIROINEN (1959). LüDI (1932) considered *Bartsia alpina* as a slowly and incompletely germinating species that required frost influence for germination. However, SöYRINKI (1938/39) failed to improve germination after the frost treatment of his material. On the other hand, wet stratification at 2°C for 180 days led to high germination in experiments of BOGENRIEDER (1974).

Gibberellic acid acts as a phytohormone in the intercellular regulation of growth and differentiation although it is not very specialized and has a variety of effects. It is believed that endogenous gibberellin level within seeds increases as the result of cold temperature and the artificial supplement of this hormone can therefore replace a cold treatment (HESS 1974). The main germination period in most alpine plants occurs after hibernation, an autumn germination immediately after seed ripening being rather exceptional (SÖYRINKI 1938/39). Winter frost being an integrated part of the life cycle of alpine plants, it is understandable that a cold treatment or the equivalent hormone treatment is often necessary to break seed dormancy.

Both mechanical scarification and the gibberellin treatment improved the germination in many of the species investigated by the present author, whereas chemical scarification and stratification, respectively, proved to be effective just in one species. In previous studies, the mechanical scarification was considered as the most frequent factor in breaking dormancy, the gibberellin treatment being given less importance (SÖYRINKI 1938/39, AMEN 1966, FOSSATI 1976, 1980, WEILENMANN 1980). The two latter authors investigated plants from silicate and carbonate alpine soils. They found virtually no differences in the germinating behaviour of seeds from same species respectively originating from silicate and carbonate. It seems therefore that the different reaction of the seeds from serpentine soils observed in the present study is not directly related to the substratum; however, the influence of the serpentine might be indirect. The serpentine flora is not very diversified and generally only a few families dominate. The variety of species available for investigation within a serpentine area is accordingly much more limited than on other substrata. In the present investigation, 42% of the species represented only two families, viz. the *Compositae* and *Caryophyllaceae*, prevailing in our study area. Therefore, one must be careful when describing and comparing general germinating behaviour of plant associations from various soils, for possible differences might be largely due to the choice of species for a given investigation.

The germination and development of the species sown in the serpentine soil in the greenhouse was rather restricted. This soil dries out rapidly leading to large fluctuations in soil moisture, and the complete dying-off of *Senecio doronicum* may probably be attributed to this feature. The influence of these conditions upon growth and development of the other species studied is rather difficult to assess. *Anthyllis alpestris* and *Silene willdenowii* demonstrated that normal development was possible. *Silene willdenowii* flowered after 100 days and had by this time a fully developed root system. The rapid growth and development of the young plants of this species has previously been noted by various authors (e.g. FOSSATI 1979). The genetically fixed tendency to develop an extensive rooting system in plants from serpentine soil represents a characteristic adaptation, necessary to extract sufficient water and nutrients from this rather extreme substrate (EGGER and SCHOOP-BROCKMANN 1979). Plants in the field showed the same tendencies in the present study.

Most of the plants transferred onto garden soil developed much better than those grown in serpentine soil. These results support the opinion that plants growing upon serpentine soils have been forced onto this substratum through competitive weakness, but nevertheless possess a considerable growth potential (KRUECKEBERG 1954, WEILENMANN 1981). Only *Silene willdenowii* proved to be an exception, developing more rapidly on the serpentine than on the garden soil.

In general, the plants studied within the experimental plot in the field appeared to be healthier and stronger than those kept in the greenhouse. For example, *Leontodon hyoseroides* had the best germination in the field, yet only a few seeds germinated in the greenhouse and even those showed very little of subsequent development. These results are contrary to those of FOSSATI (1980), who dealt, however, with different plants from different substrata.

Of the eight species that failed to germinate in the field, a delayed germination may be expected for *Gentiana campestris* and *G. kochiana*. FOSSATI (pers. communication) observed that *Gentiana kochiana* germinated in nature only in the third or fourth year after sowing.

Although sown on naked soil, the seedlings from our field trial exhibited a remarkably low mortality. It should be noted that the conditions of this trial were not very different from natural state of affairs, for serpentine soils have most frequently a very open vegetation contrasting to silicate soils which are often well-covered by vegetation. Distinct differences in seedling mortality, observed by FOSSATI (1980), not only depended on the substratum and the origin of the plants (silicate or carbonate soils), but also were related to vegetation cover: FOSSATI (1980) found a higher mortality in the naked soils than in soils covered by vegetation. Particularly high losses observed on naked soils in summer were attributed by FOSSATI to temporary dessication (see also BONDE 1968). On the other hand, SÖYRINKI (1938/39) considered the autumn frosts and the spring snow-melt to be the most critical periods for young, incompletely established plants. It is certainly possible that the seedlings and young plants within our trial plot had not yet reached their most critical life phase by the time of the last control. Nevertheless, they remained effectively untouched by two very disadvantageous factors occurring during the short study period, viz. the naked soil and summer dessication. The successful adaptations evolved under the extreme alpine conditions have apparently conferred a certain toughness to the plants studied.

The results obtained in the present study demonstrate that the germinating behaviour and early developmental phases in the taxa investigated are exceedingly variable and specific. The diversified strategies apparently led to an optimal exploitation of ecological niches available within alpine serpentine soil. It is, however, impossible to present the adaptations and survival strategies of the plants studied in a simple model. Our results show that complex ecological factors influencing germination and subsequent development often have cumulative, yet sometimes compensatory effects. Although only a long-term research may lead to satisfactory interpretations, the flexibility of life strategies, characteristic for tough alpine plants, emerges already from our brief study. It would be important to know whether the plants which we have found doing well on serpentine soils would be suitable for the revegetation of artificially graded ski slopes. This problem being rather essential in the extensively damaged region of Davos, further studies in the subject are indispensable.

Summary

The study deals with germinating behaviour and early developmental phases of 21 alpine species from serpentine soils near Davos. In the laboratory, the germinating behaviour on blotting-paper of non-treated seeds was studied; attempts were made to improve the germination and/or break a possible seed dormancy by various pretreatments. The germination and development of seeds sown on the parent serpentine soil was observed in the greenhouse as well as in an experimental plot in the study area (2280 m a.s.l.).

The results obtained demonstrated the variability in the germinating behaviour of the plants studied. Of the 21 species, none of the seeds of five species germinated within the trial period of 100 days. Seeds of eleven other species germinated under 50%; seeds of four species germinated above 50% and only one germinated in 100%. Various pretreatments resulted in an improved germination in the eight species studied. For example, mechanically scarified seeds of *Cerastium latifolium* germinated very well, as did the seeds of *Gentiana campestris* and *Bartsia alpina* after the gibberellin treatment. Successful germination of *Daphne striata* was induced by pretreatment with sulphuric acid. Except for *Silene willdenowii*, the germination and development of young plants in the greenhouse was rather restricted. Of the 20 species sown in the field, the seeds of seven species failed to germinate within the first year. Seeds of seven species germinated under 10%, those of six species in more than 10%. The mortality of the young plants in the field was surprisingly low, suggesting a successful adaptation to the extreme alpine conditions.

In conclusion, the variability observed in germination strategies and a possibility of using some apparently well-adapted species for the revegetation of the artificially graded alpine ski runs are briefly discussed.

Zusammenfassung

21 alpine Arten von Serpentinböden bei Davos wurden auf ihr Keimverhalten und ihre frühen Entwicklungsphasen untersucht. Im Labor wurde das Keimverhalten von unbehandelten Samen auf Filterpapier geprüft und versucht die Keimung mit verschiedenen Vorbehandlungen zu verbessern und/oder eine allfällige Keimruhe zu brechen. Die Keimung und Entwicklung von Samen, ausgesät auf Serpentinerde, beobachtete man sowohl im Gewächshaus als auch in einer Versuchsfläche im Untersuchungsgebiet (2280 m ü.M.).

Die erhaltenen Resultate zeigten die Variabilität im Keimverhalten der untersuchten Pflanzen. Von den 21 untersuchten Arten keimten bei fünf nach der Versuchsperiode von 100 Tagen keine Samen. Bei elf keimten weniger als 50%, bei vier mehr als 50% und bei einer Art sogar 100% aller Samen. Verschiedene Vorbehandlungen konnten bei den acht weiter untersuchten Arten die Keimung verbessern. Z.B. keimten mechanisch skarifizierte Samen von *Cerastium latifolium* sehr gut wie auch die Samen von *Gentiana campestris* und *Bartsia alpina* nach einer Gibberellinbehandlung. Die erfolgreiche Keimung von *Daphne striata* konnte durch eine Schwefelsäurebehandlung ausgelöst werden. Mit *Silene willdenowii* als Ausnahme war die Keimung und Entwicklung der jungen Pflanzen im Gewächshaus eher verzögert. Von den 20 im Felde ausgesäten Arten haben bei sieben nach dem ersten Jahr keine Samen gekeimt. Bei weiteren sieben Arten keimten weniger als 10% und bei sechs Arten mehr als 10% aller ausgesäten Samen. Die Sterblichkeit der Jungpflanzen im Felde war überraschend klein, was auf eine erfolgreiche Anpassung an die extremen Verhältnisse deuten könnte.

Abschliessend wird die Bedeutung der Variabilität von Keimungsstrategien und die Verwendung einiger gut angepasster Pflanzenarten für die Wiederbegrünungsversuche in der alpinen Stufe diskutiert.

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