

Performance of some alpine grasses in single-tiller cloning experiments and in the subsequent revegetation trials above the timberline = Verhalten einiger alpiner Gräser in Einzeltriebklonierungs- und Begrünungsversuchen oberhalb der

Waldgrenze

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**Performance of some alpine grasses
in single-tiller cloning experiments and in the subsequent
revegetation trials above the timberline**

**Verhalten einiger alpiner Gräser
in Einzeltriebklonierungs- und Begrünungsversuchen
oberhalb der Waldgrenze**

by

Krystyna M. URBANSKA, Brigit HEFTI-HOLENSTEIN and Gabriella ELMER

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1. INTRODUCTION

The superiority of native species over introduced taxa in revegetation of alpine disturbances has been demonstrated by American authors (see e.g. BROWN et al. 1978) as well as by the studies carried out by the alpine research group of the Geobotanical Institute, Swiss Federal Institute of Technology, Zürich (see e.g. URBANSKA 1986a,b, URBANSKA and SCHUETZ 1986). Our long-term research focuses upon growth and reproduction of alpine plants. Its aim is, on the one hand, to learn more about life-history strategies of plants inhabiting extreme alpine ecosystems; on the other hand, we try to find out which species native of the Alps are the best suited to the biological erosion control above the timberline.

From the very beginning, our primary concern has been not only the selection of suitable species, but also the amount of sampling that had to be done in the alpine vegetation belt to provide us with the material indispensable for experimental research. The senior author argued elsewhere (URBANSKA 1986b) that a concept of repairing damage at one site by inflicting damage upon another one does not make much sense. To solve this problem, various methods of cloning have been worked out by our group, among them the single-tiller cloning (STC) that proved particularly useful for alpine grasses (URBANSKA 1986b).

Cloning has practical advantages because a large amount of physiologically independent ramets may be obtained from a rather limited initial material. It also offers an interesting technique for studies in experimental population biology and ecology because

- genetic variance among the progeny is controlled (ramets cloned from a single parent form a genetically uniform family group);
- the donor plants selected in the wild for cloning are usually well-established and reproducing which means that they successfully passed the stabilizing selection. Studies on behaviour of such genotypes in a new ecological situation (different site conditions, altered size of the genet and ramet as well as the population density) are thus particularly interesting.

The present paper deals with the behaviour of eleven alpine grasses subjected to STC treatment, the ramet populations being established at a

later date in machine-graded ski runs above the timberline.

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2. MATERIAL

The species presented in this paper are representative of the alpine vegetation. They differ from one another as to the form of their clonal growth (Table 1); all are successful and frequently occur in extreme alpine sites (Table 2).

The samples taken from natural populations consisted most frequently of three small (not exceeding 10 cm in diameter) tussocks or tiller groups per population. The family groups resulting from the single-tiller cloning represented thus, at the most, only a few genotypes. The genet identity has not been defined, except for two series of Poa alpina where the ramets grown from single propagule-derived tillers corresponded to one genotype in either group.

The material was collected above the timberline in the surroundings of Davos (Grisons, E Switzerland), most of the samples being taken within the middle- or high-alpine vegetation belt. In view of a possible racial differentiation (see e.g. GASSER 1986, LANDOLT 1985, SCHUETZ and URBANSKA 1984, URBANSKA 1985, 1986a), all samples were taken from the same area and substratum in which experimental ramet populations were later established. Some of the samples were actually collected in close vicinity of the ski runs selected as revegetation sites.

The samples were transferred to Zürich (about 400 m a.s.l.) and planted under competition-free conditions prior to cloning.

Table 1. Clonal growth in the alpine grasses studied
 Tab. 1. Klonales Wachstum der untersuchten alpinen Gräser

I = intravaginal, E = extravaginal, X = from the stock nodes
 * = tiller growth, ** = creeping rhizome

Species	Clone form	*	Stolons	Lateral expansion
<i>Agrostis gigantea</i>	loose mats	E	present	extensive
<i>Agrostis rupestris</i>	dense firm tussocks	I	absent or rare	limited
<i>Agrostis schraderiana</i>	loose mats	I	present	extensive
<i>Festuca pumila</i>	dense firm tussocks	I	none	medium
<i>Phleum alpinum</i>	medium-dense tussocks	I	present	medium
<i>Poa alpina</i>	dense firm tussocks	I	none	pronounced
<i>Sesleria coerulea</i>	loose tussocks	I	**	medium
<i>Sesleria disticha</i>	dense firm tussocks	I	none	limited
<i>Trisetum distichophyllum</i>	loose mats	X	present	extensive
<i>Trisetum spicatum</i>	dense tussocks	I	none	limited

Table 2. Occurrence of the species studied within the alpine area of Davos

Tab. 2. Vorkommen der untersuchten Arten im alpinen Gebiet von Davos

Si = silicate, Ca = carbonate, * the material studied

Species	Site	Substratum
<i>Agrostis gigantea</i>	half-stabilized scree	Ca*
<i>Agrostis rupestris</i>	scree, rock crevices, pastures	Si*, Ca*
<i>Agrostis schraderiana</i>	coarse scree, boulder fields	Si*
<i>Festuca pumila</i>	summits, ridges, wind-exposed scree	Ca*
<i>Phleum alpinum</i>	low grassland, alpine pastures	Si*, Ca*
<i>Poa alpina</i>	scree, low grassland, pastures	Si*, Ca*
<i>Poa cenisia</i>	mobile scree	Si*, Ca
<i>Sesleria coerulea</i>	girdled grassland, scree	Ca*
<i>Sesleria disticha</i>	wind-exposed slopes and ridges	Si*
<i>Trisetum distichophyllum</i>	mobile scree, boulder fields	Ca*, Si*
<i>Trisetum spicatum</i>	wind-exposed scree, moraines	Si*, Ca*

3. GREENHOUSE TRIALS

3.1. SINGLE-TILLER CLONING (STC) treatment

The single-tiller cloning involved the separation of tillers within a given tussock (Fig. 1a). The yield of tillers was considerable in nearly all samples, an average number of tillers per tussock being 130 for most species; the yield of propagule-derived single tillers in the viviparous Poa alpina (Fig. 1b) was also exceedingly high (URBANSKA 1986b).

Single tillers, with or without root were planted in compartments of a ROOTRAINER (purchased at Spencer-Lemaire's, Edmonton, Canada) filled with garden soil. ROOTRAINER segments consisting of five compartments each were then placed together on larger trays (Fig. 2). Occasional gaps between the wall of the ROOTRAINER and the wall of the tray were filled up with the garden soil. The commercial soil mixture used in the trials consisted of 70% peat, 12% brown earth, 6% sand, and 10% perlite granules. Plants originating from calciferous alpine substratum were cultivated in the same garden soil but a small amount of lime was added.

The cloned series were watered and placed in an unheated greenhouse chamber under normal day/night light conditions. On sunny days, protection against overheating was provided by mobile screens.

After the study period of four to six weeks, the STC series made in late autumn either remained in the cold greenhouse or were placed in unheated but covered garden frames to overwinter. The series cloned in late spring were usually placed in open garden frames for about two weeks. Older series were fertilized with the commercial Hauert medium (1% Mg, 0.02% B, 0.04% Fe, 0.3% Mn, 0.005% Cu, 0.005% Mo, 0.005% Zn) used in the concentration of 7 g per 10 l water. Numerous series were cut prior to the field trials.

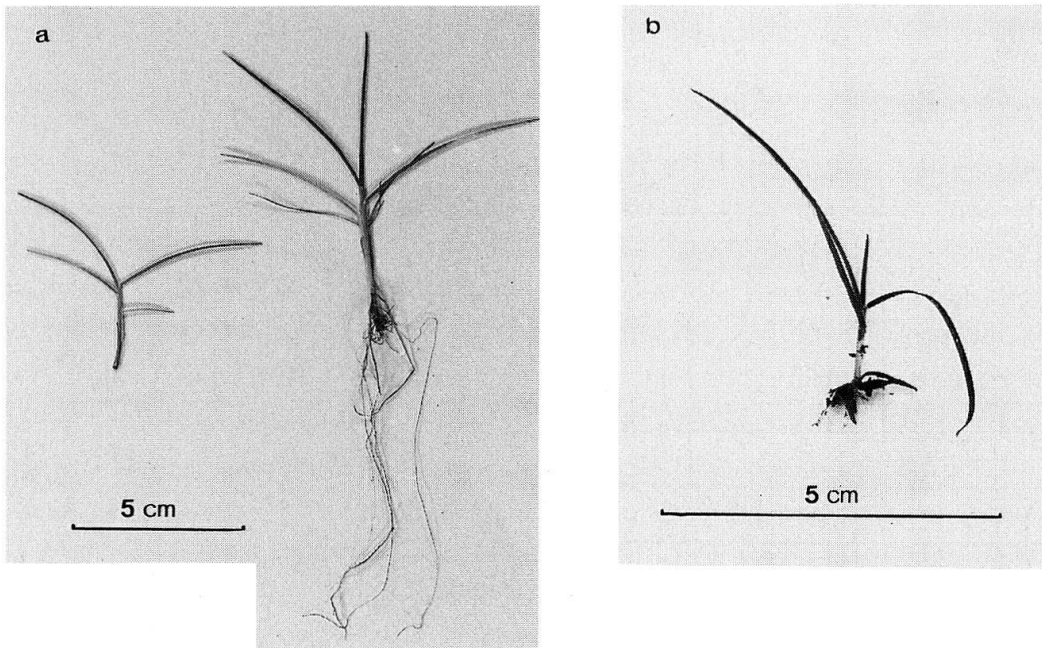


Fig. 1. Single tillers
Abb. 1. Einzelne Triebe

- a. Poa cenisia
- b. Propagule-derived tiller of the viviparous Poa alpina
Triebe aus der Brutzwiebel von Poa alpina

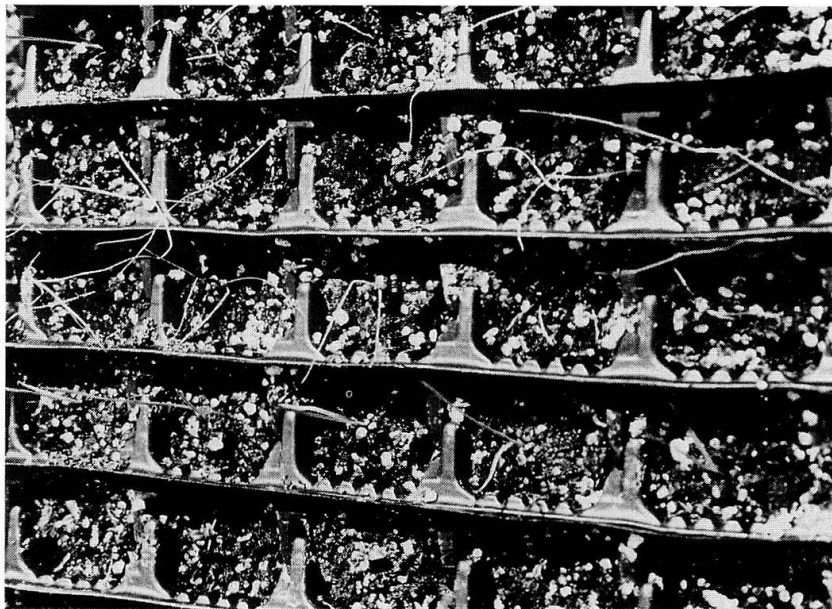


Fig. 2. Single tillers planted in the ROOTRAINER
Abb. 2. Im ROOTRAINER eingepflanzte einzelne Triebe

3.2. SURVIVAL AND RECOVERY OF INITIAL TILLERS

The initial tillers usually remained inactive for some time after the cloning. Their survival and recovery was, on the whole, very good; out of the 2838 tillers cloned, only 278 were lost. On the other hand, the species studied often differed from one another in their survival and recovery pattern, and also in global losses of initial tillers (Figs. 3 to 6, Table 3).

Festuca pumila was the only species in which 100% survival of initial tillers was observed. In eight species studied, the global mortality of initial tillers was between 1 and 10 percent, whereas five series experienced mortality between 13.7 and 17.7 percent. Global losses of initial tillers exceeded 20% only in Agrostis rupestris from dolomite (Table 3).

Table 3. Survival/recovery in initial tillers and development of ramets after the STC treatment. Global evaluation of greenhouse trials.

Tab. 3. Ueberlebens- und Erholungsverhalten der "initial tillers" sowie Entwicklung der Ramets nach der STC-Behandlung. Globale Auswertung von Gewächshausversuchen.

I = initial tillers, N = new tillers, * = mostly replaced by new ones

Species	Number of tillers				
	IT	Dead IT	N	Dead N	Total
<i>Agrostis gigantea</i> (Ca)	279	2	521	0	798
<i>Agrostis rupestris</i> (Si)	92	2*	253	0	343
<i>Agrostis rupestris</i> (Ca)	225	49	611	0	787
<i>Agrostis schraderiana</i> (Si)	238	3	397	0	632
<i>Festuca pumila</i> (Ca)	100	0	50	0	150
<i>Phleum alpinum</i> (Si)	216	36*	155	0	335
<i>Phleum alpinum</i> (Ca)	58	3*	25	0	80
<i>Poa alpina</i> (Si)	122	2*	160	0	280
<i>Poa cenisia</i> (Si)	300	53	434	0	681
<i>Sesleria coerulea</i> (Ca)	92	12	30	0	110
<i>Sesleria disticha</i> (Si)	100	5*	28	0	123
<i>Trisetum distichophyllum</i> (Si)	263	36*	238	0	465
<i>Trisetum distichophyllum</i> (Ca)	145	23*	75	0	197
<i>Trisetum spicatum</i> (Si)	508	50*	420	0	878
<i>Trisetum spicatum</i> (Ca)	100	2	86	0	184

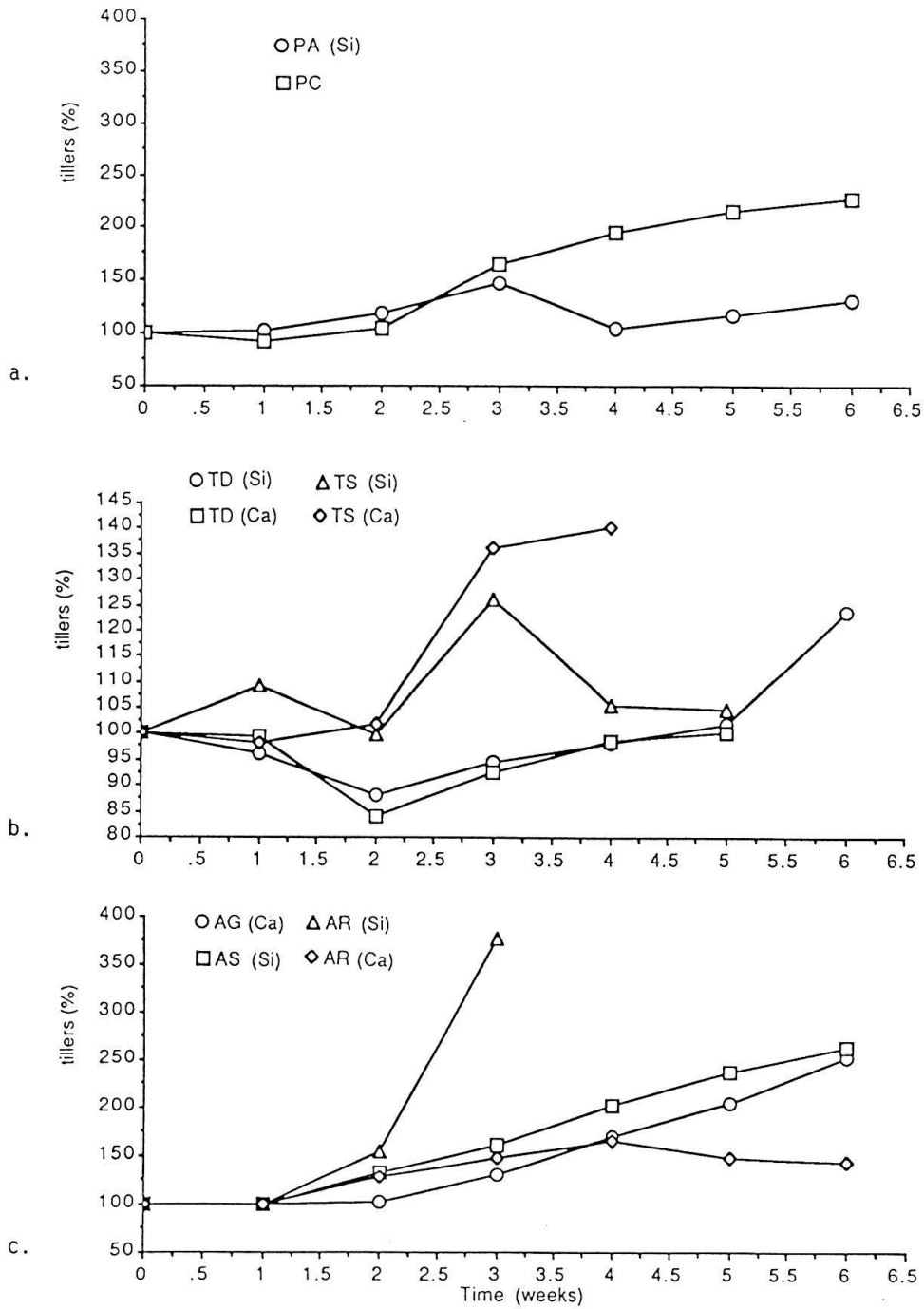
The losses occurring in the initial tiller cohorts did not always result in the loss of given ramets. It is interesting to note, however, that the initial tillers lost were not replaced by new ones in the series which manifested the highest mortality (see Table 3, the series not marked with asterisks).

3.3. DEVELOPMENT OF RAMETS

The development of ramets usually started within the second week after the STC treatment. By the time the new tillers began to appear, no distinct losses occurred anymore in most series, but in some species studied different patterns were observed. For instance, Poa alpina originating from silicate and cloned from tussocks lost two tillers only within the fourth week after cloning (Fig. 3a). Trisetum spicatum from silicate began to grow almost immediately after the STC treatment, and experienced some mortality of initial tillers within the second week; a week of good growth followed, but in the fourth and fifth week after cloning numerous tillers were lost again (Fig. 3b). Curiously enough, the sample originating from dolomite which is not the representative substratum of this species within the research area, experienced only negligible losses (Fig. 3b). Agrostis rupestris from carbonate (Fig. 3c) lost some tillers only after four weeks of stabilization and growth.

The initial tillers which recovered after cloning actively contributed to the ramet development in most of the series studied. On the other hand, production of new tillers per ramet greatly varied from one species to another (Table 4); rather consistent behaviour was observed in this respect e.g. in Agrostis rupestris from silicate and A. gigantea, whereas some other series (e.g. Poa cenisia) showed great fluctuations.

The development of ramets was conspicuously slow in some series; for instance, the two Sesleria species studied did not manifest much growth both within the observation period (Fig. 4, Table 4), and also at later stages. However, most of the species studied which did not grow well within the first six weeks developed vigorous and dense ramets later on (ELMER unpubl., HEFTI-HOLLENSTEIN unpubl.; see also Figs. 7-8).



Figs. 3a-c. Ramet development: cumulative gains and losses
 Abb. 3a-c. Entwicklung der Ramets: Gesamtgewinne und Verluste
 a. *Poa alpina* (PA) and *Poa cenisia* (PC)
 b. *Trisetum distichophyllum* (TD) and *Trisetum spicatum* (TS)
 c. *Agrostis gigantea* (AG), *Agrostis rupestris* (AR) and
Agrostis schraderiana (AS)

Si = silicate, Ca = dolomite

Table 4. Production of new tillers per ramet after the STC treatment. Greenhouse trials.

Tab. 4. Entstehung von neuen Trieben per Ramet nach der STC-Behandlung. Gewächshausversuche.

Species	Number of new ramets		
	Minimum	Maximum	Average
Agrostis gigantea (Ca)	2	5	1.9
Agrostis rupestris (Si)	2	5	2.8
Agrostis rupestris (Ca)	1	7	2.7
Agrostis schraderiana (Si)	2	6	1.7
Festuca pumila (Ca)	0	2	0.5
Phleum alpinum (Si)	0	2	0.7
Phleum alpinum (Ca)	0	2	0.4
Poa alpina (Si)	1	3	1.3
Poa cenisia (Si)	2	12	1.4
Sesleria coerulea (Ca)	0	2	0.3
Sesleria disticha (Si)	0	2	0.3
Trisetum distichophyllum (Si)	0	8	0.9
Trisetum distichophyllum (Ca)	0	7	0.5
Trisetum spicatum (Si)	0	7	0.8
Trisetum spicatum (Ca)	0	8	0.9

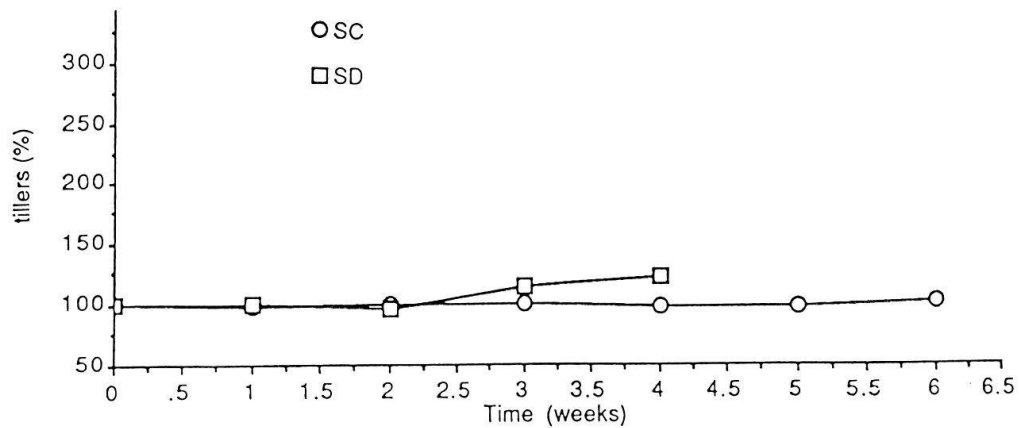


Fig. 4. Ramet development in Sesleria coerulea (SC) and Sesleria disticha (SD): cumulative gains and losses.

Abb. 4. Die Entwicklung der Ramet von Sesleria coerulea und Sesleria disticha (SD): Gesamtgewinne und Verluste.

3.4. ONSET OF FLOWERING

Flowering within the observation period occurred in Poa alpina, P. cenisia, and Sesleria disticha. Poa alpina originating from silicate and carbonate and grown from propagule-derived tillers began to produce culms with propagules by the fourth week after cloning, and by the fifth week about 85% of the ramets reached a well-advanced reproductive stage (URBANSKA unpubl.). The ramets of Poa alpina from silicate grown from single tillers obtained by cloning of tussocks developed some culms already by the second week of the trial; the flowering ramets represented 16.2% of the material studied (HEFTI unpubl.). Poa cenisia developed inflorescences by the sixth week after cloning; 9.9% of the ramets flowered. It is interesting to note that the ramets of the latter species obtained from a repeated cloning of the first series flowered already within the first week after the STC treatment (ELMER unpubl.). Sesleria disticha produced flowers in three ramets only, but the first inflorescence emerged by the end of the first week after cloning.

4. FIELD TRIALS

In early summer, ramets were transferred from Zürich to an acclimatization plot at Davos-Clavadel (1860 m a.s.l.). The material remained within the subalpine belt for about three weeks, no more observation being carried out during this period. The ramets were occasionally watered and protected from overheating, but otherwise not managed.

4.1. ESTABLISHMENT OF RAMET POPULATIONS ABOVE THE TIMBERLINE

The ramet populations were established in two alpine areas respectively



Fig. 5. The experimental revegetation sites upon dolomite: Strela, about 2400 m a.s.l. Summer aspect: the ramet populations protected by biologically degradable CURLEX blanket (in the foreground).

Abb. 5. Die wiederbepflanzten Versuchsflächen auf Dolomit: Strela, ca. 2400 m ü.M. Sommeraspekt: Die Ramet-Populationen sind geschützt mit biologisch abbaubaren CURLEX-Netzen (im Vordergrund).



Fig. 6. The experimental revegetation sites upon dolomite: Strela, about 2400 m a.s.l. Winter aspect: the ski run maintained by RATRAC machines.

Abb. 6. Die wiederbepflanzten Versuchsflächen auf Dolomit: Strela, ca. 2400 m ü.M. Winteraspekt: Die mit RATRAC-Maschinen bearbeitete Skipiste.

representing siliceous and calciferous substratum. The machine-graded ski runs selected as experimental revegetation sites were located at Jakobshorn (silicate, about 2450 m a.s.l.), and Strela (dolomite, about 2400 m a.s.l.; Figs. 5-6).

In all, twelve experimental plots have been established to date. Six plots were planted in 1985, the remainder one year later. Half of the plots are located upon silicate, the other half upon dolomite. The planting was done in two series each year, one soon after the snow had melted and the other in early summer.

Each of the ramets planted consisted of several to numerous tillers (Figs. 7-8) and some of them were already reproducing (Fig. 9). The

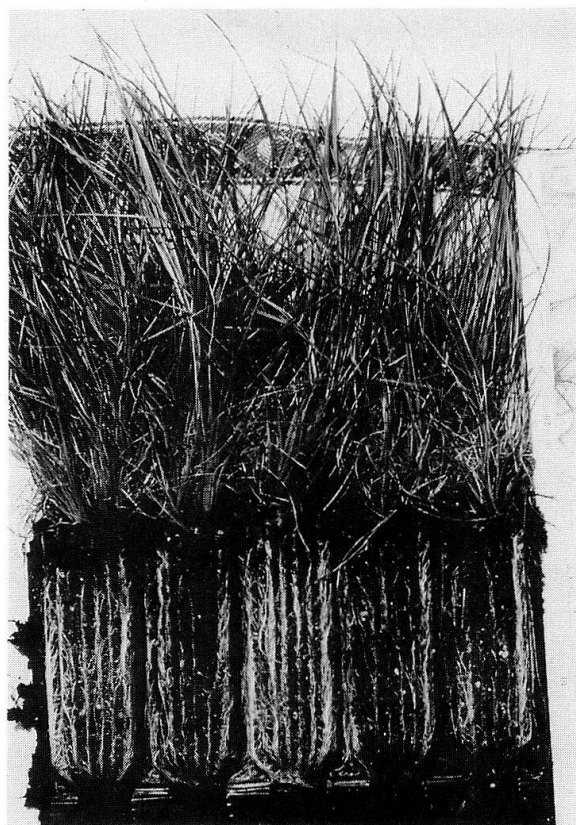


Fig. 7. The STC-derived ramets just before planting.
Open segment of the ROOTRAINER containing five ramets of Trisetum spicatum.

Abb. 7. Die STC-Ramets kurz vor dem Einpflanzen.
Offene Unterteilung des ROOTRAINERS mit fünf Trisetum spicatum-Ramets.

ramets represented family groups of various relative ages, depending on the time of STC treatment; the oldest series were about nine months old whereas the youngest ones barely reached the age of seven weeks. Root-system development in older ramets was very advanced (Figs. 7-8); on the other hand, roots in younger ramets did not completely fill up the ROOT-RAINER compartments.

The ramets were planted by hand, both single-species and mixed-species neighbourhoods being established in a precise design (Fig. 10). To avoid interference among tillers of a given ramet, we opted for a medium density viz. 50 ramets per m².

The ramets planted on silicate corresponded to eight species and totalled 1130 whereas the population established on dolomite totalled 1279 ramets of seven species in a different combination (for the selection of species, see Table 3). The surface of ski runs revegetated by the

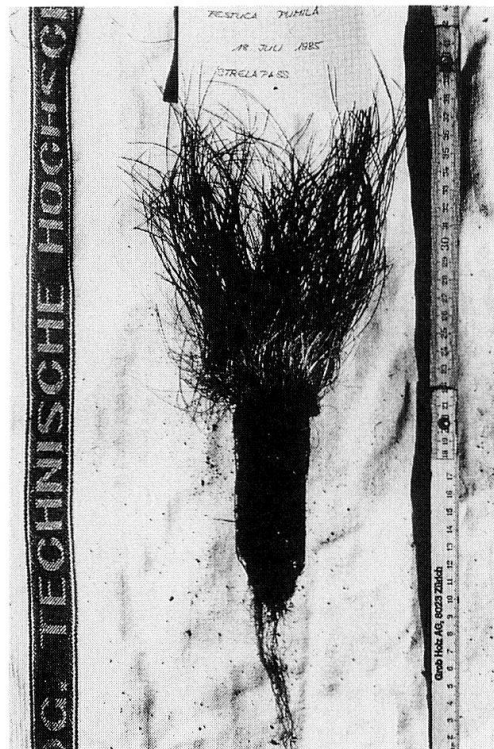


Fig. 8. The STC-derived ramets just before planting. Single ramet of Festuca pumila, about nine months old. Note the exceedingly well-developed root system.

Abb. 8. Die STC-Ramets kurz vor dem Einpflanzen. Einzelner Festuca pumila-Ramet (ca. 9 Wochen alt) mit aussergewöhnlich gut entwickeltem Wurzelsystem.

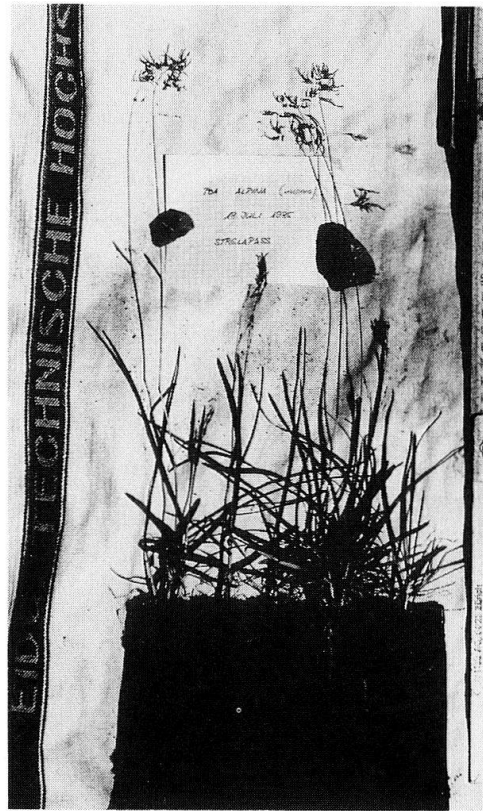


Fig. 9. Poa alpina: ramets with well-developed culms bearing viviparous propagules just before planting.

Abb. 9. Poa alpina: Ramets mit gut entwickelten Stengeln und viviparen Brutzwiebeln kurz vor dem Einpflanzen.

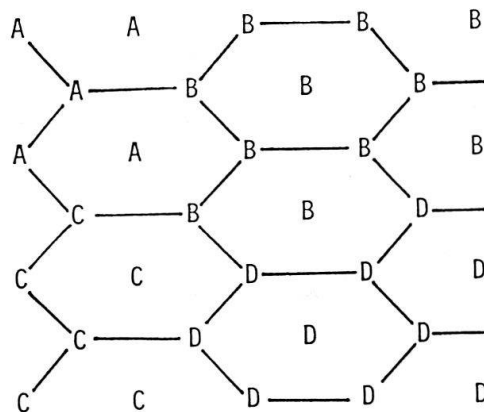


Fig. 10. Single-species and mixed-species neighbourhoods designed for field trials.

Abb. 10. Anordnung der Rein- und Mischbestände in Feldversuchen.

grasses discussed in this paper was 22.5 m² on silicate, and 25.5 m² on dolomite.

The ramets were planted in soil mainly consisting of raw substratum; plots on silicate had more fine soil than those on dolomite where some ramets were bedded in virtually bare rock. The revegetated surfaces were covered with the biologically degradable CURLEX blanket (product of American Excelsior, Texas), and watered copiously. No further management measures were undertaken.

In late autumn, winter and early spring, the experimental sites above the timberline were occasionally visited and checked for development and persistence of the snow as well as possible mechanical damage from skis or ski-run maintenance machines.

4.2. SURVIVAL AND GROWTH OF RAMETS

The ramet populations were controlled five to six times throughout a given vegetation period at about two-week intervals. The ramets were then counted and notes on their survival, general growth, and flowering were made. The check-ups were carried out without lifting the CURLEX blanket, and it is possible that some developing inflorescences were overlooked.

Survival of 100 percent was found in all the series established. Of the 2409 ramets planted, only seven were disturbed by ski run maintenance (RATRAC machines cut through the blanket and shifted the ramets of Festuca pumila), but they recovered rapidly and could be identified later in the season.

Growth of the ramets was estimated according to an arbitrary six-grade scale where '0' coded no growth, '+' equalled a very limited ramet development, '++' corresponded to a well-defined growth, and the three highest grades (+++, ++++ and +++++) respectively denoted an increasing lateral expansion of ramets.

All the ramet populations established in early summer did not manifest any growth within the first week after planting. About two weeks later, all ramets on silicate showed either a limited or a well-defined growth. On dolomite, two of the species planted in 1985 viz. Festuca pumila and

Trisetum distichophyllum still remained inactive but the other series grew similarly to those on silicate. About seven weeks after planting, growth increase was recorded in most series except for the population of Trisetum distichophyllum planted in 1985 on dolomite. By about nine weeks after planting, most series were still growing but populations of Agrostis gigantea, A. schraderiana and Poa cenisia planted in 1986 were already dormant. Later controls revealed an apparently complete winter dormancy, both in the experimental populations as well as in the neighbouring natural vegetation.

The ramet populations planted in autumn did not show any growth during the few weeks following their establishment and preceding the end of the vegetation season.

In the following summer, the ramets began to grow very soon after the snow had melted; both the early summer and the autumn series behaved alike in this respect. The growth was a little more pronounced in the former populations but all the ramets were active. The two subsequent controls revealed a further increase in the growth of ramets in a large majority of the populations studied. By the end of the first ten days of September, a general decrease in growth was observed; populations of Poa alpina, Sesleria coerulea, and Trisetum spicatum on dolomite had become dormant by that time. The census of September 27, 1986, revealed a very limited growth in about half of the populations established whereas the others had apparently entered their winter dormancy phase.

As far as the growth during the first summer after planting is concerned, Agrostis rupestris, A. schraderiana, Poa alpina and P. cenisia were the best performers on silicate; on the other hand, A. gigantea, Festuca pumila, and Trisetum spicatum positively manifested the highest relative vigour on dolomite.

The second vegetation period brought about a great improvement in the ramet development, and only Sesleria disticha consistently showed a very limited tiller production. On silicate, the best relative growth was recorded in Poa alpina, Phleum alpinum and Trisetum distichophyllum; on the other hand, Trisetum spicatum developed rather slowly. On dolomite, Poa alpina and Trisetum spicatum were the most successful but they became dormant by the beginning of September; Trisetum distichophyllum grew slowly and experienced a transient dormancy phase towards the end of August.

4.3. FLOWERING

One of the most amazing results obtained in the present study was the flowering of the ramets under field conditions. It was found to date in nine species studied, some of them known as notoriously slow to develop flowers in the wild (e.g. Festuca pumila, URBANSKA unpubl., Trisetum distichophyllum, URBANSKA and SCHUETZ unpubl.).

As far as the first appearance of flowers in populations established on silicate is concerned, Agrostis rupestris, Poa alpina, Poa cenisia and Sesleria disticha flowered already during their first alpine summer i.e. immediately or soon after planting. Trisetum spicatum and Phleum alpinum planted in autumn flowered during the following summer. On dolomite, Poa alpina in most series, Sesleria coerulea and Trisetum spicatum flowered during the first summer after planting whereas Festuca pumila and Trisetum distichophyllum developed flowers only in their second summer above the timberline.

Percentages of flowering ramets differed from year to year, from one species to another, and also from one series to another. For instance, Agrostis rupestris planted on silicate in early summer 1985 performed exceedingly well (Fig. 10a) but the ramets established on dolomite did not as yet show any flowering. Poa alpina planted in early summer 1985 on silicate flowered to 100% during the first and the second summer (Fig. 10b); on the other hand, the ramets planted in autumn 1985 flowered only to 2.5% during the following summer and those established in early summer 1986 did not produce flowering culms at all. On dolomite, the ramets of Poa alpina planted in early summer 1985 followed exactly the same pattern of flowering as the population on silicate, but only 30% of the ramets flowered in the second summer. The population established in autumn 1985 flowered to 45% during the following summer, and the series planted in early summer 1986 did not flower at all so far. Trisetum spicatum planted on dolomite in early summer 1985 flowered to 50% during the following weeks and the flowering percentage improved only slightly one year later (Fig. 10c); the series planted in autumn 1985 had only 25% of flowering ramets whereas the population established in early summer 1986 did not flower during the first season.

Emergence of inflorescences in Sesleria disticha and S. coerulea followed opposite patterns (Fig. 11). Sesleria disticha planted in early

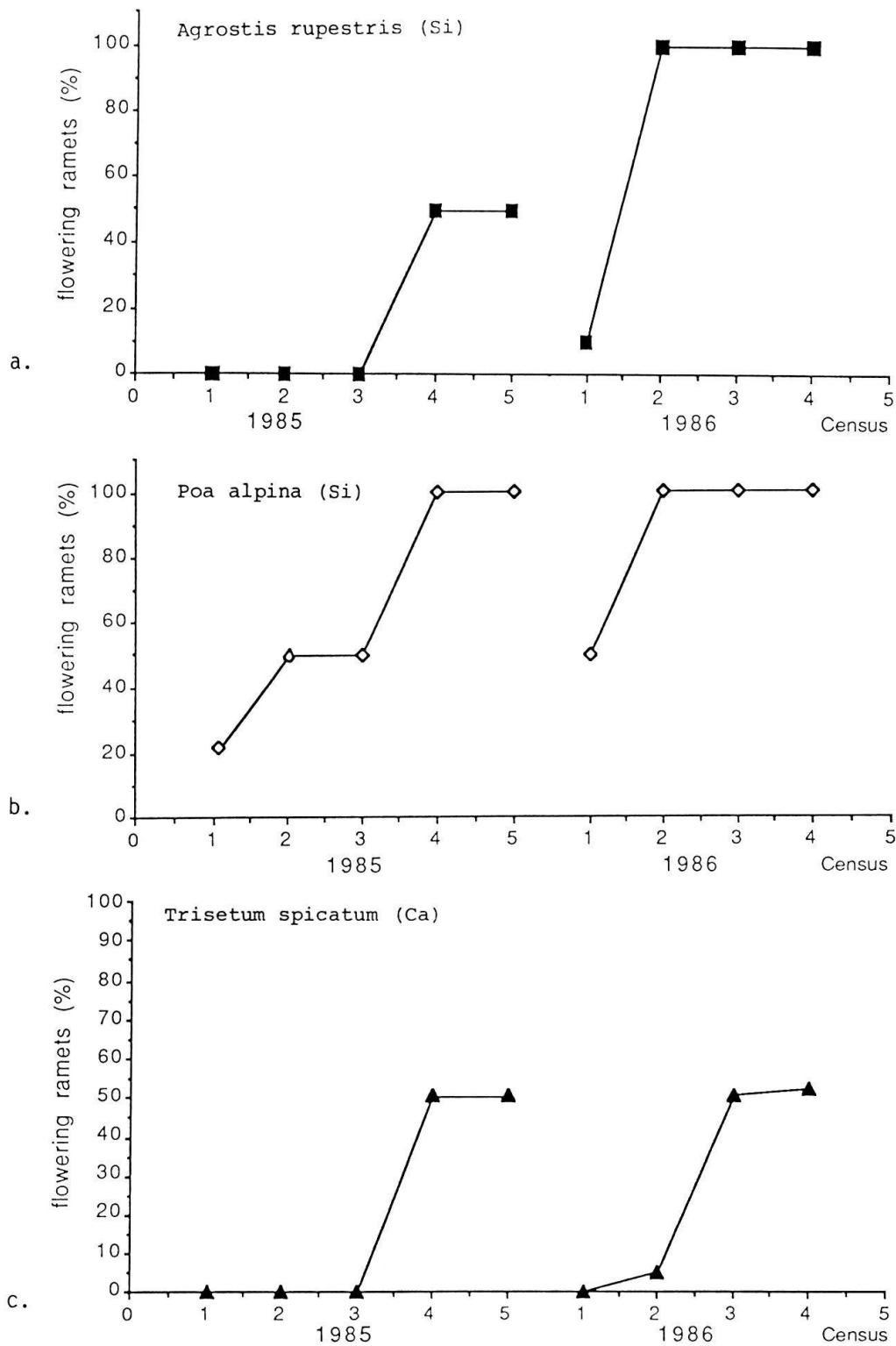


Fig. 11. Flowering in some experimental populations on silicate (Si) and on dolomite (Ca).

Abb. 11. Blütenentwicklung in einigen Versuchspopulationen auf Silikat (Si) und auf Dolomit (Ca).

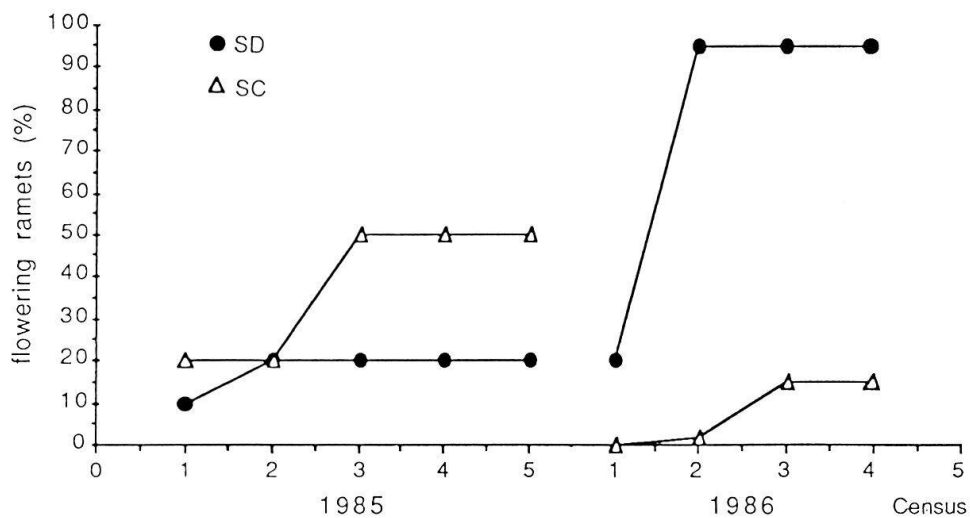


Fig. 12. Flowering of *Sesleria disticha* (SD) und *S. coerulea* (SC)
Fig. 12. Blütenentwicklung bei *S. disticha* (SD) und *S. coerulea* (SC)



Fig. 13. *Trisetum spicatum* planted upon dolomite: relatively small ramets producing up to six culms each. Note the structure of the biologically degradable CURLEX blanket. Photo taken in the second vegetation period after planting.

Abb. 13. *Trisetum spicatum* auf Dolomit gepflanzt: relativ kleine Ramets mit je bis zu sechs Stengeln. Die Struktur des biologisch abbaubaren CURLEX-Netzes ist sichtbar. Das Foto wurde in der zweiten Vegetationsperiode nach dem Einpflanzen gemacht.

summer 1985 flowered to 20% during the following weeks but reached 95% in the second season; contrary to this pattern, Sesleria coerulea flowered to 50% during the first summer after planting, but the flowering diminished in the second season to 15%, in spite of the excellent weather.

Another remarkable aspect of flowering was the relative abundance of flowering culms observed in some experimental populations. Agrostis rupestris on silicate developed five to six culms per ramet; in natural populations, this abundance is sometimes observed in old tussocks which consist of very numerous tillers, but young plants usually form only one to two culms per tussock (SCHUETZ unpubl.). Trisetum spicatum planted upon dolomite developed up to six culms per ramet (Fig. 12); this behaviour is very unusual because only one inflorescence per tussock was found in most plants forming the natural populations from which the cloned ramets originated. Sesleria disticha also produced more inflorescence per ramet than did average tussocks of a comparable size in the wild; this abundance was rather striking since the ramets of S. disticha showed very limited growth not only in the first season after planting but also in the second one.

5. DISCUSSION

The results obtained in the present study relate both to basic as well as applied research. On the one hand, they contribute to a better understanding of population dynamics in plants with clonal growth; on the other hand, they bring information useful in revegetation research which forms a part of ecosystem reconstruction science.

The generally low tiller losses after the STC treatment suggest that alpine grasses have a very high potential for regeneration after damage. The differences observed within a given series are due, at least partially, to the conditions of the initial tillers since some of them were planted without roots, and some others were very weak from the beginning. The leaf and root biomass may represent a factor deciding between

recovery or death of a given initial tiller; it may also influence temporal and spatial patterns of the subsequent ramet development.

Some differences in the development of ramets observed in the material studied may be, on the other hand, related to the genetic make-up of given individuals. For instance, the family groups of Agrostis rupestris from silicate developed strong ramets rather rapidly, whereas those originating from dolomite grew much more slowly and experienced some losses. The material used represented, at the best, only three genotypes in each series; it cannot therefore be decided whether this difference in behaviour is due to a local differentiation of populations inhabiting different alpine substrata, or simply accidental. Patterns of the clonal growth may, however, be very varied even within a single population as demonstrated e.g. by the elegant study of HARBERD (1961, 1962) on Festuca rubra and F. ovina.

Another interesting aspect revealed in the present study is the reproductive performance of the ramets derived from the STC treatment. Detailed data on reproductive size of ramets in natural and experimental populations are rather scarce, and those on alpine species virtually non-existent. However, even the limited information available clearly shows the differences occurring between the genets grown from seed and ramets which result from the clone fragmentation or remain interconnected. Genets of alpine species reportedly have small reproductive size (see e.g. FOSSATI 1980). As far as the perennials are concerned, Silene willdenowii flowered for the first time in its third year (SCHUETZ in prep.), whereas Biscutella levigata did not reach the reproductive phase before the fourth growing season (GASSER 1986). Poa laxa grown from seeds in a greenhouse flowered much earlier. The first culms appearing already in hundred-day-old plants (SCHUETZ unpubl.). The ramets resulting from the STC treatment were rather small when flowering for the first time after cloning, but some species developed culms already within the first six weeks, and others flowered within less than one year after cloning. The accelerated onset of flowering is to some extent comparable to the reproductive behaviour of Solidago canadensis where interconnected ramets grown from rhizomes began to flower earlier than those grown from seed (HARTNETT and BAZZAZ 1985). It should be remembered, however, that the tussocks which constitute the initial material for cloning already reached the reproductive phase in the wild, even if their absolute age could not be defined. On the other hand, reproductive

behaviour of the genets discussed above refers to the individuals monitored from their birth.

It seems that a drastic clone fragmentation may influence not only the onset of flowering but also the actual production of flowers. The number of culms per ramet developed in the series issued from STC treatment tended to be higher than that in the naturally-developed clones or large clone parts. This tendency was particularly clear in e.g. Trisetum spicatum (URBANSKA unpubl.), or T. distichophyllum (HEFTI unpubl., SCHUETZ and URBANSKA unpubl.). Our results support, albeit indirectly, the opinion of COOK (1979) that the clone fragmentation may reduce the probability of genet death: they strongly suggest that fragmentation of clones in alpine grasses is beneficial to genets not only in terms of vegetative growth but also in relation to the intensified reproduction by seed with the resulting considerable prolongation of the genet life-span (see also HARPER 1977). It will be most interesting to study the fate of genets recruited from the seeds already produced and self-sown by the ramets in our experimental populations.

No particular differences in number of culms per ramet were observed among single-species and mixed-species neighbourhoods. In this respect, alpine grasses differ from e.g. Solidago canadensis where three different neighbouring species differentially influenced interconnected sib-ramets (HARTNETT and BAZZAZ 1985). On the other hand, the growth and reproductive performance varied both within a given family group and among groups. For instance, in Poa alpina 100% flowering was observed but the culms did not appear simultaneously in all ramets. In Trisetum spicatum and numerous other species, some ramets flowered but the others have remained in a non-reproducing state so far. These differences further demonstrate that the ramets which are no longer interdependent react **individually** towards e.g. the differential resource limitation; fragmentation of clones should therefore be considered as equivalent to reproduction (see URBANSKA 1985). On the other hand, interconnected ramets all form a single individual, both physiologically and ecologically.

The experiment populations of ramets studied in our programme resemble older natural populations in which ramets occur at medium densities, with neighbouring ramets of the same clone intermixed with ramets of other species. The limited number of genets used in our trials also corresponds to later successional stages (see e.g. ABRAHAMSON 1975, WILLIAMS 1975); in this respect, alpine grasses studied may be compared to

e.g. Trifolium repens (HARBERD 1963), Holcus mollis (HARBERD 1967) or Pteridium aquilinum (OINONEN 1967) since in these species older populations were dominated by a single, or very few, clones. It may be expected that populations of this kind already experienced a strong stabilizing selection and consist of well-established genotypes. The amazing success of the ramets planted in the alpine vegetation belt supports this opinion well.

The points discussed so far refer to the population biology and population ecology. The potential value of our study to research on biological erosion control above the timberline should now be briefly commented upon.

The study represents a part of no-, or minimum-maintenance approach to alpine revegetation at disturbed sites. Planting of ramet populations that represent various species increases the immediate species diversity at a given site which then may serve as an epicenter for a future spread of plants and microorganisms. Our results demonstrate that the genetic diversity of such populations may increase rather rapidly since the ramets begin to reproduce by seed very soon after planting.

The ramets of native species planted above the timberline are not influenced in their establishment by availability of safe sites, and they have an important starting capital of biomass and/or resources. They do not require extensive management except for an initial protection from grazing. Our study shows, as expected, that ramets of alpine plants are well adapted to the low nutrient budget of the alpine belt, the plants apparently being able to use space and resources more efficiently than the introduced lowland species. For this reason, the success of alpine revegetation should be evaluated in terms of growth efficiency rather than by direct growth rates (see also CANHAM and MARKS 1985). The behaviour of ramets studied further demonstrates the limitations of an assessment exclusively based in yield, especially when only above-ground parts are taken into consideration. Alpine species are mostly low-growing and invest heavily in underground structures (see e.g. LANDOLT 1967, URBANSKA 1986a,b, URBANSKA and SCHUETZ 1986); this characteristic growth form has to be considered when revegetation trials above the timberline are being evaluated. We propose therefore that not only the growth efficiency but also reproductive efficiency be included in the concept of revegetation success.

Revegetation by planting represents a means of plant establishment

alternative or conjunctive with seeding (DEPUIT 1986). It is admittedly very costly, especially as far as the labour costs are concerned. In the long run, however, it may prove less expensive than a repeated seeding combined with extensive management. Our preliminary results suggest that planting of ramet populations which include carefully selected alpine species may be a useful strategy for revegetation of local, particularly erosion-endangered sites above the timberline. Further studies are in progress.

SUMMARY

Regeneration, growth patterns, and reproductive behaviour were studied in eleven alpine grasses subjected to the single-tiller treatment (STC). The results obtained both in greenhouse and in the field are presented.

Survival and recovery of initial tiller were generally good. The losses occurring in the initial tiller cohorts not always resulted in the loss of given ramets. Development of ramets varied from one species to another and sometimes also within one species. Numerous ramets issued from the STC treatment produced inflorescences soon after cloning.

The ramet populations were established above the timberline in machine-graded ski runs. The ramet survival was 100%. Differences in growth pattern were observed both within and between species, some taxa being particularly good performers. One of the most amazing aspects of behaviour observed in the field was the rapid and successful flowering.

The results obtained are important to the research on the biological erosion control above the timberline. They are of a particular interest in the minimum maintenance approach to the revegetation of alpine disturbances.

ZUSAMMENFASSUNG

Elf alpine Grasarten wurden vegetativ vermehrt durch "single-tiller cloning (STC) und die Regeneration, das Wachstumsmuster und das Fortpflanzungsverhalten untersucht. Die Ergebnisse aus Gewächshaus- und Feldversuchen wurden dargestellt.

Die Ueberlebens- und Erholungsrate der einzeln gepflanzten Triebe erwies sich allgemein als sehr gut. Die allfällig auftretenden Schäden hatten nicht immer den Verlust des gesamten Ramets zur Folge. Die Entwicklung des Ramets unterschied sich von einer Art zur anderen und gelegentlich sogar innerhalb einer Art. Zahlreiche Ramets, die nach der Klonierung (STC) entstanden, brachten schon bald Blütenstände hervor.

Die Populationen der Ramets wurden oberhalb der Waldgrenze in Skipistenplanierungsflächen ausgepflanzt. Die Ueberlebensrate betrug 100%. Unterschiede im Wachstumsverhalten wurden sowohl innerhalb wie zwischen den

Arten beobachtet. Einige Taxa zeigten besonders gutes Wachstum. Sehr eindrücklich bei diesen Feldversuchen war das rasche und erfolgreiche Blühen der Arten.

Die erhaltenen Ergebnisse bilden einen wichtigen Beitrag zur Erforschung der biologischen Erosionsbekämpfung oberhalb der Waldgrenze. Sie sind besonders interessant im Hinblick auf die Feststellung des minimalen Unterhaltes für die Wiederbegrünung gestörter Flächen in der alpinen Stufe.

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