Experimental research of alpine communities with use of reciprocal transplantations

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3. Experimental research of alpine communities with use of reciprocal transplantations

Andrej V. Sennov and Vladimir G. Onipchenko

3.1. INTRODUCTION

The main question of plant ecology can be stated as "What prevents certain species of plants from living in certain places?" In the broadest sense this question could be answered in two ways. First, some species cannot occupy a place merely due to historical reasons. Second, the species' survival in the community can be opposed by present ecological factors, both biotic and abiotic.

The transplantation method has been used for plant community investigation for a long time. At first, it was applied for separate plant individuals and in this form was rather widespread. Transplanted plants were often used as phytometers. Research carried out by Bonnier (see Clements 1905) was probably among the earliest, to use the phytometer technique. In the early twentieth century, Clements (1905) expounded general directions for experimental investigations of plant communities. Among those techniques the method of introduction of new species into an alien community occupied a prominent place. Later, Clements and Hall (1918) described this method as useful in the research of competitive relationships between plant species. Development of the turf cut transplantation method instead of transplantations of plant phytometers was started in 1910 by Clements. The basis of this method was documented by the year 1924 (Clements and Weaver 1924).

To define whether conditions of growth and the natural habitat of a species are optimal, it is necessary to consider a rate of its competition with other species (Ellenberg 1953, 1954). Shennikov (1942) used pieces of cut turf, transplanted from one plant community to another to estimate the influence of interspecific competition on the viability of plant a species, i.e. narrowing its of potential ecological niche. As a result of this investigation, Shennikov concluded that it is possible to distinguish two kinds of natural areals and ecological optima (which are usually comparable); with interspecific competition and without. The former was called "ecological," and the latter "phytocoenotic" optimum. SHENNIKOV (1942) proved that there was a significant divergence between "ecological" and "phytocoenotic" areal for some species. Later ELLENBERG (1953, 1954) used the terms "physiological" and "ecological" areal to describe the range of ecological conditions in which species can grow without and with interspecific competition, resp. To avoid confusion between SHENNIKOV and ELLENBERG's terms, RABOTNOV (1983) suggested "auto-" and "synecological" areal and optimum for the same phenomena. Independently, in the field of general ecology, the same things have been called "fundamental" and "realized" ecological niches resp. (HUTCHINSON 1958).

It seems that the field transplantation technique is one of the best methods suited for the research of species coexistence mechanisms and behaviour of plant species under different ecological conditions. Unfortunately, only a few publications describing the usage of this method are known to the authors (GIGON 1971, KLÖTZLI 1980; MAY et al. 1982, DEL MORAL 1983, PARTRIDGE and WILSON 1988). It seems strange that this method, although very simple, available and important, has not found widespread application (PIGOTT 1982, RABOTNOV 1987b). Probably, this can be connected with the fact, that this method is very time consuming, since it is necessary to observe the transplanted pieces of cut turf for at least several years in order to obtain reliable results. During the first years of the experiments only transient dynamics of a community can be observed (TILMAN 1988). A new ecological equilibrium can be established after several generations of main dominants (LIKENS 1987).

A main purpose of this investigation was to find out how much recent environmental conditions are favourable for both existing and brought in plant species, or in other words, to determine the role of biotic and abiotic factors in maintaining the structure of some alpine communities. Elucidation of this problem also may be reached by investigating of reactions of different species to the changes in their environment caused by their introduction into other types of communities, which differ in their ecological parameters.

Acknowledgements
We wish to thank I. Malyshev for the field assistance.

3.2. METHODS

The experiments included reciprocal transplantation of turf cuts between four investigated communities:

a) alpine lichen heaths (ALH)

b) *Festuca varia* dominated grasslands (FVG)

c) *Geranium gymnocaulon - Hedysarum caucasicum* dominated meadows (GHM)

d) snow bed communities (SBC).

These communities are described in chapter 1 of this volume.

Within each community a rectangular experimental area of 8x13 m was selected, with its shorter side parallel to the base of the mountain. Areas with homogeneous vegetation were selected.

Within each area, rows of squares, 50x50 cm with 1 m spacing between them, were chosen in such way that the squares included most characteristic species of the community. The chosen squares formed eight rows with five squares in each (Fig. 3.1). Sample plots of 25x25 cm were marked within each square by means of aluminium tent-pegs and fishing line for shoot number counting.

The 160 squares (40 squares per community) obtained in this manner were distributed in the following way: Ten squares in each community were used as a control and the other 30 were transplanted by tens into three other communities in a random manner.

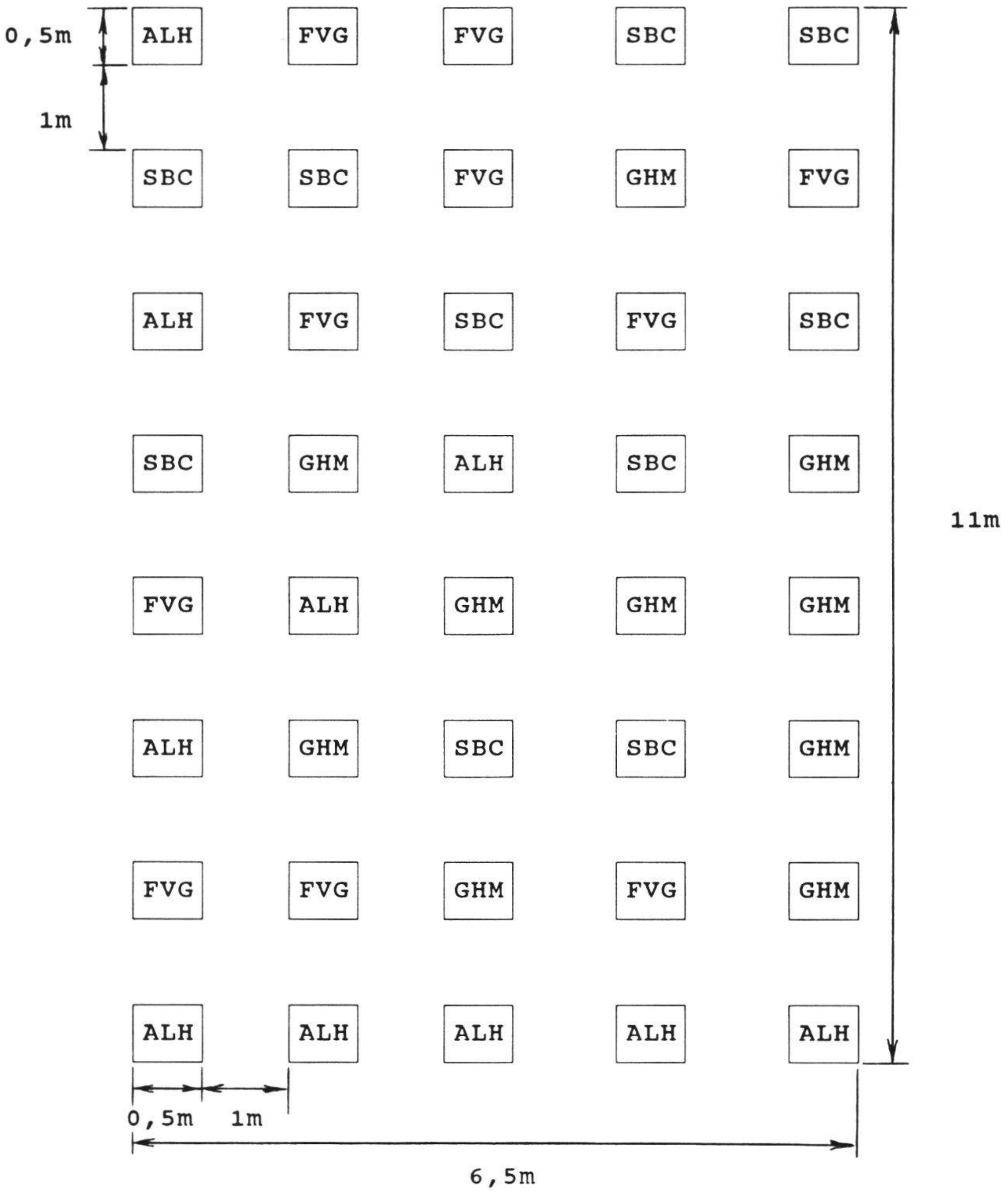
The translocations were carried out as follows: each transplanted sod was dug out as deep as the humus layer (approximately 15-25 cm). Then the turf cut was exchanged with a cut from another community.

The periphery surface of the turf cuts were wrapped with polyethylene stripes to prevent lateral penetration from roots of the surrounding plants, avoiding the additional influence of root competition.

The control squares were also dug out, wrapped around the edges in the same way, and turned around 180 degrees, and put back into the previous place.

The translocations were conducted during two weeks in the summer of 1989. Counting of plant shoots was started in 1988 and continued each subsequent year until July and August of 1992. The vegetative and generative shoots of each species were counted as well as juvenile individuals. Plants with small leaves and which were supposedly in the early stages of development or had low vitality were considered as juvenile individuals.

Fig. 3.1. Scheme of the experimental area in alpine lichen heaths (ALH).



The data resulting from 5 years of counting were evaluated in the following manner. For each type of translocation and control experiment the total amount of individuals of each plant species for each year was calculated. For species with unidirectional changes within four years (either increasing or decreasing amounts) a ratio between the total plant shoots during the last year of observations (1992) and the total during the year of transplantation (1989) for each square was calculated for each square:

$$R = \frac{\text{Sum in 1992}}{\text{Sum in 1989}}$$

average value of this ratio for each species and standard error of the average value.

The calculated data made it possible to detach random oscillations of quantity from naturally determined data using the t-test (a comparison with the initial condition).

A relative coefficient (K) was used to compare plant response to translocations with a control:

$$K = \frac{N_{t2} \times C_{t1}}{N_{t1} \times C_{t2}}$$

N_{t1} is the shoot density on experimental plots at the beginning of the experiment (1989), N_{t2}-shoot density on the experimental plots after some years (e.g. 1992), C_{t1}-shoot density on the control plots at the beginning of the experiment, C_{t2} - the same as in the $_{t2}$ period. The coefficient, discussed in chapter 7, was counted only when all density parameters exceeded 10.

Morphological changes of one species were studied from each community: *Helictotrichon versicolor* from ALH, *Festuca varia* from FVG, *Geranium gymnocaulon* from GHM and *Taraxacum stevenii* from SBC. The length of the longest leaf in several *Helictotrichon versicolor* and *Taraxacum stevenii* plants and the height of generative shoots of *Geranium gymnocaulon* and *Festuca varia* were measured. Both control and transferred experimental plots were studied and a total of at least 30 measurements was carried out in each community. Based on these data, average values and standard error were calculated. To detach the reliable values from the insignificant, the t-test was used.

3.3. RESULTS AND DISCUSSION

3.3.1. Transplantations of alpine lichen heaths (ALH)

There were slight changes in the floristic composition of experimental and control plots after transplantations of ALH sod (Table 3.1 and 3.2). Only a few rare species (*Anthyllis vulneraria* on control, *Alchemilla caucasica* and *Gentiana biebersteinii* after transplantation to GHM) were no longer found

Table 3.1. Dynamics of shoots in the ALH, in the control and transplanted to SBC variants for four experimental years.
Used abbreviations: v = vegetative shoots, g = generative shoots, j = juvenile plants. Probability of distinction between the initial (1989) and 1992 years (t-test): * p >95%, ** p >99%, *** p >99,9%. ALH = alpine lichen heaths, SBC = snow bed communities.

		ALH-Control					ALH→SBC				
Year		89	90	91	92	t	89	90	91	92	t
Anemone speciosa	v	26	19	20	16	*	19	22	26	25	
Arenaria lichnidea	v	81	65	70	58		117	115	139	139	
Campanula	v	44	39	45	56		39	41	34	56	
biebersteiniana	j	39	42	36	43		44	39	41	41	
Campanula collina	v	28	76	62	66	*	22	31	28	32	
Carex umbrosa											
+ C. sempervirens	v	138	151	175	184	**	174	182	229	339	**
Carum caucasicum	g	10	7	8	9	*	9	7	6	10	
	j	24	33	31	35		36	27	61	49	
Eritrichium	v	21	41	40	15		14	10	8	5	***
caucasicum	j	30	26	34	48		8	12	13	8	***
Euphrasia ossica	g	102	84	26	47	*	106	13	46	4	***
Festuca ovina (x10)	v	67	69	90	111	***	55	57	69	128	***
	g	11	8	53	42		10	0	6	63	
Gentiana djimilensis	v	86	89	91	79		45	42	82	95	
Helictotrichon											
versicolor	v	54	51	46	71		48	45	33	62	
Minuartia circassica	v	34	26	24	2		97	103	72	112	***
	g	3	1	3	21		9	0	3	2	***
Plantago saxatilis	v	16	4	7	5	***	6	1	2	4	
Ranunculus oreophilus	v	15	19	21	21		6	7	18	10	
	g	3	6	5	8		20	15	10	14	
Trifolium polyphyllum	v	92	82	86	95		13	26	51	62	
Vaccinium vitis-idaea	v	478	373	393	470		554	176	82	76	***
Sum of shoots (x10)		231	228	253	282		227	179	199	281	
Number of species:											
general		25	27	28	28		29	32	33	35	
appearing		-	4	2	1		-	4	2	3	
disappearing		-	2	1	1		-	1	1	1	

2-3 years after the beginning of the experiment.

The ALH species fall into three groups according to their response to transplantations (Tab. 3.9).

1) Shoot density of the main dominants (*Festuca ovina*, *Carex umbrosa* and *C. tristis*, *Antennaria dioica*, *Trifolium polyphyllum*) and variegated oat (*Helictotrichon versicolor*) increased considerably when transplanted into

Table 3.2. Dynamics of shoots in the ALH transplanted to GHM and FVG variants for four experimental years.
* p >95%, ** p >99%, *** p >99,9%. ALH = alpine lichen heaths, GHM = *Geranium gymnocaulon* - *Hedysarum caucasicum* dominated meadows, FVG = *Festuca varia* dominated grasslands.

		ALH→GHM					ALH→FVG				
Year		89	90	91	92	t	89	90	91	92	t
Anemone speciosa	v	20	14	17	14	*	22	20	22	20	
	g	11	8	10	10		7	13	3	6	
	j	7	15	10	8		7	14	14	4	**
Antennaria dioica	v	126	139	107	151		86	93	113	135	*
Campanula	v	53	45	60	70		34	39	113	49	
biebersteiniana	g	16	11	10	16		7	5	1	8	*
	j	4	27	18	14		50	27	31	24	
Campanula collina	v	52	94	80	84	**	32	48	49	57	***
Carex umbrosa											
+ *C. sempervirens*	v	122	165	213	381	***	184	225	239	367	***
Carum caucasicum	v	18	10	8	5	**	6	4	7	6	
	j	22	75	29	38		26	63	38	14	
Eritrichium caucasic.	v	23	16	3	2	***	28	21	15	15	
Euphrasia ossica	g	137	50	15	23	***	94	40	4	4	***
Festuca ovina (x10)	v	51	74	102	144	***	69	76	110	221	***
	g	28	4	70	78		30	9	116	95	
Gentiana djimilensis	v	100	55	35	59		133	89	75	64	*
Helictotrichon											
versicolor	v	65	75	93	167	***	62	61	85	112	
Luzula spicata	v	15	18	27	43	*	10	11	22	21	
Pedicularis chroor.	v	7	1	1	1	***	1	3	0	1	
Ranunculus oreophilus	v	16	18	15	15		15	13	10	27	
	j	14	25	27	28		23	29	19	10	*
Trifolium polyphyllum	v	40	43	32	32		56	88	81	81	
Vaccinium vitis-idaea	v	434	356	104	84	***	544	492	174	105	***
Sum of shoots (x10)		199	220	219	300		232	238	249	359	
Number of species:											
general		28	31	33	33		28	31	32	32	
appearing		-	5	3	1		-	4	3	3	
disappearing		-	2	1	1		-	1	2	3	

the more productive FVG and GHM (Table 3.9). Apparently, these species have different syn- and autoecological optima and can grow successfully under the more favourable conditions of alpine grasslands and meadows without the competition of more vigorous plants (*Festuca varia, Nardus stricta* et al.).

2) Long living semirosette plants (*Anemone speciosa* and *Campanula bie-*

Table 3.3. Dynamics of shoots in the FVG, in the control and transplanted to SBC variants for four experimental years.
* p >95%, ** p >99%, *** p >99,9%. FVG = *Festuca varia* dominated grasslands, SBC = snow bed communities.

		FVG-Control					FVG→SBC				
Year		89	90	91	92	t	89	90	91	92	t
Anthemis iberica	v	1	2	3	1		20	13	23	43	
Antennaria dioica	v	9	18	26	26		14	11	10	16	
Anthoxanthum odoratum	v	35	37	67	96	*	28	20	58	119	*
Campanula collina	v	4	6	5	7		17	25	26	23	
Carex atrata	v	9	5	8	18		2	5	6	0	
Festuca brunnescens	v	47	59	53	54		29	22	71	47	*
Festuca ovina	v	148	214	377	297		234	168	115	140	
	g	6	2	31	5		17	1	2	1	*
Festuca varia (x10)	v	154	175	256	315	***	218	173	169	250	
	g	126	14	69	21	***	95	13	13	53	
Gentiana djimilensis	v	13	11	12	14		34	14	25	34	
	g	0	8	3	7		2	13	1	2	
Deschampsia flexuosa	v	102	83	87	57		221	194	122	239	
Minuartia aizoides	v	141	237	213	220		63	43	88	144	**
	g	10	8	8	0		0	1	2	3	
Nardus stricta (x10)	v	108	141	165	217	*	115	86	72	96	
	g	65	46	42	54		9	5	10	12	
Scorzonera cana	v	13	15	9	8		19	21	16	25	
	g	0	1	3	0		10	4	7	5	
	j	0	2	4	3		4	10	9	6	
Viola oreades	v	18	10	1	2	***	31	21	3	6	***
Sum of shoots (x10)		340	398	530	626		430	330	314	451	
Number of species:											
general		21	23	22	21		23	27	28	25	
appearing		-	4	1	1		-	6	3	2	
disappearing		-	2	2	2		-	2	2	5	

bersteiniana) demonstrated a significant tolerance to different ecological conditions. Their shoot density did not noticeably change, but the number of plants with generative shoots decreased and one without generative shoots increased in most experimental variants. It is believed that the ecological conditions of ALHs are more favourable for these species than the conditions of other communities. A longer observation period is necessary to prove this suggestion.

3) A few typical but minor components of the ALH (*Vaccinium vitis-idaea, Eritrichium caucasicum, Euphrasia ossica*) demonstrated negative

Table 3.4. Dynamics of shoots in the FVG transplanted to GHM and ALH variants for four experimental years.
* p >95%, ** p >99%, *** p >99,9%. ALH = alpine lichen heaths, GHM = *Geranium gymnocaulon - Hedysarum caucasicum* dominated meadows, FVG = *Festuca varia* dominated grasslands.

		FVG→GHM					FVG→ALH				
Year		89	90	91	92	t	89	90	91	92	t
Anthoxanthum odoratum	v	47	67	96	134	*	44	46	54	61	
	g	3	7	9	4	*	4	7	13	5	
Campanula biebersteiniana	v	6	15	13	15		0	0	4	1	
Campanula collina	v	7	10	7	9		6	13	14	16	
Carex umbrosa	v	0	0	7	13		13	1	13	15	
Euphrasia ossica	g	0	1	0	1		0	3	2	8	
Festuca brunnescens	v	99	104	216	200		58	58	60	87	***
	g	25	5	40	4	***	3	4	15	6	
Festuca ovina	v	78	93	80	78		47	48	127	103	
Festuca varia (x10)	v	135	163	226	349	***	179	200	169	171	
	g	103	14	107	106		85	47	216	24	***
Gentiana djimilensis	v	0	14	14	8		48	40	59	63	**
Leontodon hispidus	v	10	18	8	7		14	16	9	2	***
Deschampsia flexuosa	v	202	426	722	772	**	180	259	243	287	*
	g	20	0	11	15		3	5	22	2	
Minuartia aizoides	v	42	76	58	42		210	125	133	159	
Nardus stricta (x10)	v	57	114	106	110		86	122	98	81	
Ranunculus oreophilus	v	4	7	3	0		2	8	5	4	
	j	0	1	14	16		12	7	11	10	
Scorzonera cana	v	29	37	19	17	*	21	38	21	15	
	j	0	1	7	7		9	1	30	11	
Viola oreades	v	71	0	2	0		37	7	16	26	
Sum of shoots (x10)		274	375	485	614		350	398	379	349	
Number of species:											
general		23	25	25	23		21	22	23	23	
appearing		-	6	2	2		-	2	2	1	
disappearing		-	4	2	4		-	1	1	1	

responses to transplantation to all other communities. There is a good correlation between their experimental behaviour and natural distribution among the communities (Tab. 3.9).

There seems to be two main causes for the relative decrease of species performance in the experimental plots. First, the new microclimate (for example, the length of vegetative season, temperature regime etc.) can be less favourable than the original. Second, some ALH plants can increase their competition ability and suppress other components of the ALH more seriously. The

reason for this could not be distinguished within these experiments.
Apparently, the first cause is more important for the first years of the experiment because the process of transplantation is accompanied by disturbances. The reaction of most species is somewhat slow in the alpine zone, so competition relationships can be weakened for several years. The attempt was made to minimize the influence of the surrounding vegetation by means of root isolation and wide borders between the investigated plots and the original community. In spite of this, some aboriginal species did infiltrate the experimental plots of ALH, e.g., *Agrostis vinealis, Carum alpinum, Catabrosella variegata, Sibbaldia procumbens* in SBC; *Geranium gymnocaulon, Hedysarum caucasicum* and *Matricaria caucasica* in GHM; *Agrostis vinealis, Carum alpinum, Geranium gymnocaulon, Viola oreades* in FVG. They infiltrated the plots mainly by seeds and some of them by rhizome. The total floristic diversity of the plots increased slightly (Tab. 3.1 and 3.2). These observations support the suggestion that competition is not very strong during the first years after transplantation and some species can show their potential responses to the ecological conditions.
The same reasoning can be applied to the species which increase their performance on the experimental plots. In all cases, the behaviour of species under conditions of "depleted" competition can be estimated.
Of course, there can be other reasons for changes in species composition on transplanted plots such as the influence of consumers, apparent competition (CONNEL 1990) and others. More detailed experiments should be carried out to study these processes.

3.3.2. Transplantations of *Festuca varia* dominated grasslands (FVG)

Festuca varia and *Nardus stricta* are the main dominants of FVG. These species display very similar behaviour on experimental plots (Table 3.3, 3.4, 3.9). Shoot density of the species did not change significantly according to control when transplanted to GHM, but it decreased approximately twice when transplanted to a more severe environment like ALH or SBC. So it can be suggested that the auto- and synecological optima of the species are similar.
The behaviour of other FVG-species varies. *Deschampsia flexuosa* and *Festuca brunnescens* displayed positive reactions when transplanted to other communities. It is interesting that the species are very rare or absent in ALH, but their shoot density increases in this community. Apparently, severe

ecological conditions are less important for the species than the influence of main dominants (*Festuca varia* and *Nardus stricta*).
Anthoxanthum odoratum responded the same to transplantation to GHM as to control treatment. The shoot number decreased when transplanted to ALH, but slightly increased in SBC. *Minuartia aizoides* reacted positively to transplantation to SBC, where it is one of the most abundant species.
Floristic diversity of the experimental plots remained almost constant during the period of observation. A few rare species disappeared from the plots, for example: *Anthyllis vulneraria, Carex atrata, Matricaria caucasica* in SBC; *Anthyllis vulneraria* and *Viola oreades* in GHM. And a few new species appeared, for example: *Carum caucasicum, Sibbaldia procumbens, Taraxacum stevenii* in SBC; *Campanula biebersteiniana, Carum caucasicum, Euphrasia ossica, Pedicularis chroorrhyncha* in ALH. In the first year after transplantation, juvenile individuals of *Geranium gymnocaulon* and *Hedysarum caucasicum* had infiltrated from the surrounding GHM, but they died in the following year. So the structure and composition of FVG stayed very conservative under similar ecological conditions of GHM. It seems that *Festuca varia* has the similar competitive ability under GHM conditions as in its original community.

3.3.3. Transplantations of *Geranium gymnocaulon - Hedysarum caucasicum* dominated meadows (GHM)

This community type has properties similar to FVGs. Many species can grow in both GHMs and FVGs, but with differing frequency (Table 3.9). Still, the reaction of the GHM species to the transplantation differed from that of the FVG. The shoot density of most GHM species did not considerably change or even slightly increased when transplanted to similar communities (FVG and SBC, but decreased seriously when transplanted to more severe conditions of ALH, Tables 3.5, 3.6, 3.9). Such behaviour is typical for *Hedysarum caucasicum, Anthoxanthum odoratum, Minuartia aizoides,Veronica gentianoides, Scorzonera cana, Carum meifolium.* The ecological conditions of GHMs are almost favourable for these species, but they can be slightly suppressed by the main dominant *Geranium gymnocaulon.*
Geranium gymnocaulon displayed a significant tolerance to the wide spectrum of ecological conditions. The shoot density of this species did not change greatly in any variants (Table 3.9). By means of several morphological features of *Geranium gymnocaulon*, it was possible to ascertain that the

Table 3.3. Dynamics of shoots in the FVG, in the control and transplanted to SBC variants for four experimental years.
* p >95%, ** p >99%, *** p >99,9%. FVG = *Festuca varia* dominated grasslands, SBC = snow bed communities.

		FVG-Control					FVG→SBC				
Year		89	90	91	92	t	89	90	91	92	t
Anthemis iberica	v	1	2	3	1		20	13	23	43	
Antennaria dioica	v	9	18	26	26		14	11	10	16	
Anthoxanthum odoratum	v	35	37	67	96	*	28	20	58	119	*
Campanula collina	v	4	6	5	7		17	25	26	23	
Carex atrata	v	9	5	8	18		2	5	6	0	
Festuca brunnescens	v	47	59	53	54		29	22	71	47	*
Festuca ovina	v	148	214	377	297		234	168	115	140	
	g	6	2	31	5		17	1	2	1	*
Festuca varia (x10)	v	154	175	256	315	***	218	173	169	250	
	g	126	14	69	21	***	95	13	13	53	
Gentiana djimilensis	v	13	11	12	14		34	14	25	34	
	g	0	8	3	7		2	13	1	2	
Deschampsia flexuosa	v	102	83	87	57		221	194	122	239	
Minuartia aizoides	v	141	237	213	220		63	43	88	144	**
	g	10	8	8	0		0	1	2	3	
Nardus stricta (x10)	v	108	141	165	217	*	115	86	72	96	
	g	65	46	42	54		9	5	10	12	
Scorzonera cana	v	13	15	9	8		19	21	16	25	
	g	0	1	3	0		10	4	7	5	
	j	0	2	4	3		4	10	9	6	
Viola oreades	v	18	10	1	2	***	31	21	3	6	***
Sum of shoots (x10)		340	398	530	626		430	330	314	451	
Number of species:											
general		21	23	22	21		23	27	28	25	
appearing		-	4	1	1		-	6	3	2	
disappearing		-	2	2	2		-	2	2	5	

species grew better in GHM and SBC than in ALH and FVG (Table 3.10). *Nardus stricta* responded to transplantation to GHM very much the same as to FVG. The shoot density of *Festuca brunnescens* slightly increased in ALH, but decreased in FVG.

Agrostis vinealis possesses a great vegetative mobility and a wide ecological areal. Its shoot number increased after transplantation to every community (Tables 3.5, 3.6, 3.9). This species can be considered as a pioneer species for secondary successions in the alpine zone (see also chapter 6). *Matricaria caucasica* is another species with "ruderal" (according to GRIME 1979)

Table 3.4. Dynamics of shoots in the FVG transplanted to GHM and ALH variants for four experimental years.
* p >95%, ** p >99%, *** p >99,9%. ALH = alpine lichen heaths, GHM = *Geranium gymnocaulon - Hedysarum caucasicum* dominated meadows, FVG = *Festuca varia* dominated grasslands.

		FVG→GHM					FVG→ALH				
Year		89	90	91	92	t	89	90	91	92	t
Anthoxanthum odoratum	v	47	67	96	134	*	44	46	54	61	
	g	3	7	9	4	*	4	7	13	5	
Campanula biebersteiniana	v	6	15	13	15		0	0	4	1	
Campanula collina	v	7	10	7	9		6	13	14	16	
Carex umbrosa	v	0	0	7	13		13	1	13	15	
Euphrasia ossica	g	0	1	0	1		0	3	2	8	
Festuca brunnescens	v	99	104	216	200		58	58	60	87	***
	g	25	5	40	4	***	3	4	15	6	
Festuca ovina	v	78	93	80	78		47	48	127	103	
Festuca varia (x10)	v	135	163	226	349	***	179	200	169	171	
	g	103	14	107	106		85	47	216	24	***
Gentiana djimilensis	v	0	14	14	8		48	40	59	63	**
Leontodon hispidus	v	10	18	8	7		14	16	9	2	***
Deschampsia flexuosa	v	202	426	722	772	**	180	259	243	287	*
	g	20	0	11	15		3	5	22	2	
Minuartia aizoides	v	42	76	58	42		210	125	133	159	
Nardus stricta (x10)	v	57	114	106	110		86	122	98	81	
Ranunculus oreophilus	v	4	7	3	0		2	8	5	4	
	j	0	1	14	16		12	7	11	10	
Scorzonera cana	v	29	37	19	17	*	21	38	21	15	
	j	0	1	7	7		9	1	30	11	
Viola oreades	v	71	0	2	0		37	7	16	26	
Sum of shoots (x10)		274	375	485	614		350	398	379	349	
Number of species:											
general		23	25	25	23		21	22	23	23	
appearing		-	6	2	2		-	2	2	1	
disappearing		-	4	2	4		-	1	1	1	

properties. It has a more strict preference to GHMs and reactions negatively to transplantation to other communities.

The floristic diversity of the investigated plots did not change significantly. It slightly diminished in control plots only due to disappearance of a few rare species (*Campanula biebersteiniana, Cerastium purpurascens, Gentiana biebersteiniana, Gentiana oschtenica, Gnaphalium supinum* and *Taraxacum confusum*). There were some changes in the floristic composition of a variant of transplantation to ALH. Such minor components, as *Minuartia recurva,*

Table 3.5. Dynamics of shoots in the GHM, in the control and transplanted to SBC variants for four experimental years.
* p >95%, ** p >99%, *** p >99,9%. GHM = *Geranium gymnocaulon - Hedysarum caucasicum* dominated meadows, SBC = snow bed communities.

		GHM-Contr.					GHM→SBC				
Year		89	90	91	92	t	89	90	91	92	t
Agrostis vinealis	v	114	90	82	144		12	24	17	36	
Anthoxanthum odoratum	v	174	166	196	254		210	141	175	277	
	g	10	11	25	10	**	3	1	3	16	
Campanula collina	v	12	11	16	6		10	15	14	17	
Carex atrata	v	14	19	19	24		7	10	8	16	
Carum meifolium	v	16	26	17	7	***	42	52	28	53	
	j	0	0	0	27		25	59	74	81	
Festuca brunnescens (x10)	v	37	67	51	63		96	99	98	130	*
	g	53	2	74	14	*	95	11	20	130	
Geranium gymnocaulon	v	187	194	224	216		166	206	194	229	**
	g	13	33	9	0		26	7	14	4	**
Hedysarum caucasicum	v	43	53	15	19	***	31	65	30	27	
	g	34	0	2	4	***	55	2	0	0	
	j	12	17	35	27		49	134	57	50	
Leontodon hispidus	v	0	0	0	0		15	11	8	12	*
Deschampsia flexuosa	v	185	363	437	341		405	206	77	191	
Nardus stricta (x10)	v	45	98	87	105	*	75	95	87	101	
Phleum alpinum	v	213	275	233	263		29	87	83	106	
	g	12	41	18	83	**	2	9	29	49	
Ranunculus oreophilus	j	27	18	22	15		18	31	15	6	***
Scorzonera cana	v	32	49	35	15	**	44	53	45	47	
	j	0	0	0	34		4	14	12	7	
Veronica gentianoides	v	25	40	36	31		20	47	33	51	
Sum of shoots (x10)		216	327	305	342		339	342	307	404	
Number of species:											
general		23	22	20	18		26	26	25	26	
appearing		-	2	1	0		-	1	1	1	
disappearing		-	3	3	2		-	1	2	0	

Erigeron venustus and *Luzula multiflora* had disappeared after several years, whereas young *Vaccinium vitis-idaea* and *Eritrichium caucasicum* plants were detected.

3.3.4. Transplantations of snow bed communities (SBC)

Heavy snow accumulation and a short vegetative season are typical for SBC (see chapter 1). *Sibbaldia procumbens* and *Taraxacum stevenii* are the main

Table 3.6. Dynamics of shoots in the GHM transplanted to FVG and ALH variants for four experimental years.
* p >95%, ** p >99%, *** p >99,9%. GHM = *Geranium gymnocaulon - Hedysarum caucasicum* dominated meadows, FVG = *Festuca varia* dominated grasslands, ALH = alpine lichen heaths.

		GHM→FVG					GHM→ALH				
Year		89	90	91	92	t	89	90	91	92	t
Anthemis iberica	v	28	41	39	50	**	35	31	16	15	**
Anthoxanthum odoratum	v	180	211	226	260	**	183	239	274	117	
Campanula biebersteiniana	v	9	17	20	18	**	14	13	12	16	
Campanula collina	v	4	17	12	15		17	27	23	28	
Carex atrata	v	4	11	20	20		20	18	20	27	
Carum meifolium	v	28	60	27	17		32	40	8	2	***
Festuca brunnescens (x10)	v	45	54	72	59	*	52	98	126	101	
	g	52	13	42	6	*	2	12	206	4	*
Festuca ovina	v	30	14	55	57		57	24	227	404	
Gentiana djimilensis	v	9	15	30	36		28	31	57	54	
Geranium gymnocaulon	v	193	230	221	194		177	265	222	181	
Hedysarum caucasicum	v	37	65	78	76		18	25	17	22	
	g	49	3	0	0		53	0	0	9	***
Leontodon hispidus	v	5	3	0	1	***	9	19	10	1	
Deschampsia flexuosa	v	150	261	397	287	*	69	103	86	71	
Matricaria caucasica	v	43	42	56	51		54	43	31	6	***
Nardus stricta (x10)	v	48	77	85	110		61	102	81	70	
	g	11	7	4	10		13	32	20	18	
Phleum alpinum	v	68	81	112	92		111	102	98	61	
	g	12	4	13	3		12	8	12	2	***
Ranunculus oreophilus	j	2	0	6	19	*	24	0	11	13	*
Scorzonera cana	v	49	77	61	92	*	28	35	37	32	
Veronica gentianoides	v	15	32	33	36		14	25	28	20	
Sum of shoots (x10)		210	275	331	330		238	334	384	312	
Number of species:											
general		28	30	26	26		28	28	28	28	
appearing		-	5	1	2		-	2	2	2	
disappearing		-	3	5	2		-	2	2	2	

dominants. The synecological areal of the species is comparatively wide, they occur in different associations (Table 3.9). These species respond positively to transplantation to other communities (Tables 3.7 and 3.8). There seems to be a significant divergence between the auto- and synecological optima of the species. *Sibbaldia procumbens* and *Taraxacum stevenii* are suppressed by stronger competitors in meadow communities. *Sibbaldia procumbens* can

Table 3.7. Dynamics of shoots in the SBC control and transplanted in GHM variants for four experimental years.
* p >95%, ** p >99%, *** p >99,9%. SBC = snow bed communities, GHM = *Geranium gymnocaulon - Hedysarum caucasicum* dominated meadows.

		SBC-Control					SBC→GHM				
Year		89	90	91	92	t	89	90	91	92	t
Agrostis vinealis	v	241	199	235	301	*	164	236	243	417	***
Anthoxanthum odoratum	v	39	40	46	45		3	9	8	19	
Carex atrata	v	22	14	15	18		9	6	12	10	
Carex oreophila	v	192	251	234	284		176	221	150	159	
	g	28	28	0	1	***	51	31	3	6	***
Catabrosella variegata	v	449	471	462	557		293	433	275	398	**
	g	74	22	22	7	***	72	24	14	5	***
Gnaphalium supinum	v	109	105	112	101		146	160	124	45	**
	g	0	5	4	2		3	5	9	0	
Minuartia aizoides	v	655	454	590	665		642	726	611	794	
	g	35	10	7	15		33	3	11	8	*
Nardus stricta (x10)	v	52	89	74	104	*	52	150	152	223	***
	g	13	13	4	2	***	59	23	41	12	
Pedicularis	v	36	10	11	17		4	2	2	0	
nordmanniana	g	48	11	30	21	*	4	1	0	0	
Phleum alpinum	v	34	37	59	64	***	2	9	7	24	
	g	1	9	4	6		1	0	2	4	
Sibbaldia procumbens	v	725	551	555	615		443	753	562	587	*
	g	27	16	9	7		28	24	3	1	***
Taraxacum stevenii	v	476	437	304	344		236	367	297	272	
	g	40	33	7	23		40	43	8	25	
	j	89	52	168	129		0	112	132	56	
Sum of shoots (x10)		392	374	369	438		298	478	414	525	
Number of species:											
general		16	17	17	16		16	18	21	22	
appearing		-	2	1	0		-	4	3	1	
disappearing		-	1	1	1		-	1	0	0	

grow on dry meadows in the Rocky Mountains, but it responded positively to experimental snow augmentation in the absence of stronger competitors (KNIGHT et al. 1979).

The shoot density of *Gnaphalium supinum* and *Carex oreophila* decreased considerably when transplanted to GHMs or FVGs. The causes of this phenomenon may be the same as for some ALH plants (see 3.3.1): either abiotic conditions or changes in interspecific interactions.

Some SBC species (*Catabrosella variegata, Phleum alpinum, Nardus stricta*) responded positively or neutrally to transplantation to GHM and

Table 3.8. Dynamics of shoots in the SBC transplanted in FVG and ALH variants for four experimental years.
* p >95%, ** p >99%, *** p >99,9%. SBC = snow bed communities, FVG = *Festuca varia* dominated grasslands, ALH = alpine lichen heaths.

		SBC→FVG					SBC→ALH				
Year		89	90	91	92	t	89	90	91	92	t
Agrostis vinealis	v	221	183	157	86		194	174	182	242	**
Carex oreophila	v	307	283	187	273		135	166	174	179	**
	g	49	46	13	19	**	22	18	10	19	
Catabrosella variegata	v	352	358	324	303		362	252	340	337	
	g	58	5	8	4	***	57	12	1	2	***
Gnaphalium supinum	v	51	45	30	30	*	206	157	193	148	
Minuartia aizoides (x10)	v	77	64	62	115	*	88	71	85	109	
	g	27	5	31	26		61	26	11	13	***
Nardus stricta (x10)	v	140	145	172	224	**	437	608	618	613	**
	g	34	11	5	3	***	2	0	0	1	
Phleum alpinum	v	13	16	21	22		36	35	26	19	*
Sibbaldia procumbens	v	729	761	561	536	*	678	966	769	885	**
	g	37	8	0	0		49	18	0	1	***
Taraxacum stevenii	v	439	349	323	318	*	303	340	228	365	
	g	35	39	8	13	**	49	15	0	2	***
	j	0	92	140	132		64	121	228	107	*
Sum of shoots (x10)		462	435	422	525		369	381	383	427	
Number of species:											
general		15	18	18	17		14	16	18	17	
appearing		-	3	2	0		-	2	2	2	
disappearing		-	0	2	1		-	0	0	3	

negatively in other cases. Therefore, several types of behaviour are typical for species of this community as well as of other investigated communities.

Floristic diversity remained almost constant on the control plots and FVG plots, but it increased slightly in ALHs and GHMs (Tables 3.7 and 3.8). *Carum caucasicum, Erigeron uniflorus, Euphrasia ossica* were found after the transplantation of sods from SBC to ALH. An increase in the number of *Euphrasia ossica* was especially noticeable.

In short, the conclusion can be made that adult plant individuals from SBCs are tolerant to be able to exist under variable conditions above timberline. They are effected by changes in environmental conditions resulting in alterations of the number of their vegetative and generative shoots and reduction of generative reproduction. After the transplantation of experimental squares into other communities, a few new species were observed.

Table 3.9. Relative coefficient (K) showing changes on experimental plots and natural distribution of alpine species among studied communities. K is determimed for 1989 and 1992 seasons, n.d. - no data, K=1 for control plots; Raunkiaer's class of frequency is counted as an average for large (see ch. 1) and small (0.25 sq.m, n=260) plots in different communities. It shows the natural distribution of the species among the communities.
ALH = alpine lichen heaths, FVG = *Festuca varia* dominated grasslands, GHM = *Geranium gymnocaulon - Hedysarum caucasicum* dominated meadows, SBC = snow bed communities.

	Frequency classes				Relative coefficient (K)			
Species name	ALH	FVG	GHM	SBC	ALH	FVG	GHM	SBC
Vaccinium vitis-idaea	IV	-	-	-	1.00	0.20	0.20	0.14
Eritrichium caucasicum	IV	I	-	-	1.00	0.52	0.11	0.37
Euphrasia ossica	II	I	II	-	1.00	0.09	0.36	0.08
Campanula collina	III	IV	I	-	1.00	1.09	1.00	0.85
Gentiana djimilensis	V	III	II	I	1.00	0.54	0.66	2.12
					1.22	1.00	n.d.	0.62
					3.34	6.03	1.00	n.d.
Trifolium polyphyllum	V	I	-	-	1.00	1.40	0.78	4.62
Helictotrichon versicolor	V	I	-	-	1.00	1.36	2.10	1.01
Carex umbrosa	V	III	I	-	1.00	1.46	2.21	1.43
+ *C. sempervirens*								
Festuca ovina	V	III	I	-	1.00	1.92	1.69	1.42
					1.09	1.00	0.54	0.29
Antennaria dioica	IV	III	I	-	1.00	1.61	1.28	1.16
Nardus stricta	-	V	III	III	0.49	1.00	0.99	0.43
					0.50	0.98	1.00	0.58
					0.71	0.79	1.94	1.00
Festuca varia	-	V	II	-	0.48	1.00	1.29	0.59
Deschampsia flexuosa	I	III	IV	I	2.96	1.00	6.65	2.01
					0.52	0.96	1.00	0.24
Festuca brunnescens	-	II	V	I	1.30	1.00	1.41	1.41
					1.21	0.77	1.00	0.89
Anthoxanthum odoratum	I	IV	V	II	0.49	1.00	0.98	1.40
					0.47	1.01	1.00	0.96
Minuartia aizoides	-	III	III	IV	0.52	1.00	0.69	1.60
					0.74	0.83	1.00	1.22
					1.01	1.51	1.21	1.00
Agrostis vinealis	I	I	I	I	1.76	1.50	1.00	2.27
					1.05	0.31	2.07	1.00
Veronica gentianoides	IV	III	III	I	0.79	1.84	1.00	2.04
Scorzonera cana	I	III	II	-	0.71	1.33	1.00	0.94
Geranium gymnocaulon	-	I	V	I	0.91	0.83	1.00	1.12
Hedysarum caucasicum	-	II	V	-	0.54	1.86	1.00	1.02
Carum meifolium	I	I	IV	II	0.13	1.05	1.00	0.96
Matricaria caucasica	-	I	IV	II	0.07	0.65	1.00	0.67
Phleum alpinum	-	I	III	II	0.33	0.77	1.00	3.25
					0.23	0.85	4.67	1.00
Sibbaldia procumbens	-	III	IV	V	1.47	0.85	1.51	1.00
Taraxacum stevenii	II	I	I	V	1.39	1.19	1.51	1.00
Carex oreophila	-	-	I	I	0.97	0.35	0.56	1.00
Catabrosella variegata	-	-	I	III	0.75	0.69	1.02	1.00
Gnaphalium supinum	-	I	III	IV	0.80	0.61	0.32	1.00

Table 3.10. Changes of morphological traits of some alpine species after transplantation in different communities (Average value (av.) and standard error (s.e.) of leaf length for *Taraxacum stevenii* and *Helictotrichon versicolor*, height of generative shoots for *Festuca varia*, height of plants for *Geranium gymnocaulon*, mm).
ALH = alpine lichen heaths, FVG = *Festuca varia* dominated grasslands, GHM = *Geranium gymnocaulon - Hedysarum caucasicum* dominated meadows, SBC = snow bed communities.

	ALH		FVG		GHM		SBC	
	av.	s.e.	av.	s.e.	av.	s.e.	av.	s.e.
Festuca varia	548	33.6	538	37.3	581	25.1	413	19.2
Taraxacum stevenii	30	0.8	47	0.9	59	1.8	53	0.9
Geranium gymnocaulon	70	3.9	95	5.2	149	12.2	162	7.3
Helictotrichon versicolor	117	5.5	150	4.4	159	7.1	105	5.7

3.3.5. Morphological changes of separate species

The value of the investigated parameters changed considerably between plots (Table 3.10). The sizes of the studied plants decreased in the following sequences:

Helictotrichon versicolor	GHM, FVG > ALH, SBC
Festuca varia	GHM, FVG, ALH > SBC
Geranium gymnocaulon	SBC, GHM > FVG > ALH
Taraxacum stevenii	GHM > SBC > FVG > ALH

The sequences show that almost all studied species were larger in meadows than in other communities. This observation supports our above mentioned conclusions about the behaviour of these species under experimental conditions. The dominants of highly productive meadows and grasslands have their optima in the same communities, but species from semiextreme conditions (ALH, SBC) often improve their growth in other communities.

Based on a study of the calcifuge-calcicole problem in alpine grasslands, GIGON (1983, 1987) concluded that "the largest proportion of species restricted to the less extreme habitats does not occur on the more extreme ones because of abiotic factors... On the other hand, the largest part of the species restricted to the more extreme habitats does not occur on the less extreme ones because of competition."(GIGON 1987, p. 241). The present results confirm his point of view.

SUMMARY

Field observations and the analysis of the results of reciprocal transplantation between four alpine communities allowed the following conclusions.

1) The complex vegetation of each community is rather stable and keeps its composition and structure practically unchanged for several years after having been transplanted into alien ecological conditions above timberline.
2) Responses of the species to transplantation are varied. As a rule, dominants of ALHs and SBCs (communities, developing under semiextreme ecological conditions) responded positively when transplanted to more productive meadows and grasslands in absence of competition with native plants. On the other hand, dominants of alpine meadows and grasslands demonstrated negative responses when transplanted to the more severe conditions of an ALH or SBC.
   Some species developed best in their original communities (*Vaccinium vitis-idaea, Eritrichium caucasicum* in ALH, *Gnaphalium supinum* in SBC). Still, many species can grow successfully in several communities.
   (ALH = alpine lichen heaths, SBC = snow bed communities)
3) In each case (including control squares) the introduction of new species to transplanted plots was observed. The species seemed to infiltrate the experimental plots in the form of seeds from a transplanted community situated nearby or from surrounding vegetation of the experimental area.