Demographic studies

4. DEMOGRAPHIC STUDIES

4.1. METHODS

In sites where Biscutella levigata was particularly abundant, two 1 m^2 plots codified as A and B were selected within each population sector (Fig. 1). They were permanently marked with plugs. The plots were mapped once a month in July, August, and September; not all plots could be mapped at each monthly census (Table 17) on account of the snow cover lasting longer than usual in the spring, as well as of an intermittent snowfall during the vegetation season.

Three different age-state variants sensu RABOTNOV (1978) were distinguished:

Seedlings. (Fig. 31, codified as S). The seedlings were first identified by their cotyledons. Young plants were named seedlings during the whole first season of their life, even if they subsequently lost their cotyledons.

Non-reproducing rosettes. (Fig. 31, codified as N). All rosettes without inflorescences notwithstanding their real age were included in this category.

Reproducing rosettes. (Fig. 31, codified as R). This category comprised all rosettes with inflorescences disregarding their chronological age.

Without destroying the plots it could not be decided, whether the rosettes originated from various seeds or root suckers. For this reason, all rosettes were considered as ramets, only the seedlings and the subsequently developing young plants being recognized as genets i.e. distinct genotypes.

Special attention was paid to various reproductive phases occurring in a given reproducing rosette. The following reproductive units were taken into consideration:

- flower buds
- flowers
- unripe fruits
- ripe fruits
- seeds.

An aluminium frame (1 m x 1 m) divided into 100 1 dm^2 squares by an elastic cord was used during each census. The number of all age-state variants and reproductive units was exactly determined in each of the small squares per plot.

Fig. 31. Age-state variants of Biscutella levigata (after GASSER 1983).
Abb. 31. Altersvarianten von Biscutella levigata

S = Seedlings - Keimlinge
N = Non-reproducing rosettes - Nichtreproduzierende Rosetten
R = Reproducing rosettes - Reproduzierende Rosetten

The raw data (number of genets, ramets, and reproductive units per 1 dm^2) was stored in a computer; all further calculations were made by computer. Most programs used were produced by the author and they are stored at the Geobotanical Institute.

4.1.1. Spatial distribution

To assess the distribution pattern of Biscutella levigata in the plots studied, the sum of all age-state variants was used (seedlings, non-reproducing, and reproducing rosettes). The following parameters were calculated:

$$\textbf{Density} = \frac{N}{100} = \frac{\text{total number of plants per } m^2}{\text{total number of small quadrats}}$$

$$\textbf{Abundance} = \frac{N}{Q} = \frac{\text{total number of plants per } m^2}{\text{total number of occupied small quadrats}}$$

The abundance is the measure of density in the patches.

$$\textbf{Index of dispersion} = \frac{\text{variance}}{\text{mean}}$$

$$\text{variance} = s^2 = \frac{\text{sum of } (x_i - xq)^2}{\text{number of sub-plots} - 1}$$

where x^i is the number of plants in the i-th sub-plot

$$\text{mean} = xq = \frac{\text{total number of plants per } m^2}{\text{number of sub-plots}}$$

The index of dispersion was calculated for four different sub-plots codified in Fig. 32:

a. 1 dm^2 sub-plot
b. 4 dm^2 sub-plot
c. horizontal column sub-plot
d. vertical column sub-plot.

If the distribution was mosaic-like ("contagious" sensu GREIG-SMITH 1983), random, or regular, significance was assessed by reference to the table of χ^2. For detailed descriptions, the reader is referred to GREIG-SMITH (1983).

For comparison, the same parameters were calculated separately for each given age-state variant. If many individuals per m^2 were observed, index of dispersion was calculated for 1 dm^2; if there were only a few individuals, index of dispersion was calculated for 4 dm^2.

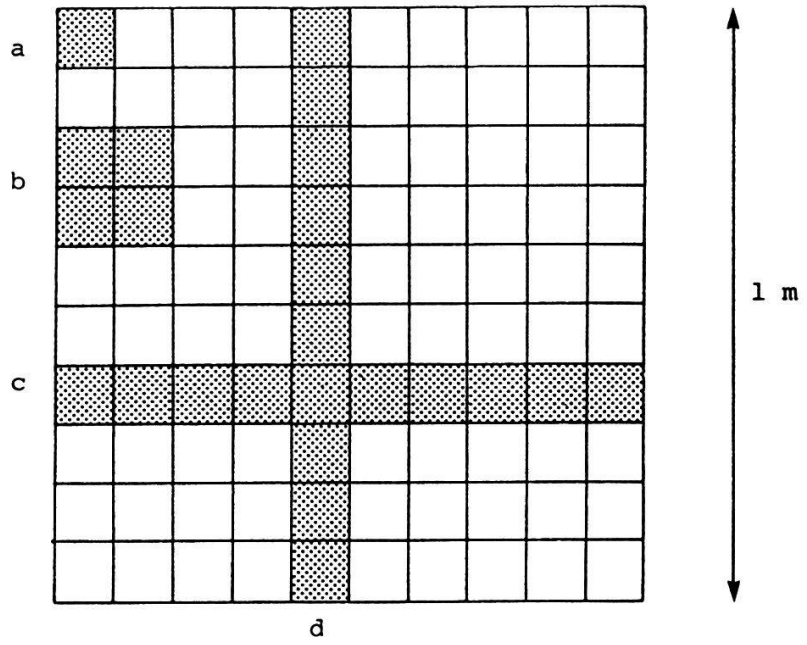


Fig. 32. Four different sub-plots used for calculation of index of dispersion. Explanations see text.
Abb. 32. Die vier verschiedenen Teilflächen, die für die Berechnung des Dispersionsindex verwendet wurden.

4.1.2. Temporal distribution

The evaluation of behaviour of genets was based upon data collected in 1982, 1983, and 1984 (Table 17). In order to recognize seedlings they were marked individually with a thread, a different colour being used for each year. The number of seedlings counted in July 1982 was considered as 100% and the subsequent gains and losses were calculated as percentages of this. The fate of young genets was followed for a maximum of three seasons.

To assess the behaviour of ramets viz. non-reproducing and reproducing rosettes during one vegetation season the census data of 1983 were taken, and the net number of rosettes as well as cumulative gains and losses were calculated.

The behaviour over several years is represented by the sum of the age-state variants per one m^2 plot and based on the data gathered during the August census of 1982, 1983, and 1984. If a 1 m^2 plot was not scored in August, the data obtained at the end of July or beginning of September were taken into consideration. Gains and losses over several years were not calculated, because the number of ramets dying during the winter could not be observed.

Table 17. Demographic census in different plots.
Tab. 17. Kontrollen der verschiedenen Flächen.

J = July, A = August, S = September
DOL = dolomite, SER = serpentine, SIL = acidic silicate

Plot code	Census											
	1981			1982			1983			1984		
	J	A	S	J	A	S	J	A	S	J	A	S
DOL 1A	+	+	+	+	+	+	+	+	+	+		+
1B		+	+	+	+	+	+	+	+	+		+
DOL 2A					+	+	+	+	+	+		+
2B					+	+	+	+	+	+		+
DOL 3A					+	+	+	+	+		+	
3B					+	+	+	+	+		+	
DOL 4A	+	+	+	+	+	+	+	+	+	+		+
4B	+	+	+	+	+	+	+	+	+	+		+
DOL 5A	+	+	+	+	+	+	+	+	+	+		+
5B		+	+	+	+	+	+	+	+	+		+
DOL 6A	+	+	+	+	+	+	+	+	+	+		+
6B	+	+	+	+	+	+	+	+	+	+		+
DOL 7A					+	+	+	+	+		+	
7B					+	+	+	+	+		+	
DOL 8A	+	+	+	+	+	+	+	+	+		+	
8B	+	+	+	+	+	+	+	+	+		+	
DOL 9A					+	+	+	+	+		+	
9B					+	+	+	+	+		+	
DOL 10A					+	+	+	+	+		+	
10B					+	+	+	+	+		+	
DOL 11A					+	+	+	+	+		+	
11B					+	+	+	+	+		+	
DOL 12A		+	+	+	+	+	+	+	+		+	
12B					+	+	+	+	+		+	

Table 17. (continued)

Plot code	Census											
	1981			1982			1983			1984		
	J	A	S	J	A	S	J	A	S	J	A	S
SER 1A		+	+	+	+	+	+	+	+		+	+
1B		+	+	+	+	+	+	+	+		+	+
SER 2A				+		+	+	+	+	+		+
2B				+		+	+	+	+	+		+
SER 3A				+		+	+	+	+		+	
3B				+		+	+	+	+		+	
SER 4A	+	+	+	+	+	+	+	+	+	+		+
4B				+		+	+	+	+	+		+
SER 5A	+	+	+	+	+	+	+	+	+		+	
5B				+		+	+	+	+		+	
SER 6A	+	+	+	+	+	+	+	+	+		+	+
6B		+	+	+	+	+	+	+	+		+	+
SER 7A				+		+	+	+	+		+	
7B				+		+	+	+	+		+	
SER 8A	+	+	+	+	+	+	+	+	+	+		+
8B	+	+	+	+	+	+	+	+	+	+		+
SER 9A	+	+	+	+	+	+	+	+	+	+		+
9B	+	+	+	+	+	+	+	+	+	+		+
SER 10A				+		+	+	+	+		+	
10B				+		+	+	+	+		+	
SER 11A		+	+	+	+	+	+	+	+		+	
11B				+		+	+	+	+		+	
SIL A				+		+	+	+	+		+	
B				+		+	+	+	+		+	

In the assessment of the behaviour of the reproductive units, the data of 1983 were used.

4.2. RESULTS

4.2.1 Spatial distribution

Global evaluations for all age-state variants. Three-dimensional representations of distribution pattern of Biscutella levigata are exemplified by DOL 1A, a plot in dolomite grassland, and SER 8A, a serpentine plot

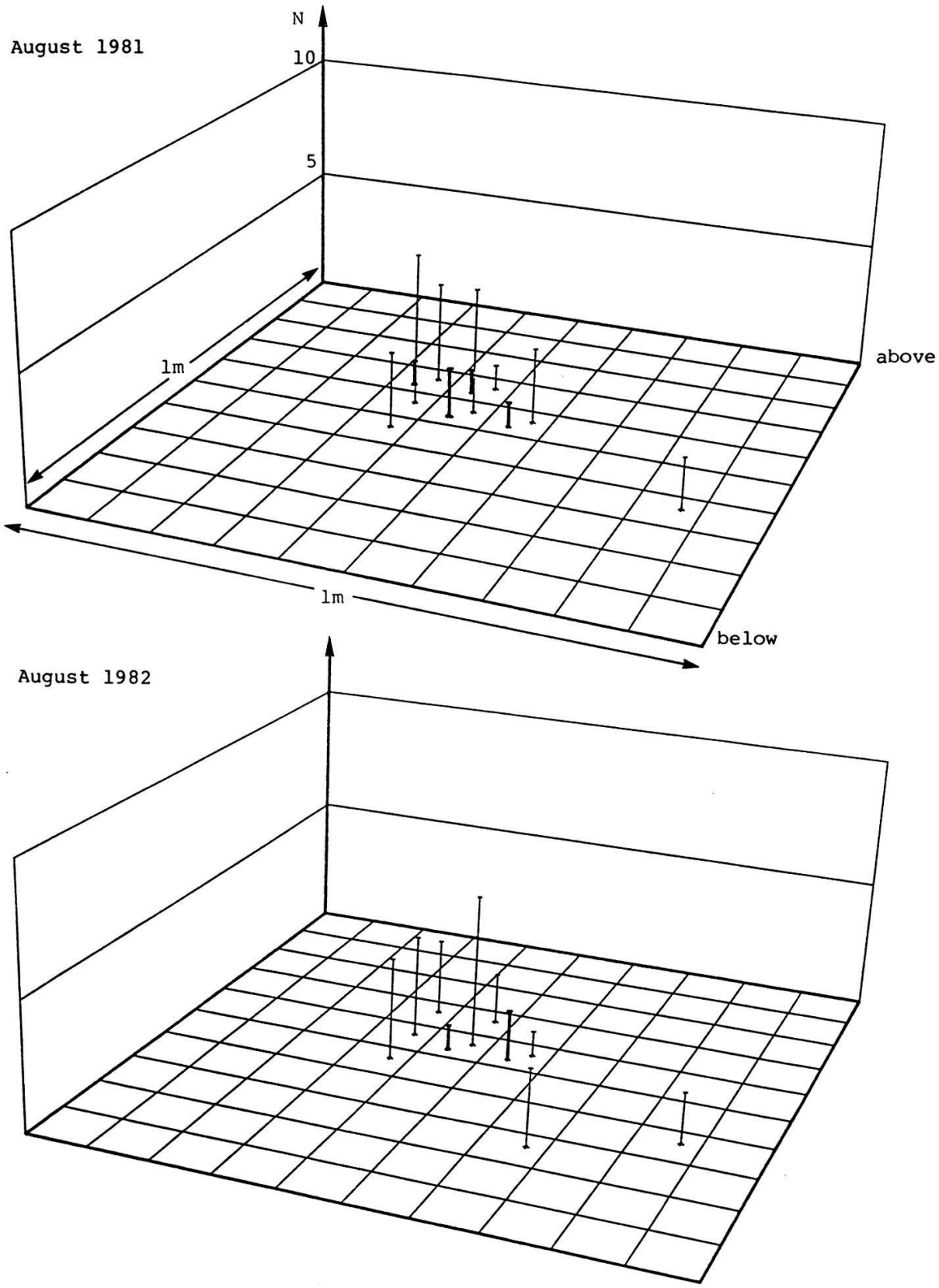


Fig. 33. Distribution pattern of the age-state variants of B. levigata in DOL 1A over 4 years.

Abb. 33. Verteilungsmuster der Altersvarianten von B. levigata in DOL 1A während 4 Jahren.

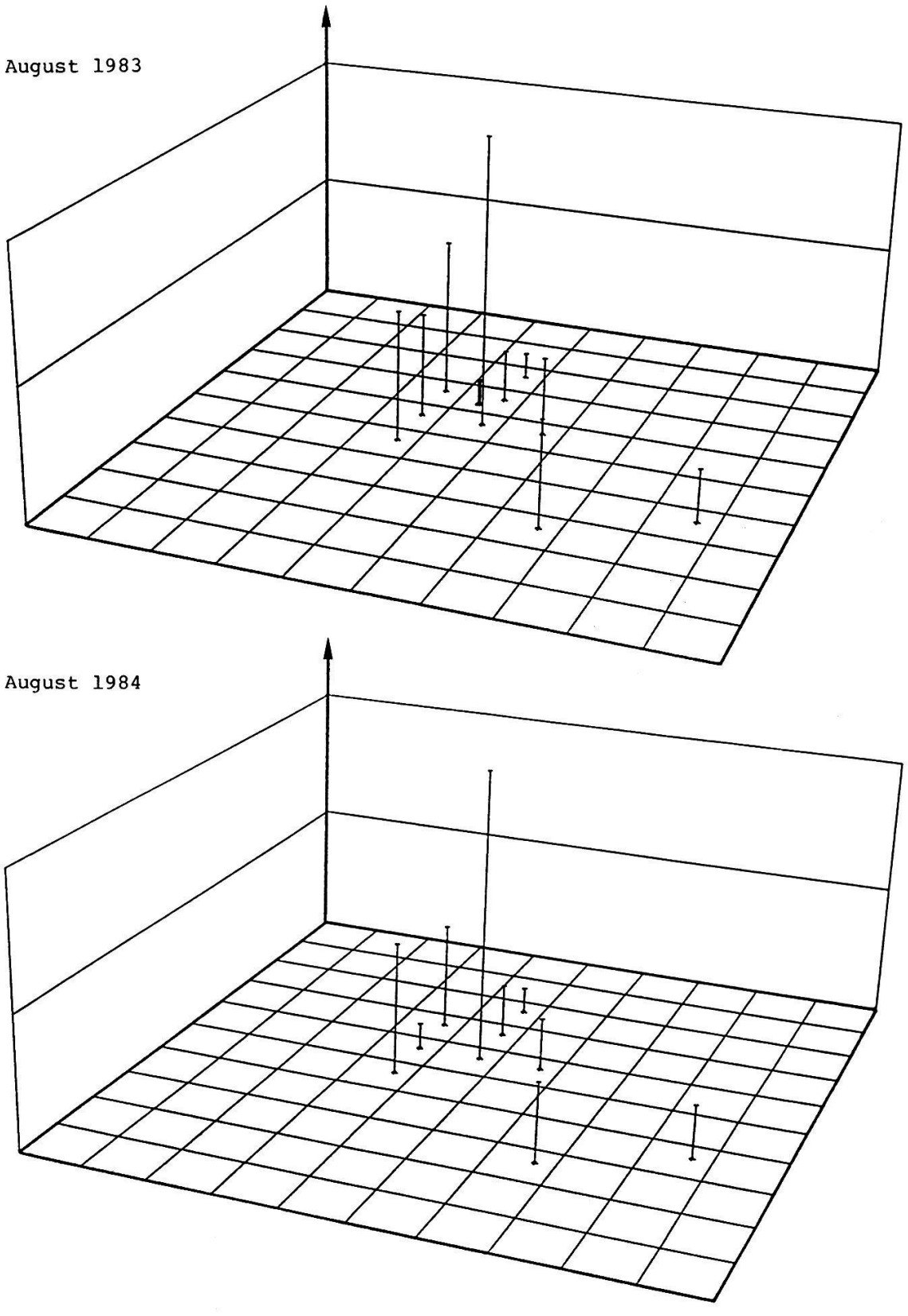


Fig. 33 (continued)

..... Seedlings - Keimlinge
—— Non-reproducing rosettes - Nichtreproduzierende Rosetten
—— Reproducing rosettes - Reproduzierende Rosetten

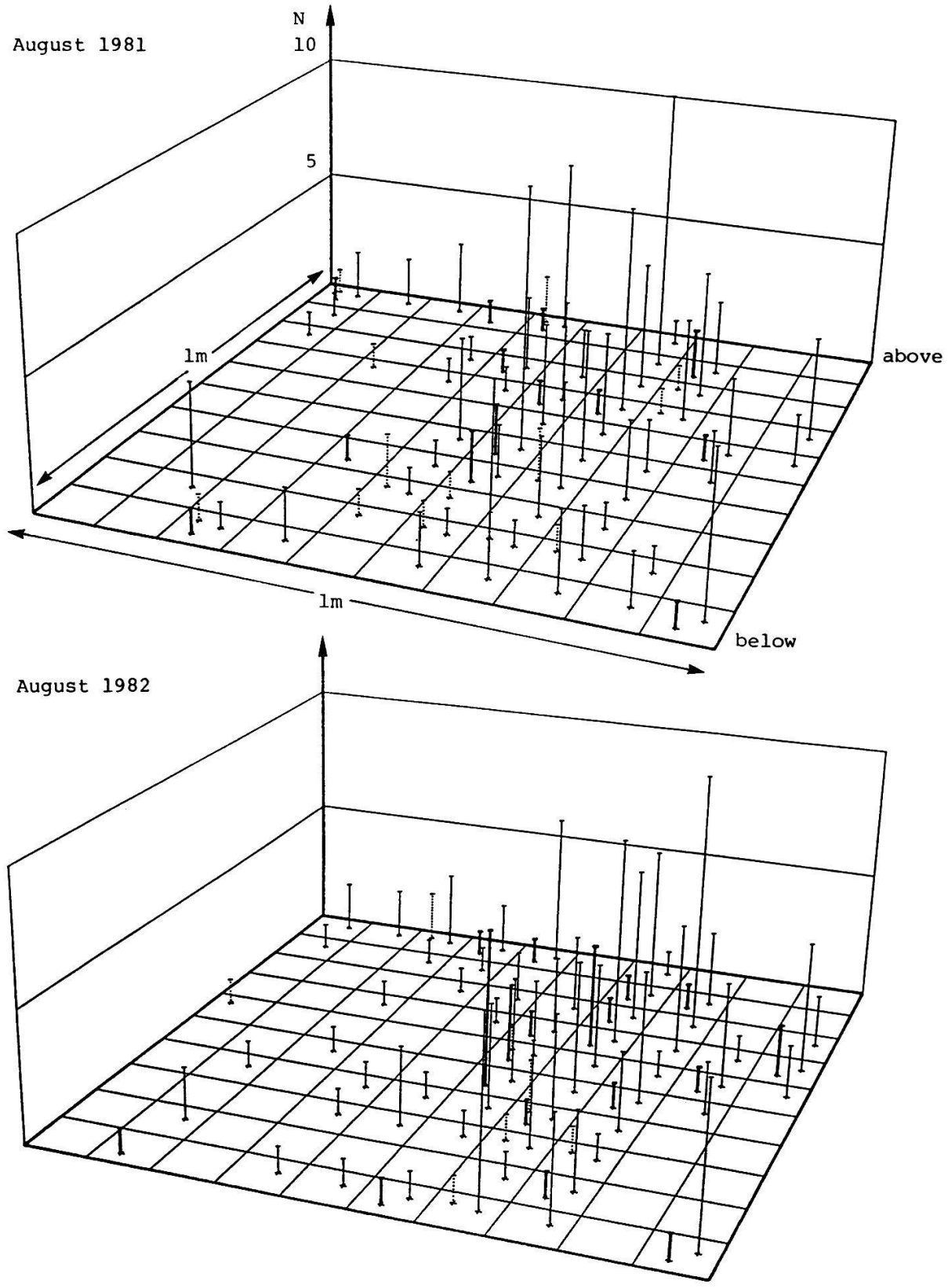


Fig. 34. Distribution pattern of the age-state variants of B. levigata in SER 8A over 4 years.

Abb. 34. Verteilungsmuster der Altersvarianten von B. levigata in SER 8A während 4 Jahren.

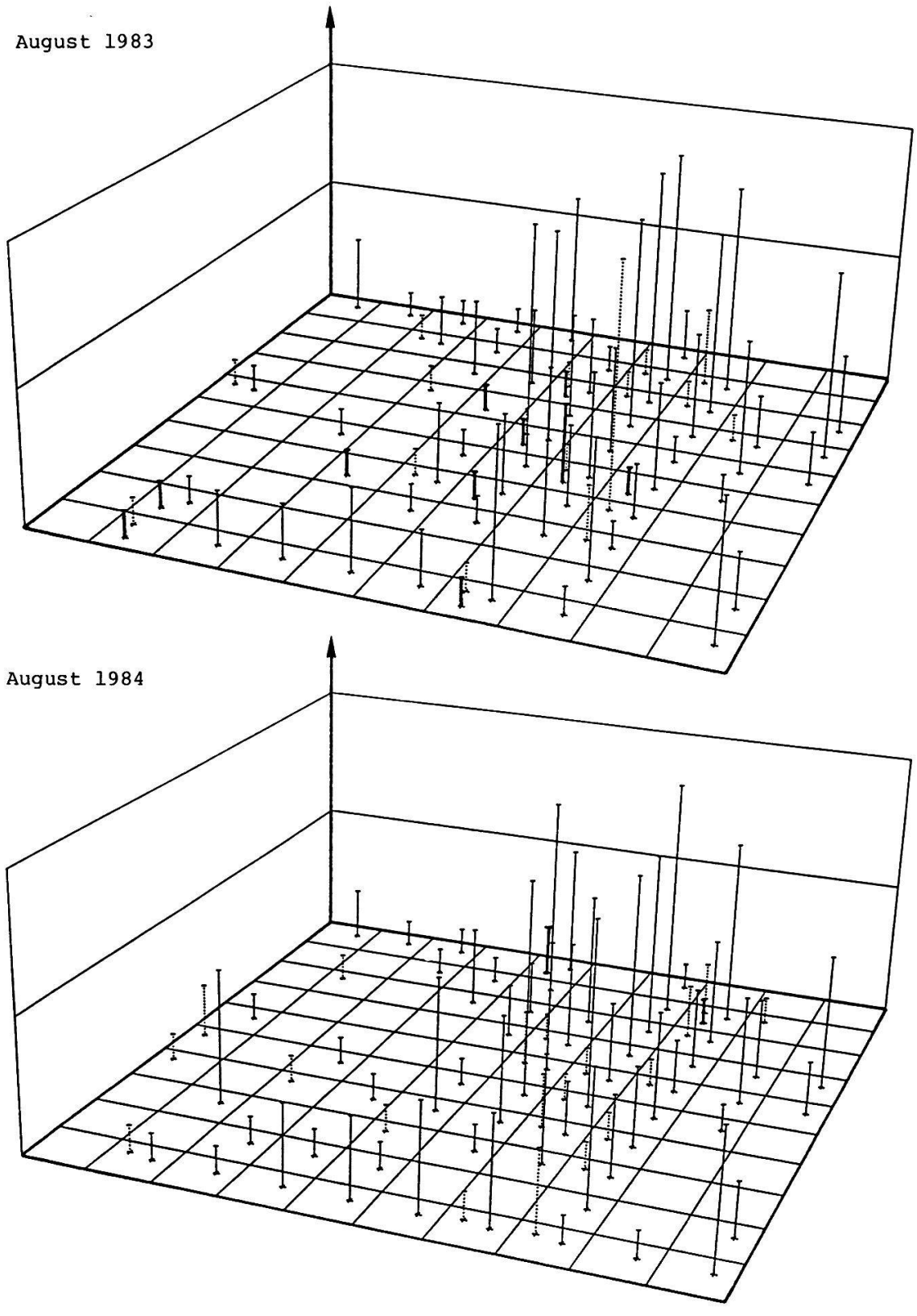
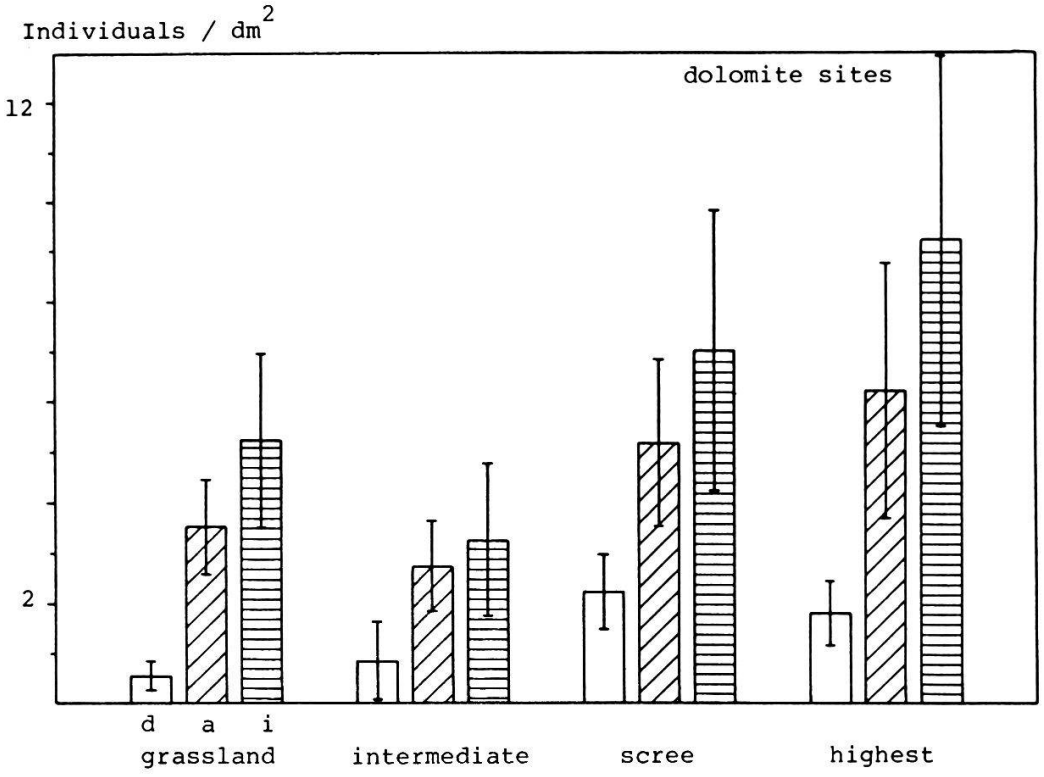


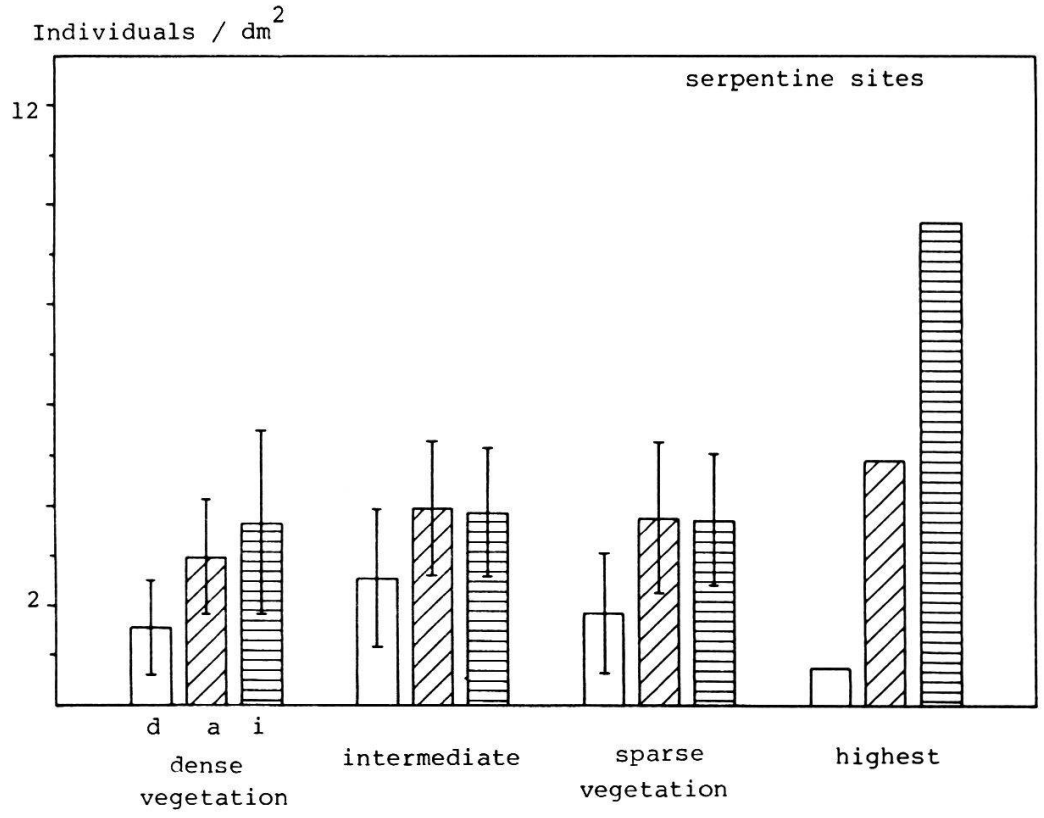
Fig. 34 (continued)

..... Seedlings - Keimlinge

—— Non-reproducing rosettes- Nichtreproduzierende Rosetten

—— Reproducing rosettes - Reproduzierende Rosetten


Individuals / dm2
dolomite sites
12
2
d a i
grassland
intermediate
scree
highest


Individuals / dm2
serpentine sites
12
2
d a i
dense vegetation
intermediate
sparse vegetation
highest

with thin vegetation (Figs 33, 34). As far as the density is concerned, distinct differences occurred between particular local sectors on dolomite (Table 18, Fig. 35). In grassland, a low density was observed whereas many more individuals per area were found on scree slopes. Large fluctuations from plot to plot were observed in intermediate and highest sectors. The differences between the niches were statistically signifi-

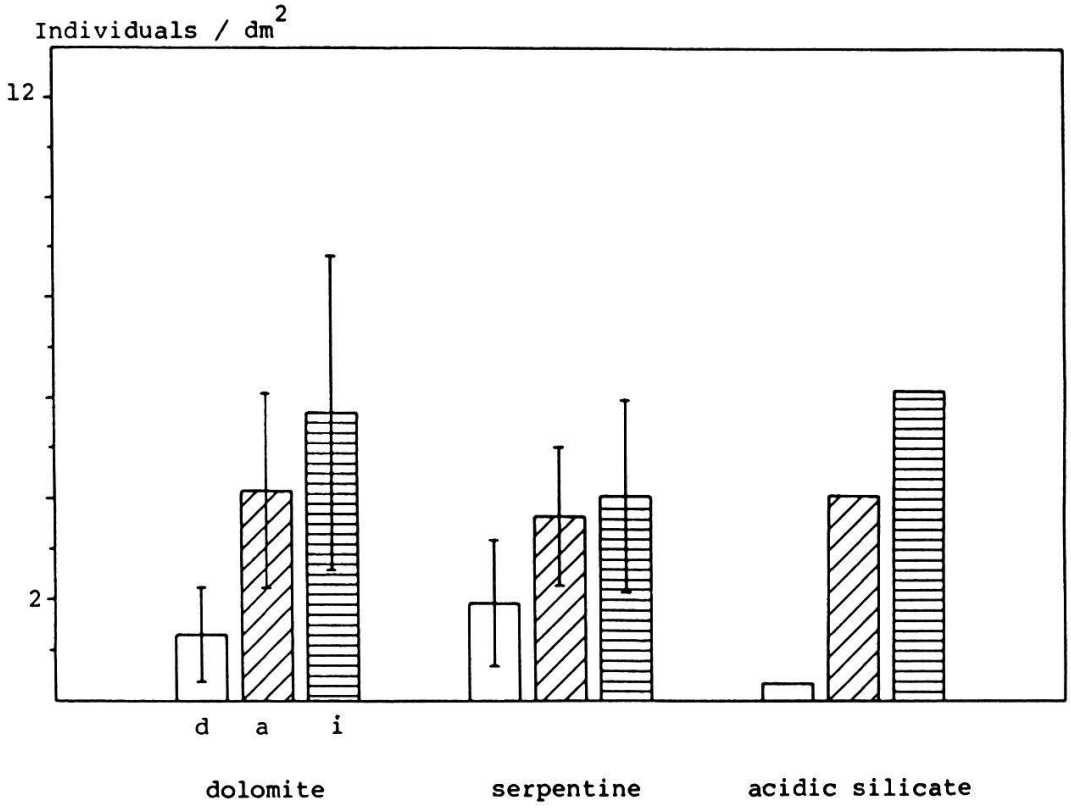


Fig. 37. Global evaluations of density (d), abundance (a), and index of dispersion (i) (± S.D.) of all three age-state variants on dolomite, serpentine, and acidic silicate. Census of August 1983.

Abb. 37. Dichte (d), Abundanz (a) und Dispersionsindex (i) (± s_x) von den drei Altersvarianten auf Dolomit, Serpentin und saurem Silikat. Zählung vom August 1983.

Figs 35,36. (p. 58). Global evaluations of density (d), abundance (a), and index of dispersion (i) (± S.D.) of all three age-state variants on various sites on dolomite and serpentine. Census of August 1983.

Abb. 35,36. (S. 58). Dichte (d), Abundanz (a) und Dispersionsindex (i) (± s_x) von den drei Altersvarianten auf den verschiedenen Dolomit- und Serpentinflächen. Zählung vom August 1983.

Table 18. Global evaluations of density, abundance, and index of dispersion (± S.D.) of all three age-state variants. Census of August 1983.

Tab. 18. Dichte, Abundanz und Dispersionsindex (± s_x) von den drei Altersstadien. Zählung vom August 1983.

Site	Dolomite	Serpentine
	Density Individuals / dm2	
grassland / dense veg.	0.56 ± 0.30	1.56 ± 0.98
intermediate	0.89 ± 0.86	2.56 ± 1.39
scree / sparse veg.	2.28 ± 0.74	1.84 ± 1.22
highest	1.82 ± 0.65	0.74
all sectors	1.31 ± 0.96	1.92 ± 1.25
acidic silicate	0.37	
	Abundance Individuals / dm2	
grassland / dense veg.	3.53 ± 0.95	2.98 ± 1.16
intermediate	2.77 ± 0.91	3.96 ± 1.36
scree / sparse veg.	5.20 ± 1.68	3.75 ± 1.49
highest	6.25 ± 2.57	4.91
all sectors	4.15 ± 1.94	3.67 ± 1.34
acidic silicate	4.07	
	Index of dispersion (1 dm2)	
grassland / dense veg.	5.26 ± 1.72	3.68 ± 1.88
intermediate	3.26 ± 1.51	3.88 ± 1.30
scree / sparse veg.	7.02 ± 2.80	3.71 ± 1.31
highest	9.29 ± 3.75	9.67
all sectors	5.71 ± 3.12	4.05 ± 1.89
acidic silicate	6.19	

cant (P <1%, Table 22). On serpentine, B. levigata grew more densely but no significant differences as compared to dolomite were calculated (Figs 36, 37). Owing to great fluctuations, no significant differences between the niches were observable within all serpentine sectors. The two plots studied from silicate corresponded to the lowest densities found in the course of the present study (Fig. 37).

The abundance in all sectors was distinctly higher than the density notwithstanding the substrata. In grassland and on scree slopes the abundance was higher than on the intermediate and on the highest sectors. The differences between the niches were significant upon dolomite (P <1%). On the other hand, no significant differences between the niches were observed on serpentine (Tables 18, 22, Fig. 36). The differences between dolomite and serpentine were also not significant. The abundance on silicate was comparable to the other substrata.

The index of dispersion showed the same tendencies as those revealed in

the abundance. In scree slopes and in the highest sectors on dolomite where the index was very high, B. levigata formed a distinct mosaic pattern. In grassland, the rosettes had a more mosaic-like distribution than in the intermediate sectors where the lowest indices were found (Table 18, Fig. 35). The differences were significant (P <1%, Table 22). On serpentine the index of dispersion was more or less the same as in the intermediate sectors on dolomite, only the highest plot on serpentine showing a distinct mosaic-like distribution (Fig. 36). The differences of index of dispersion between the niches on serpentine were, in contrast to density and abundance, statistically significant (P <5%, Table 22). Behaviour of Biscutella levigata in the two silicate plots studied was more or less the same as on the other substrata.

Separate evaluations for each age-state variant. Evaluations carried out separately for each given age-state variant revealed a rather complex situation. The densities of seedlings were very low and significantly

Table 19. Seedlings: Density, abundance, and index of dispersion (±S.D.). Census of August 1983.
Tab. 19. Keimlinge: Dichte, Abundanz und Dispersionsindex (± s_x). Zählung vom August 1983.

Site	Dolomite	Serpentine
	Density Individuals / dm2	
grassland / dense veg.	0	0.07 ± 0.049
intermediate	0.013 ± 0.028	0.17 ± 0.16
scree / sparse veg.	0.072 ± 0.076	0.22 ± 0.24
highest	0	0
all sectors	0.022 ± 0.49	0.15 ± 0.17
acidic silicate	0	
	Abundance Individuals / dm2	
grassland / dense veg.	0	1.12 ± 0.24
intermediate	1.05 ± 0.08	1.32 ± 0.42
scree / sparse veg.	1.16 ± 0.19	2.02 ± 1.51
highest	0	0
all sectors	1.11 ± 0.15	1.47 ± 0.91
acidic silicate	0	
	Index of dispersion (4 dm2)	
grassland / dense veg.	-	1.25 ± 0.40
intermediate	1.42 ± 0.73	2.01 ± 1.53
scree / sparse veg.	1.14 ± 0.32	2.80 ± 1.88
highest	-	-
all sectors	1.26 ± 0.50	2.02 ± 1.49
acidic silicate	-	

different within the niches on dolomite (P <5%) and between dolomite and serpentine (P <1%). On the other hand, The abundance of seedlings and index of dispersion were higher but no significant differences occurred (Tables 19, 22). Patterns in density and abundance of non-reproducing rosettes were generally similar to those revealed in global evaluations. However, significant differences between dolomite and serpentine were found in the index of dispersion (P <5%, Tables 20, 22). As far as reproducing rosettes only are concerned, the density on serpentine was higher than on dolomite (P <1%). Also the density differences between various dolomite niches were significant (P <1%), whereas on serpentine no distinct differences appeared. The abundances and the index of dispersion followed distinct patterns within either of the substrata studied; differences between niches were not significant on dolomite, but significant on serpentine (P <1%, Tables 21, 22).

Table 20. Non-reproducing rosettes: Density, abundance, and index of dispersion (± S.D.). Census of August 1983.
Tab. 20. Nichtreproduzierende Rosetten: Dichte, Abundanz und Dispersionsindex (± s_x). Zählung vom August 1983.

Site	Dolomite	Serpentine
	Density Individuals / dm2	
grassland / dense veg.	0.54 ± 0.31	1.29 ± 0.78
intermediate	0.81 ± 0.85	1.96 ± 1.16
scree / sparse veg.	1.99 ± 0.79	1.40 ± 0.91
highest	1.73 ± 0.59	0.42
all sectors	1.19 ± 0.89	1.53 ± 0.99
acidic silicate	0.30	
	Abundance Individuals / dm2	
grassland / dense veg.	3.45 ± 0.99	2.67 ± 0.92
intermediate	2.53 ± 0.84	3.20 ± 1.11
scree / sparse veg.	4.78 ± 1.91	3.17 ± 1.08
highest	5.98 ± 2.33	4.20
all sectors	3.90 ± 1.89	3.09 ± 1.03
acidic silicate	3.22	
	Index of dispersion (1 dm2)	
grassland / dense veg.	5.20 ± 1.68	3.72 ± 1.99
intermediate	3.03 ± 1.24	3.25 ± 1.15
scree / sparse veg.	6.69 ± 2.78	3.46 ± 1.15
highest	9.01 ± 3.63	7.42
all sectors	5.48 ± 3.02	3.64 ± 1.60
acidic silicate	5.50	

Distribution of B. levigata plants calculated in 1 dm^2 and 4 dm^2 subplots always corresponded to a statistically significant not random pattern ($P < 0.1\%$). The test of horizontal and vertical distribution revealed mostly a mosaic-like pattern and only in a few 1 m^2 plots a random distribution was observed; however, no influence of direction or slope gradient could be recognized (Table 23).

4.2.2. Temporal distribution

Genets. The number of seedlings in dolomite grassland and within the highest sectors was very small and seedlings did not appear every year (Table 24). The number of individuals within intermediate sectors on

Table 21. Reproducing rosettes: Density, abundance, and index of dispersion (± S.D.). Census of August 1983.
Tab. 21. Reproduzierende Rosetten: Dichte, Abundanz und Dispersionsindex (± s_x). Zählung vom August 1983.

Site	Dolomite	Serpentine
	Density Individuals / dm2	
grassland / dense veg.	0.033 ± 0.026	0.20 ± 0.22
intermediate	0.068 ± 0.048	0.43 ± 0.20
scree / sparse veg.	0.23 ± 0.17	0.22 ± 0.16
highest	0.090 ± 0.059	0.12
all sectors	0.10 ± 0.12	0.29 ± 0.21
acidic silicate	0.07	
	Abundance Individuals / dm2	
grassland / dense veg.	1.11 ± 0.13	1.26 ± 0.33
intermediate	1.41 ± 0.40	1.85 ± 0.37
scree / sparse veg.	1.59 ± 0.33	1.44 ± 0.30
highest	1.40 ± 0.23	4.00
all sectors	1.40 ± 0.34	1.67 ± 0.35
acidic silicate	1.75	
	Index of dispersion (4 dm2)	
grassland / dense veg.	1.10 ± 0.12	1.20 ± 0.26
intermediate	2.01 ± 1.09	3.10 ± 1.10
scree / sparse veg.	2.83 ± 1.00	2.42 ± 0.91
highest	1.85 ± 1.01	8.53
all sectors	2.04 ± 1.07	2.62 ± 1.76
acidic silicate	2.01	

dolomite decreased regularly from census to census but the the population became stabilized in the third year. Many seeds germinated only in August or September (Table 24, Fig. 38). As far as the dolomite scree is concerned, losses of seedlings and young plants were rather irregular; a particularly great reduction was observed after the first winter and in July of the second year after seedling emergence. The survival of genets followed type II of DEEVEY (1947). The germination in August and September was lower. A very large number of seedlings was found in 1984 (Table 24, Fig. 38).

A great reduction in number of genets during their first winter as well as in the second summer and winter was characteristic for the serpentine sectors with high vegetation density. On the other hand, no more young plants died in their third summer. Only a few new seedlings were found during August and September census (Table 25, Fig. 38). In the intermediate sectors and sectors with thin vegetation on serpentine, a great amount of seedlings germinated in 1983 and 1984, but pronounced losses

Table 22. Differences in density, abundance, and index of dispersion within and between dolomite and serpentine subpopulations. Niveau of significance is indicated. Census of August 1983.

Tab. 22. Unterschiede in Dichte, Abundanz und Dispersionsindex innerhalb und zwischen Subpopulationen auf Dolomit und Serpentin; das Signifikanzniveau ist angegeben. Zählung vom August 1983.

aov = analysis of variance
S = seedlings, N = non-reproducing, R = reproducing rosettes

	All age-states	S only	N only	R only
Density				
DOL aov	1%	5%	1%	1%
SER aov	-	-	-	-
all sites aov	1%	5%	5%	1%
DOL-SER t-test	-	1%	-	1%
Abundance				
DOL aov	1%	-	1%	-
SER aov	-	-	-	1%
all sites aov	1%	-	1%	1%
DOL-SER t-test	-	-	-	-
Index of dispersion	($1dm^2$)	($4dm^2$)	($1dm^2$)	($4dm^2$)
DOL aov	1%	-	1%	-
SER aov	5%	-	-	1%
all sites aov	1%	-	1%	1%
DOL-SER t-test	-	-	5%	-

occurred during the first years of their life (Table 25, Fig. 38). Contrary to the situation in sectors with dense vegetation, only about 14% were counted after three years. On serpentine the genets had also a Deevey's type II survivorship curve. No seedlings at all were found in the highest sectors on serpentine and on acidic silicate.

Ramets. The net number of non-reproducing rosettes during one vegetation season always remained more or less stable, with only a slight maximum in August, gains being apparently equivalent to losses. On account of

Table 23. Probability of mosaic-like vs. random distribution of ramets; niveau of significance is indicated. Census of August 1983.
Tab. 23. Wahrscheinlichkeit für gehäufte Verteilung gegen Zufallsverteilung von Ramets; das Signifikanzniveau ist angegeben. Zählung vom August 1983.

H = horizontal column sub-plot, V = vertical column sub-plot
DOL = dolomite, SER = serpentine, SIL = acidic silicate

$1m^2$ plot	$1dm^2$	$4dm^2$	H	V	$1dm^2$ plot	$1dm^2$	$4dm^2$	H	V
DOL 1A	.1%	.1%	.1%	.1%	SER 1A	.1%	.1%	.1%	.1%
1B	.1%	.1%	.1%	.1%	1B	.1%	.1%	-	1%
DOL 2A	.1%	.1%	.1%	.1%	SER 2A	.1%	.1%	1%	1%
2B	.1%	.1%	.1%	.1%	2B	.1%	.1%	.1%	.1%
DOL 3A	.1%	.1%	.1%	.1%	SER 3A	.1%	.1%	-	5%
3B	.1%	.1%	.1%	.1%	3B	.1%	.1%	.1%	.1%
DOL 4A	.1%	.1%	1%	.1%	SER 4A	.1%	.1%	5%	5%
4B	.1%	.1%	.1%	.1%	4B	.1%	.1%	.1%	.1%
DOL 5A	.1%	.1%	-	1%	SER 5A	.1%	.1%	.1%	.1%
5B	.1%	.1%	-	.1%	5B	.1%	.1%	.1%	.1%
DOL 6A	.1%	.1%	.1%	.1%	SER 6A	.1%	.1%	1%	.1%
6B	.1%	.1%	.1%	5%	6B	.1%	.1%	.1%	.1%
DOL 7A	.1%	.1%	.1%	.1%	SER 7A	.1%	.1%	.1%	.1%
7B	.1%	.1%	5%	1%	7B	.1%	.1%	.1%	-
DOL 8A	.1%	.1%	.1%	.1%	SER 8A	.1%	.1%	1%	.1%
8B	.1%	.1%	.1%	.1%	8B	.1%	.1%	.1%	5%
DOL 9A	.1%	.1%	.1%	.1%	SER 9A	.1%	.1%	.1%	.1%
9B	.1%	.1%	.1%	.1%	9B	.1%	.1%	.1%	.1%
DOL 10A	.1%	.1%	.1%	.1%	SER 10A	.1%	.1%	-	.1%
DOL 10B	.1%	.1%	.1%	.1%	10B	.1%	.1%	.1%	.1%
DOL 11A	.1%	.1%	.1%	.1%	SER 11A	.1%	.1%	.1%	.1%
11B	.1%	.1%	.1%	.1%					
DOL 12A	.1%	.1%	.1%	.1%	SIL A	.1%	.1%	.1%	1%
12B	.1%	.1%	.1%	.1%	B	.1%	.1%	.1%	.1%

the high standard deviation, there were no differences in the behaviour of dolomite and serpentine plants (Tables 26, 27). The number of reproducing rosettes decreased mostly from July through August to September; a high standard deviation was also found, but the total number was more than twice as high on serpentine than on dolomite (Tables 26, 27, Figs 39, 40).

On dolomite scree and in intermediate serpentine sectors the highest number of non-reproducing rosettes was found in September. In the intermediate and highest sectors as well as in sectors with low vegetation density on serpentine and on acidic silicate the maximum of reproducing rosettes was in August (Table 27).

The behaviour of the age-state variants over several years is exempli-

Table 24. Net number, gains, and losses of genets (seedlings and young plants) on dolomite.
Tab. 24. Netto Anzahl, Gewinne und Verluste von Genets (Keimlinge und Jungpflanzen) auf Dolomit.

J = July, A = August, S = September
82 = germinated in 1982, 83 = in 1983, 84 = in 1984

Grassland									Intermediate								
	1982			1983			1984			1982			1983			1984	
$6m^2$	J	A	S	J	A	S	A	S	$8m^2$	J	A	S	J	A	S	A	S
82 net	0	2	2	1	1	1	1	1	82 net	12	12	12	10	10	9	8	8
gains		2							gains	12	2	1					
losses				1					losses		2	1	2		1		
83 net				0	0	0	0	0	83 net				9	10	10	7	6
gains									gains				9	1	1		
losses									losses						1	3	1
84 net							1	1	84 net							31	31
gains							1		gains							31	3
losses									losses								3

Scree									Highest								
	1982			1983			1984			1982			1983			1984	
$6m^2$	J	A	S	J	A	S	A	S	$4m^2$	J	A	S	J	A	S	A	S
82 net	29	30	29	23	21	19	12	-	82 net	0	0	0	0	0	0	0	-
gains	29	2							gains								
losses		1	1	6	2	2	7		losses								
83 net				31	38	34	21	-	83 net				0	0	0	0	-
gains				31	7				gains								
losses						4	13		losses								
84 net							103	-	84 net							3	-
gains							103		gains							3	
losses									losses								

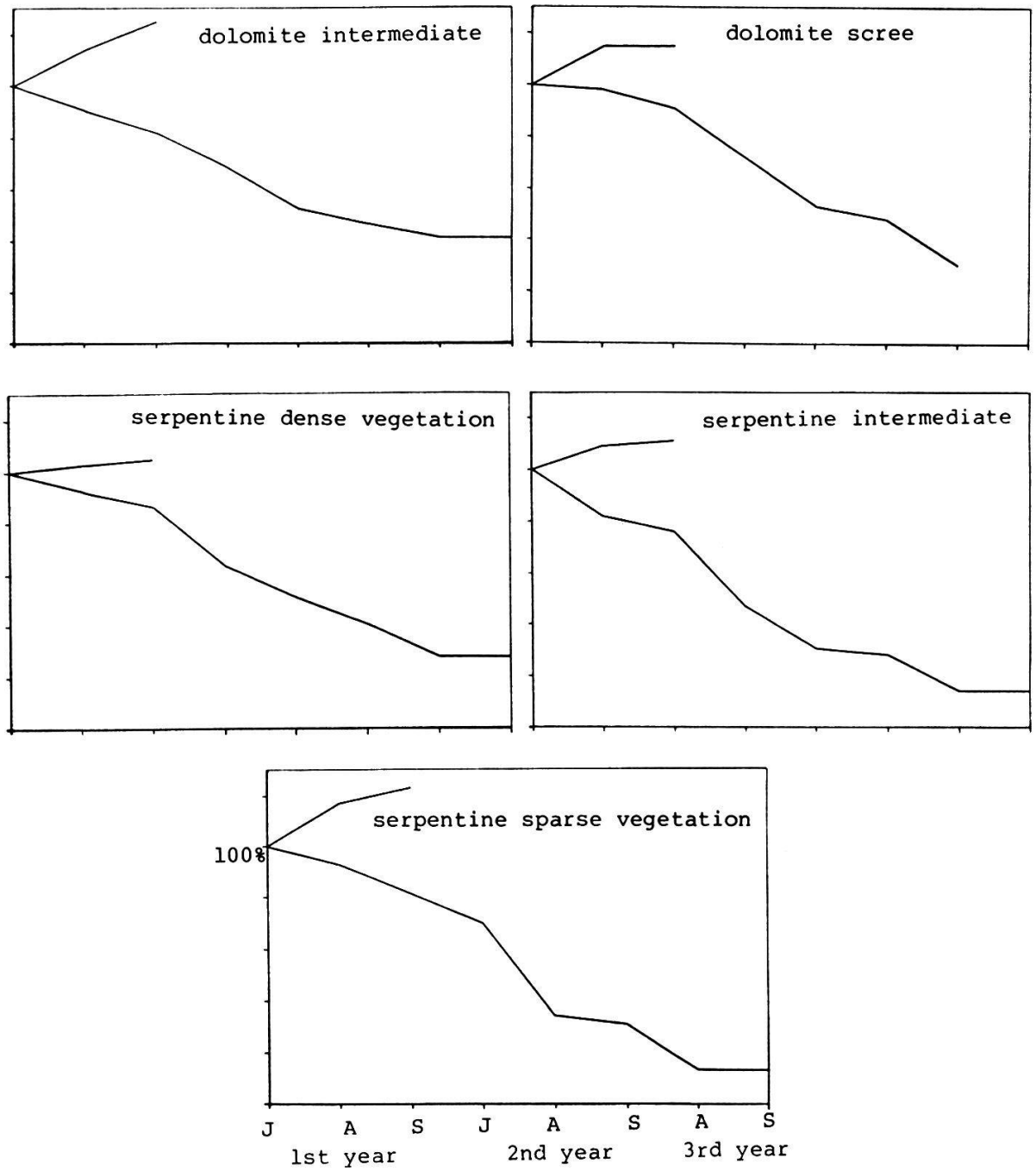


Fig. 38. Gains and survivorship curves of genets (seedlings and young plants); number of seedlings germinated in July were taken to be 100%.

Abb. 38. Gewinne und Ueberlebenskurven von Genets (Keimlinge und Jungpflanzen), die Anzahl im July gekeimter Keimlinge wurde als 100% genommen.

fied by data on two plots viz. DOL 1A and SER 8A (Figs 33, 34). The number of ramets per m^2 remained more or less stable for 4 years, a maximum in 1982 or 1983 was sometimes observed. In the plot on acidic silicate the greatest amount was found in 1984 (Figs 41, 42). Different patterns for a given age-state variant were observed. The number of non-reproducing rosettes decreased slightly from 1982 through 1983 to 1984. The number of reproducing rosettes decreased on dolomite from year to year; however, on serpentine and acidic silicate there was usually a maximum in 1983; great differences between the plots were noted.

Reproductive units. A strong reduction in number of reproductive units viz. flower buds, flowers, and fruits during a vegetation season charac-

Table 25. Net number, gains, and losses of genets (seedlings and young plants) on serpentine.
Tab. 25. Netto-Anzahl, -Gewinne und -Verluste von Genets (Keimlinge und Jungpflanzen aus Serpentin).

J = July, A = August, S = September
82 = germinated in 1982, 83 = in 1983, 84 = in 1984

Dense vegetation cover									Intermediate								
	1982			1983			1984			1982			1983			1984	
$6m^2$	J	A	S	J	A	S	A	S	$8m^2$	J	A	S	J	A	S	A	S
82 net	53	49	46	34	33	26	18	18	82 net	28	24	21	13	12	8	4	4
gains	53	1							gains	28	4						
losses		5	3	12	1	7	8		losses		8	3	8	1	4	4	
83 net				42	42	38	25	20	83 net				144	132	125	98	94
gains				42	2	2			gains				144	11	6		
losses					2	6	13	5	losses					23	13	47	4
84 net							45	45	84 net							133	129
gains							45		gains							133	1
losses									losses								5

Sparse vegetation cover									Highest								
	1982			1983			1984			1982			1983			1984	
$6m^2$	J	A	S	J	A	S	A	S	$2m^2$	J	A	S	J	A	S	A	S
82 net	22	24	22	19	17	14	6	6	82 net	0	0	0	0	0	0	0	0
gains	22	4							gains								
losses		2	2	3	2	3	8		losses								
83 net				121	133	117	49	46	83 net				0	0	0	0	0
gains				121	20	13			gains								
losses					8	29	68	3	losses								
84 net							93	94	84 net							0	0
gains							93	1	gains								
losses									losses								

terized the behaviour of Biscutella levigata in all niches. Unfortunately, the observations in serpentine sectors could not be completed.
In the dolomite grassland, only a small number of flower buds and flowers was found in July; in August, some unripe fruits occurred but in September only very few ripe yet empty fruits were left (Table 28). Many more reproductive units were observed in the scree slopes and in the highest sectors on dolomite; however, a great reduction also occurred, especially in the highest sectors. The seed production was very good on scree slopes but limited in the highest sectors. As far as the occur-

Table 26. Net number, added gains, and subtracted losses of ramets (N = non-reproducing and R = reproducing rosettes) per m^2 (± S.D.) during summer 1983 on dolomite.
Tab. 26. Netto-Anzahl mit addierten Gewinnen und subtrahierten Verlusten von Ramets (N = nichtreproduzierenden und R = reproduzierenden Rosetten) pro m^2 (± s_x) während des Sommers 1983 auf Dolomit.

Site	Month	Net number	Added gains	Subtracted losses
grassland	July	51.8 ± 28.5		
N	Aug.	54.0 ± 31.3	56.5 ± 35.1	49.3 ± 24.7
	Sept.	49.5 ± 33.3	57.8 ± 36.1	43.5 ± 25.6
	July	2.33 ± 2.88		
R	Aug.	2.17 ± 2.64	2.33 ± 2.88	2.17 ± 2.64
	Sept.	1.17 ± 1.47	2.33 ± 2.88	1.17 ± 1.47
intermediate	July	75.5 ± 81.1		
N	Aug.	80.3 ± 85.5	84.4 ± 87.4	71.4 ± 79.1
	Sept.	72.6 ± 77.4	87.6 ± 88.4	60.6 ± 70.3
	July	7.13 ± 4.94		
R	Aug.	6.75 ± 4.77	7.25 ± 5.06	6.63 ± 4.66
	Sept.	6.25 ± 4.40	7.38 ± 5.00	6.00 ± 4.41
scree slope	July	192.0 ± 92.5		
N	Aug.	196.0 ± 83.3	209.8 ± 92.1	178.2 ± 83.8
	Sept.	185.2 ± 86.8	216.8 ± 94.0	160.3 ± 85.5
	July	24.8 ± 16.7		
R	Aug.	23.3 ± 17.6	25.7 ± 17.1	22.5 ± 17.1
	Sept.	22.8 ± 18.0	26.0 ± 17.5	21.7 ± 17.1
highest site	July	162.5 ± 47.3		
N	Aug.	173.5 ± 59.1	180.3 ± 52.3	155.8 ± 54.2
	Sept.	165.0 ± 53.0	187.8 ± 50.6	139.8 ± 48.6
	July	12.0 ± 7.79		
R	Aug.	9.00 ± 5.89	12.25 ± 7.79	8.75 ± 5.56
	Sept.	7.00 ± 5.48	12.25 ± 7.79	6.75 ± 5.12

rence of the reproductive units is concerned, intermediate sectors represented a transition between dolomite grassland and scree (Table 28, Fig. 43).

The behaviour of the plants in the serpentine plots was quite comparable

Table 27. Net number, added gains, and subtracted losses of ramets (N = non-reproducing and R = reproducing rosettes) per m^2 (± S.D.) during summer 1983 on serpentine and acidic silicate.

Tab. 27. Netto-Anzahl mit addierten Gewinnen und subtrahierten Verlusten von Ramets (N = nichtreproduzierende und R = reproduzierende Rosetten) pro m^2 ($\pm s_x$) während des Sommers 1983 auf Serpentin und saurem Silikat.

Site	Month	Net number	Added gains	Subtracted losses
dense	July	112.0 ± 73.4		
vegetation N	Aug.	123.7 ± 80.9	129.0 ± 83.3	106.7 ± 71.3
	Sept.	122.7 ± 82.4	139.2 ± 88.7	95.5 ± 67.4
	July	21.0 ± 22.5		
R	Aug.	20.3 ± 21.9	22.5 ± 23.8	18.8 ± 20.6
	Sept.	17.3 ± 20.7	22.5 ± 23.8	15.8 ± 19.5
intermediate	July	168.6 ± 106.7		
N	Aug.	195.5 ± 115.3	203.0 ± 117.8	161.1 ± 104.2
	Sept.	198.8 ± 114.3	217.0 ± 120.3	150.4 ± 100.5
	July	42.9 ± 17.0		
R	Aug.	43.6 ± 20.4	47.8 ± 20.3	39.1 ± 17.0
	Sept.	41.5 ± 20.7	48.4 ± 20.5	36.0 ± 17.3
sparse	July	129.7 ± 81.6		
vegetation N	Aug.	138.2 ± 88.3	145.0 ± 91.3	122.8 ± 78.6
	Sept.	134.7 ± 82.5	153.7 ± 96.6	110.7 ± 67.7
	July	21.5 ± 15.5		
R	Aug.	22.2 ± 16.6	23.8 ± 17.7	19.8 ± 14.6
	Sept.	20.8 ± 15.1	24.5 ± 18.4	17.8 ± 12.3
highest site	July	66.5		
N	Aug.	80	83	63.5
	Sept.	78.5	86	59
	July	17.5		
R	Aug.	12	17.5	12
	Sept.	17.5	23	12
Acidic	July	29		
silicate N	Aug.	30	31	28
	Sept.	27.5	32	24.5
	July	6.5		
R	Aug.	7	7.5	6
	Sept.	6	7.5	5

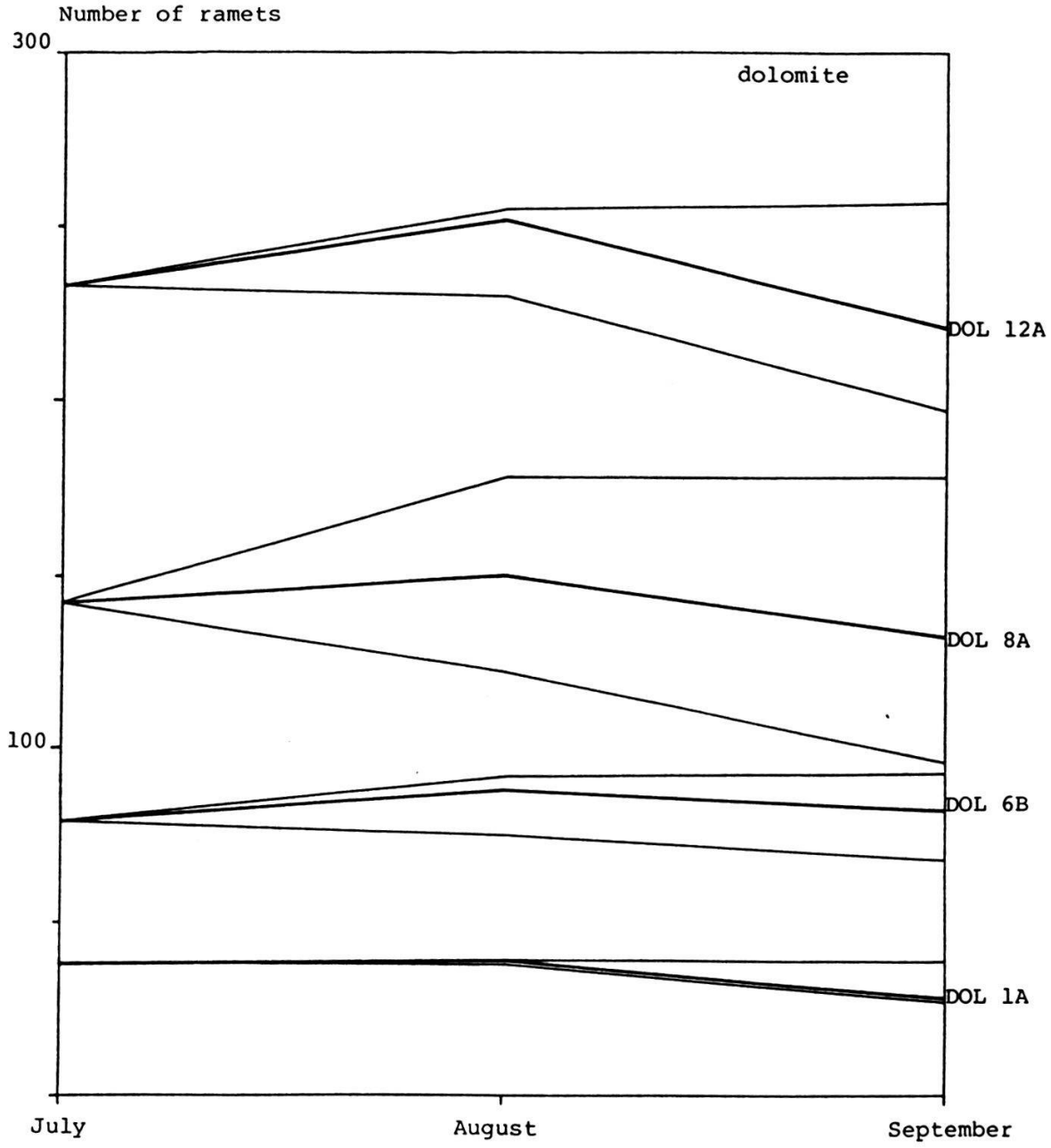


Fig. 39. Net number, added gains and subtracted losses of ramets per m^2 during summer 1983 within selected plots on dolomite.

Abb. 39. Netto-Anzahl mit addierten Gewinnen und subtrahierten Verlusten von Ramets pro m^2 während des Sommers 1983 in ausgewählten Flächen auf Dolomit.

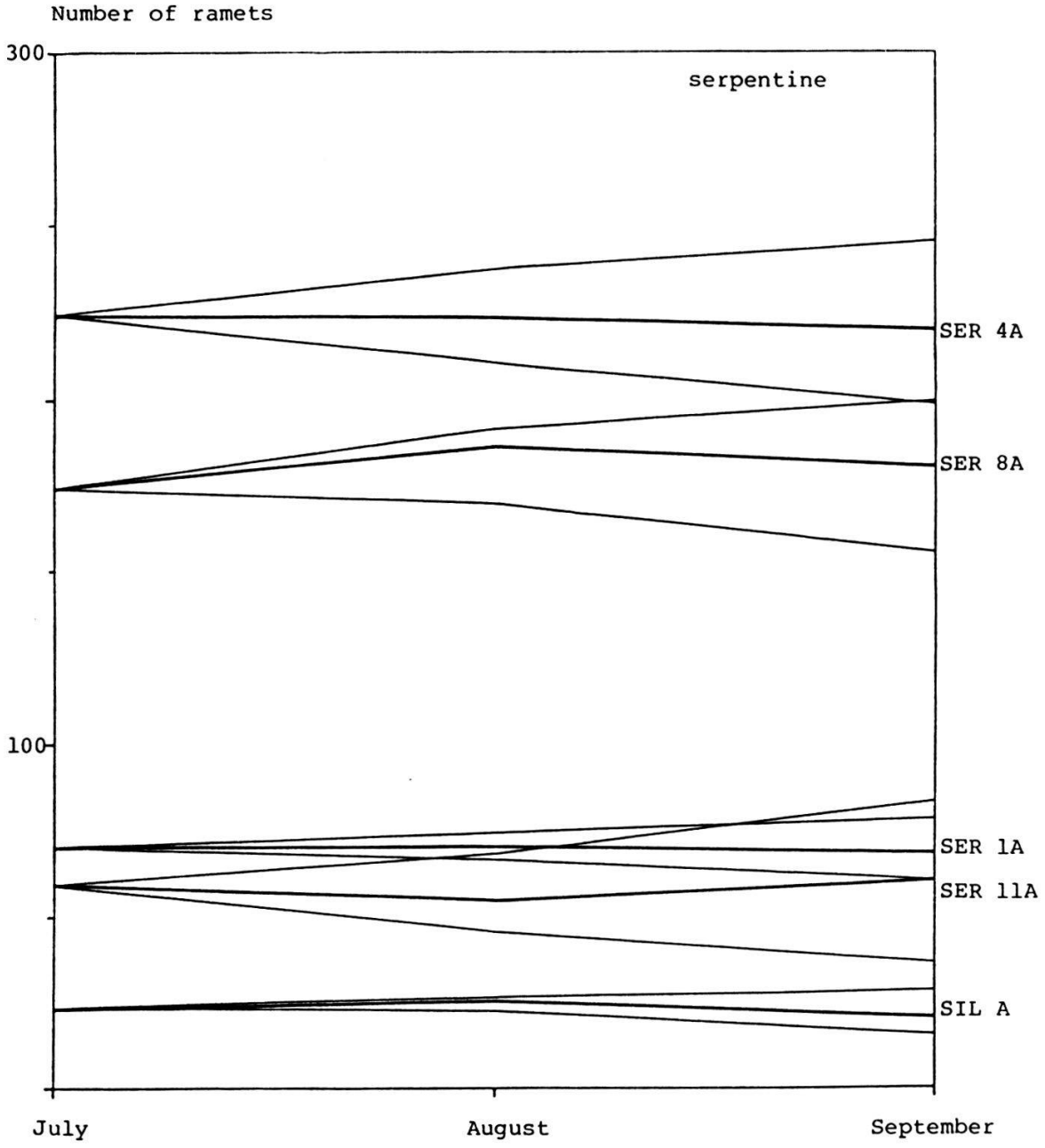
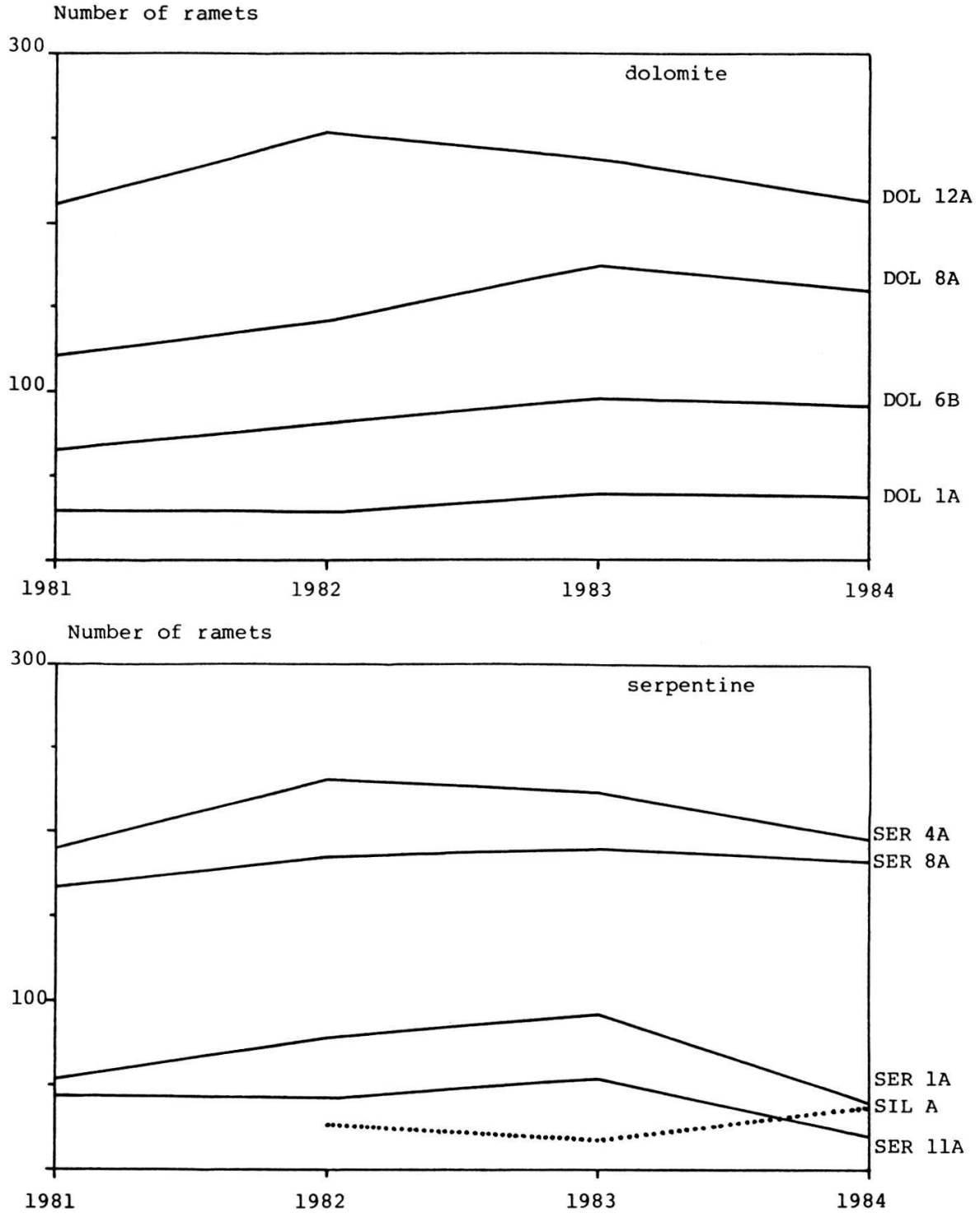


Fig. 40. Net number, added gains and subtracted losses of ramets per m^2 during summer 1983 within selected plots on serpentine and acidic silicate.

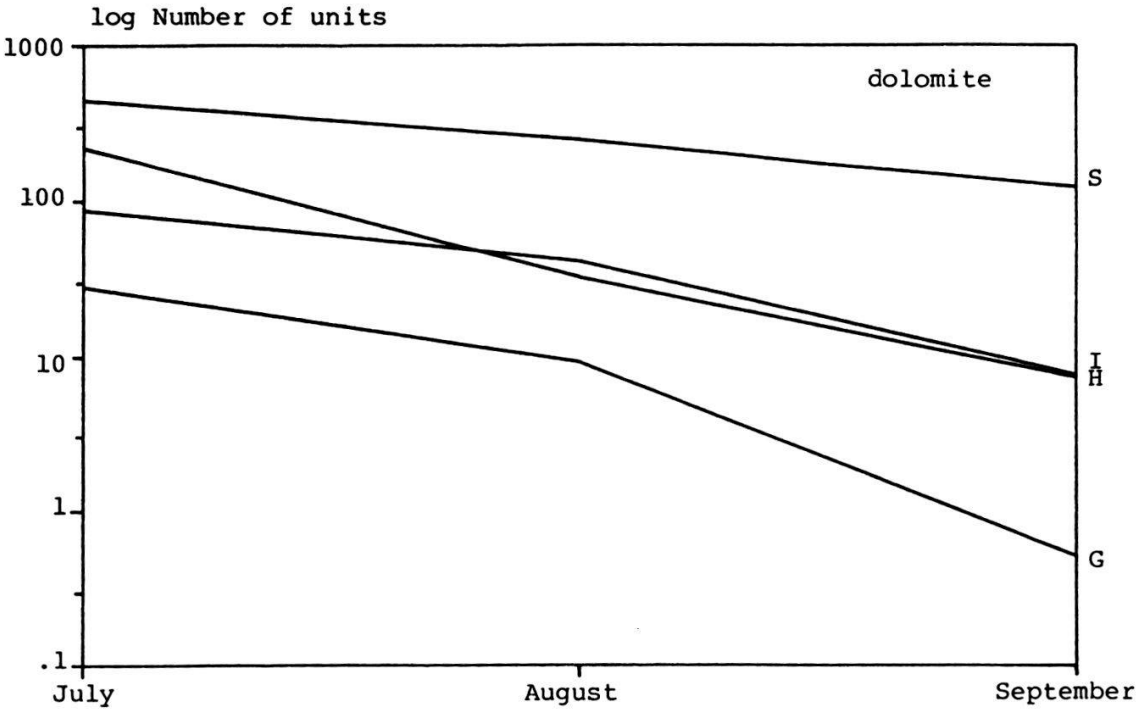
Abb. 40. Netto-Anzahl mit addierten Gewinnen und subtrahierten Verlusten von Ramets pro m^2 während des Sommers 1983 in ausgewählten Flächen auf Serpentin und saurem Silikat.

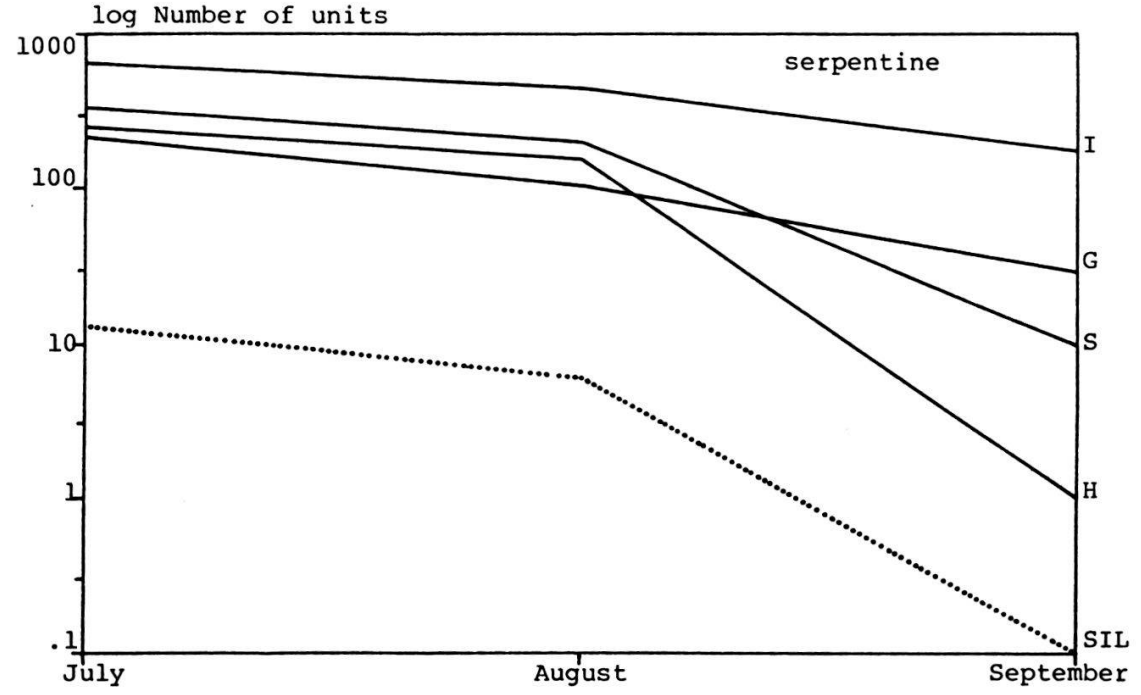


Figs 41,42. Net numbers of ramets per m^2 during 4 years within selected plots on dolomite, serpentine, and acidic silicate (SIL).
Abb. 41,42. Netto-Anzahl Ramets pro m^2 während 4 Jahren in ausgewählten Flächen auf Dolomit, Serpentin und saurem Silikat.

DOL 1A: grassland
DOL 6B: intermediate sites
DOL 8A: scree
DOL 12A: highest sites

SER 1A: dense vegetation
SER 4A: intermediate sites
SER 8A: sparse vegetation
SER 11A: highest sites





Figs 43,44. Number of reproductive units per m^2 at different sites on dolomite, serpentine, and acidic silicate in summer 1983.

Abb. 43,44. Anzahl Fortpflanzungseinheiten pro m^2 auf verschiedenen Standorten auf Dolomit, Serpentin und saurem Silikat im Sommer 1983.

G = grassland, dense vegetation
I = intermediate sites
H = highest sites
S = scree, sparse vegetation

in all sectors except the highest ones, the same tendencies as on dolomite scree slopes being observed. In July, very numerous flower buds and

Table 28. Number of reproductive units per m^2 in summer 1983.
Tab. 28. Anzahl Fortpflanzungseinheiten pro m^2 im Sommer 1983.

*) Seeds were already dispersed - Samen waren schon verstreut
**) Many reproducing rosettes were eliminated by grazing - viele reproduzierende Rosetten sind abgefressen
A = flower buds - Blumenknospen, B = flowers - Blüten, C = unripe fruits - unreife Früchte, D = ripe fruits - reife Früchte, - E = seeds (not included in the total amount) - Samen (nicht im Gesamttotal enthalten).

Site	Month	A	B	C	D	E	Total
Dolomite:							
grassland	July	8.3	19	.5	0	0	27.8
	August	0	0	9	0	0	9
	Sept.	0	0	0	.5	0	.5
intermediate	July	6.8	50.4	30.2	0	0	87.4
	August	0	0	40.1	0	0	40.1
	Sept.	0	0	0	7.4	2.5	7.4
scree slopes	July	193.3	222.5	33.2	0	0	448
	August	0	2	239.5	5.3	4.2	245.8
	Sept.	0	0	0	119	86	119
highest sites	July	191.5	26.5	0	0	0	218
	August**	0	31.5	0	0	0	31.5
	Sept.	0	0	.75	6.5	2.5	7.25
Serpentine:							
dense vegetation	July	161	40.1	15.3	0	0	216.5
	August	0	3	100.8	0	0	103.8
	Sept.	0	0	1.4	28	20.3	29.4
intermediate	July	470	132.9	47.4	0	0	650.3
	August	1.5	21	421.5	0	0	444
	Sept.	0	0	.8	178.4	71.3	179.2
sparse vegetation	July	38.8	267.3	29.3	0	0	335.4
	August	0	0	199.2	0	0	199.2
	Sept.*	0	0	0	9.8	2.7	9.8
highest sites	July	230	23	0	0	0	253
	August	0	2	152	0	0	154
	Sept.**	0	0	0	1	0	1
Acidic silicate	July	.5	11	1.5	0	0	13
	August	0	0	6	0	0	6
	Sept.	0	0	0	0	0	0

flowers were observed in sectors with dense vegetation and intermediate ones; in August, unripe fruits prevailed whereas in September mostly ripe fruits with a good seed content were found. Abundant flowers and unripe fruits were counted also in the plots with thin vegetation, but during the September census, most of the ripe fruits with the seeds were already dispersed (Table 28, Fig. 44).
Only few reproductive units were found in July and August on acidic silicate and no seed output was observed in September (Table 28, Fig. 44).

5. DISCUSSION

The present studies reveal that Biscutella levigata is predominantly allogamous and highly self-incompatible. However, its theoretically possible wide gene exchange is apparently limited, at least in some alpine subpopulations. Biology of reproduction undoubtedly plays an important role in this process; factors limiting the gene flow apparently operate both at the pollination phase as well as during seed development and their subsequent dispersal.
It seems that the limited gene flow in B. levigata is influenced by spatial and/or temporal variation in floral supply as well as by the foraging behaviour of pollinators. Populations of Biscutella levigata are variable as to their density. In the study area, population density was very low in dolomite grassland, whereas dense clusters of rosettes were found on dolomite scree. On serpentine, a rather consistent pattern in density was observed.
On the whole, about 10% of the rosettes produced inflorescences. The general pattern of production of floral structures in B. levigata is similar to e.g. Hieracium floribundum (THOMAS and DALE 1975). However, some differences between the substrata studied were noted. On dolomite, reproducing rosettes of B. levigata most frequently represented less than 10%, but the corresponding proportion on serpentine was always higher than 10%. On the other hand, no pronounced differences between