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COLONIZATION OF *SIBBALDIA TETRANDRA* CUSHIONS ON ALPINE SCREE IN THE PAMIRO-ALAI MOUNTAINS, CENTRAL ASIA

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ABSTRACT

The population of *Sibbaldia tetrandra*, a cushion plant, on the scree slope at 3800 m a.s.l. in the Pamiro-Alai Mountains consists of isolated individuals with positively skewed size distribution. Direct competition among isolated individuals is improbable. The differences in cushion size are due mainly to the age of individuals and the local site quality. Linear relationship between the growth in height of a cushion and its lateral growth was found. Frost injuries are more extensive in the small cushions, but the proportion of afflicted plants is greater in the large ones. Slightly contagious spatial pattern resulting from the environmental heterogeneity was detected. Seventeen species were observed to invade the cushions. Total biomass of intruding species is highly correlated with the cushion volume as well as with biomass. Species diversity increases with cushion area. A log-linear relationship between the number of invading species and cushion area was found. Both the number and cover of the species occurring outside of the *Sibbaldia tetrandra* cushions are negatively correlated with the cover of *Sibbaldia tetrandra*. The spatial pattern of *Sibbaldia* populations differs considerably between the study plot on a flat site and that on the scree slope. On the flat site, *Sibbaldia* forms a carpet consisting of individuals which cannot be clearly distinguished from each other. There also, the number and cover of the other species increases, and the most successful species are those which are capable of colonizing *Sibbaldia* cushions.

INTRODUCTION

Alpine habitats are well known for their exceedingly severe life conditions (e.g., Bliss, 1971; Landolt, 1983; Urbanska and Schutz, 1986; Ellenberg, 1988). They offer environments which are stressed (climate) or disturbed (unstable surface) or are combinations of both (Grime, 1979; Callaghan, 1987). Cushion plants represent life forms which are adapted to these extreme conditions (Billings and Mooney, 1968; Bliss, 1971; Alliende and Hoffmann, 1985; Ellenberg, 1988; Walter and Breckle, 1989; Callaghan, 1989). Their buds are held close to the soil surface (Rauh, 1939; Crawley, 1986) where conditions are more constant than in the surrounding air (Billings and Mooney, 1968; Larcher, 1980). Moreover, the cushion form is able to anchor the scree material (Jenny-Lips, 1930, cited by Ellenberg, 1988).

Colonization of cushion plants by other plant species has been reported from various parts of the world (Polunin, 1936; Whitehead, 1951; Griggs, 1956; Walter, 1974; Alliende and Hoffmann, 1985; Lough et al., 1987; Walter and Breckle, 1989; Filion and Payette, 1989). It has been suggested that the benefits for invading species are mainly (1) shelter from wind exposure, (2) increased local temperature, (3) provision of moisture for germination and seedling establishment, and (4) provision of organic substrates (Griggs, 1956; Bonde, 1986; Bell and Bliss, 1980; Alliende and Hoffmann, 1985). However, the relationships among the host plant and the invading species have rarely been investigated in detail up to now (Alliende and Hoffmann, 1985).

This study was carried out in an alpine community with the prevailing species *Sibbaldia tetrandra,* a cushion plant, in the Pamiro-Alai Mountains, USSR. The study addresses the following questions:

(1) What is the spatial structure of the *Sibbaldia tetrandra* population on the steep scree slope?

(2) How is the performance of invading species affected by biometric features of a cushion?

(3) What are the differences between the cushion community of a steep scree slope and that of a flat site?

STUDY AREA

The high mountain system of Pamiro-Alai (central Asia) extends from 39°N to 42°N and from 66°E to 74°E and covers an area of 600 × 150 km. Mountain peaks reach altitudes of over 5500 m a.s.l., dropping in the north to the Fergana basin at 500 m a.s.l. Pamiro-Alai belongs to the area of the Hercynian folding. Tertiary deformations control the longitudinal direction of main ridges. The mountains are built of Proterozoic and Paleozoic to Tertiary sediments (Černík and Sekyra, 1969).

The orographic snowline lies between 3900 and 4500 m a.s.l. The present glaciation limit varies from 3000 to 3500 m a.s.l. The arid climate with rainfall maxima at approximately 2500 mm is typical of the region. On the Turkestan Ridge, at an altitude of 3000 m, precipitation of only 714 mm was measured from September to July (Walter, 1974).

The study was conducted on the northern slopes of the Turkestan Ridge, in the westernmost part of the Pamiro-Alai (Figure 1). It represents an arid mountain range without a tree belt. Occurrence of woody plants is conditioned by moisture and local soil conditions (Sakirov, 1955, cited by Walter, 1974). Two vegetational limits may be distinguished in this area: (1) between 2700 and 3100 m a.s.l., long-term and extensively used pastures are found, consisting of grasses and forbs with scattered shrubs of *Juniperus seravshanica* and *J. turkestanica;* on skeleton-rich soils, the communities of thorn-cushion plants (*Tragacantha* sp., *Acantholimon* sp.) are developed; and (2) above 3000 m a.s.l., cryophilous plant communities occur. The extremely steep and rocky character of the mountains makes it impossible to distinguish more altitudinal belts here; the occurrence of plant species is determined by local habitat conditions (Afanasjev, 1956; Walter, 1974).

The study site was located on the arete between the Karasu and Uram river valleys at an altitude of 3800 m. Two research plots were situated on the northern slope (approximately 30°) covered with mobile (in the sense of Ellenberg, 1988) slate scree. The size of scree particles varied, on average, from several centimeters to several tens of centimeters.

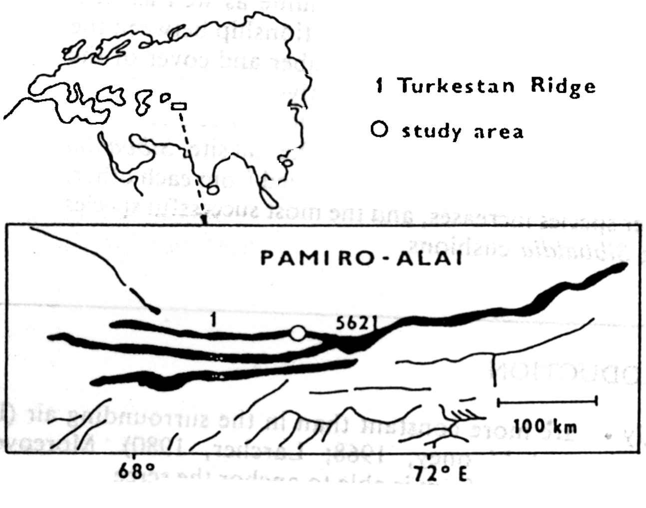

FIGURE Location of the study area in the Pamiro-Alai, USSR.

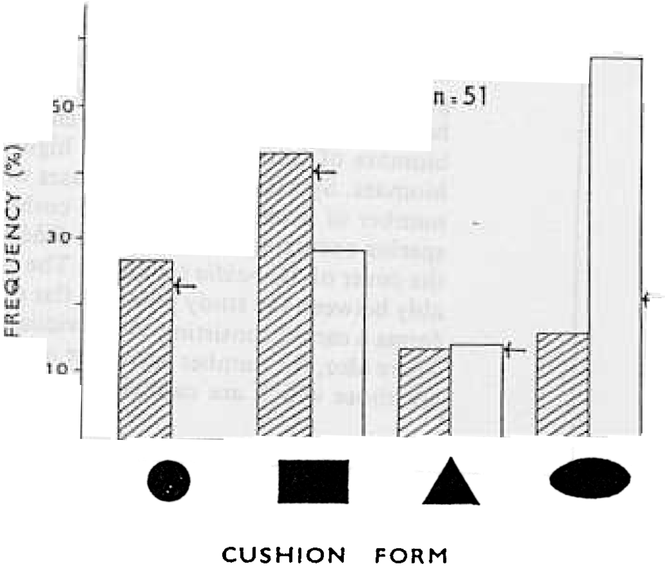

FIGURE 2. Frequency distribution of the cushion form (plot A). Size classes are indicated by hatching (cushions of area up to 10 dm^2, $n = 44$) and unshaded bars (larger cushions, $n = 7$). Arrows indicate the mean values for the whole population.

STUDY SPECIES

Sibbaldia tetrandra Bunge (Rosaceae) is a monoecious or dioecious dwarf shrub forming extensive cushions. Stems are tightly packed, covered with remainders of stipules and older leaves at their bases. Leaves are ternate, up to 5 mm in size, cuneate-obovate and shortly petioled. Flowers up to 8 mm diameter are on very short peduncles (2-4 mm). The flowering period is from June–July to August and the fruiting period from August to September (Ovchinnikov, 1975). The cushions are often wind-sheared (Walter and Breckle, 1989).

Young shoots grow from the root collar plagiotropically on the ground surface and produce a large number of rooted lateral branches (Steshenko, 1963). According to the classification by Rauh (1939) (based on the morphology of cushion plants) it belongs to the radial flat cushion which can develop to the hemispherical cushion. These are the best protected of all types against drought (Ellenberg, 1988).

The growth of *Sibbaldia tetrandra* cushion is very slow, being only 0.2 to 0.3 cm radially per year. Maximal increment observed in extremely moist and warm years was 0.5 cm (Steshenko, 1973). Measurements of cushion age, based on morphology, were presented by Steshenko (1973) who gave values of 50 to 70 yr for cushions of 18 to 20 cm diameter, and several hundred years for 1 to 2 m diameter cushions. The plant flowers initially at the age of 7 to 12 yr and flowers regularly from 15 to 25 yr of age.

Sibbaldia tetrandra is a widespread species on the Pamir, Pamiro-Alai, Tien Shan, Altai, Tibet, Himalaya, and North Mongolian mountains (Ikonnikov, 1963; Ovchinnikov, 1975). It occupies high mountain rocky and scree slopes. It is more abundant on moist northern slopes of the alpine belts where snow lies; it is one of the prevailing species of cryophilous communities (Steshenko, 1973; Ovchinnikov, 1975; Walter, 1974; Walter and Breckle, 1989).

METHODS

Two research plots, each 5 × 5 m, were established in July 1989. Plot A was situated on the steep scree slope, and plot B on flat ground.

The cushions present in plot A were located using coordinates. The following morphological characteristics of the cushions were recorded: (1) area (*A*), calculation of which was based on cushion geometry, (2) height (*H*), estimated from several randomly located measurements, and (3) volume, $V = A \cdot H$. For each cushion, the list of intruding species was recorded. Plot A was divided into 25 subplots of 1 m^2. Cover values of all species occurring outside of the *Sibbaldia* cushions, as well as the percentage cover of *Sibbaldia tetrandra*, were recorded in each subplot.

To compare the effect of slope steepness on species performance, plot B was established on flat ground occupied by stable rock debris. Cover values of all species present in the 25 1-m^2 subplots were estimated.

Ten cushions of different size were selected at random on the steep scree slope, each being characterized by the biometric criteria described above. Aboveground biomass of all intruding species was harvested from each cushion and oven-dried at 85°C until a constant weight was obtained. The diversity of species intruding the cushions was computed using the Shannon formula (see, e.g., Peet, 1974)

$$H' = -\sum_{i=1}^{S} p_i \cdot \log_2 p_i \qquad (1)$$

where p_i is a relative importance of the species *i* expressed in terms of biomass, and *S* is the number of intruding species.

One cushion of a known size was harvested to provide the following data: (1) fresh volume of the aboveground biomass, (2) total dry weight of the aboveground biomass, and (3) proportion of dry weight of current-year's shoots.

Frost injury was estimated visually. Damaged parts of cushions differed in color from the living ones.

Nomenclature follows Cherepanov (1981). Data were analyzed using linear regressions according to Sokal and Rohlf (1981).

RESULTS

SPATIAL PATTERN OF THE *SIBBALDIA TETRANDRA* POPULATION

Changes in the form of a cushion during its growth in size were observed. It was possible to compare the cushion form to some simple geometric design. Among small cushions (up to 10 dm^2), circles and oblongs were the most frequent (70.4%). Less regular forms, predominantly elliptical, were typical of the larger cushions (57.1%, see Figure 2).

On the slope, the frequency distribution of cushion area was positively skewed ($g_1 = 3.26$) with most plants concentrated in the small size classes (Figure 3). The maximum size of an isolated cushion here was ca. 70 dm^2.

A linear relationship was found ($r = 0.52$, $p < 0.01$) between the growth in height of a cushion and its lateral growth (expressed as the square root of its area) (Figure 4). The value of the correlation coefficient increased ($r = 0.65$) when the interactive regression was used (three outliers deleted).

It is possible to relate the aboveground biomass of a cushion to its volume because of negligible size variability of a single module. Fresh volume of 1 dm³ corresponded to the dry weight of 79.4 g. The proportion of current-year shoots was 15%.

Table 1 shows the frost injuries to cushions of different size classes. The afflicted parts of cushions were often located at the windward side (cf. Ellenberg, 1988). Of the cushions recorded in plot A, 41.1% were partially afflicted. The range of injury varied from 5 to 90% of the cushion area. Altogether, 8.5% of the total area covered by *Sibbaldia* cushions in plot A was afflicted. The data presented in Table 1 lead to the following conclusions: (1) the injury is more severe in small cushions, and (2) the probability of frost injury increases with cushion size, i.e., age.

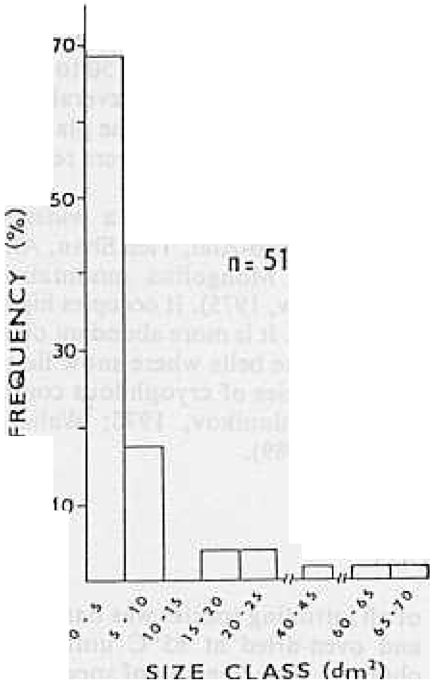

FIGURE 3. Frequency distribution of the cushion area (plot A).

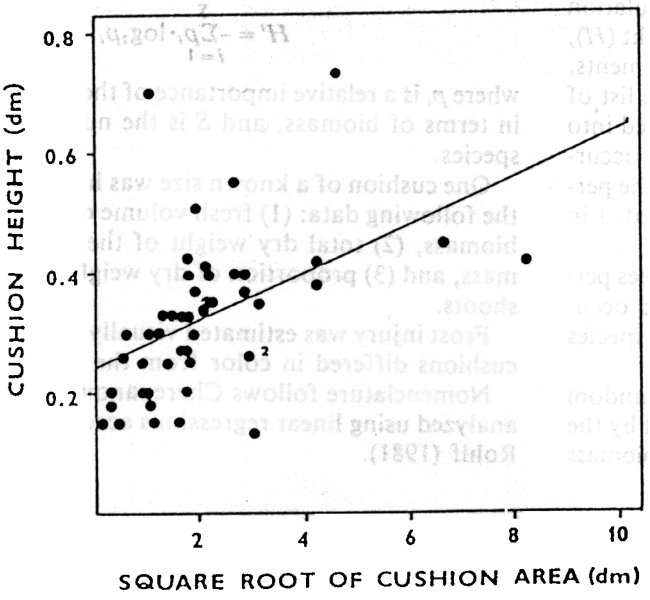

FIGURE 4. Mean cushion height plotted against cushion area (note the square root scale). The fitted regression is $y = 0.3878x + 2.448$, $r = 0.52$, $p < 0.01$.

The spacing of *Sibbaldia* cushions in plot A is presented in Figure 5. The Blackman's coefficient s^2/x was used as a measure of pattern (Kershaw, 1973; Goldsmith et al., 1986). Its value varied from 1.31 ($n = 100$) to 1.07 ($n = 25$) with regard to the number of subplots used for calculation. This indicates a slightly contagious spatial pattern.

COLONIZATION OF THE *SIBBALDIA TETRANDRA* CUSHIONS

Data on the performance of species growing on the *Sibbaldia* cushions of different size are summarized in Table 2.

TABLE 1
Frost injury of Sibbaldia tetrandra *cushions in relation to their size*

Size class (dm²)	Total number of cushions	Afflicted cushions		Extent of injury (mean percentage of cushion area)
		Number	%	
0– 5	35	11	31.4	36.4
5–10	9	6	66.7	8.3
15–20	2	1	50.0	10.0
20–25	2	0	0.0	0.0
>25	3	3	100.0	10.0
Total				
Ratio			41	
Mean				23.3

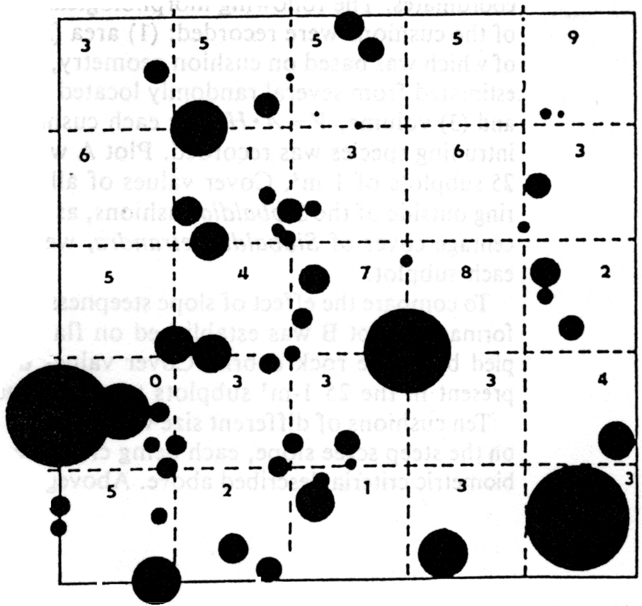

FIGURE 5. Location of the cushions in plot A (5 × 5 m). Size of the circle represents relative size of a cushion. The numbers in the plots correspond to the number of noncushion species found within the plot beyond cushions.

A linear increase in the total biomass of intruding species with the volume and biomass of *Sibbaldia* cushion was found ($r = 0.92$, $p < 0.001$, Figure 6a). However, when total biomass of intruding species was plotted against the cushion area, a less significant correlation was obtained ($r = 0.73$, $p < 0.025$).

The occurrence of *Festuca alaica* ($y = 0.046x + 0.221$, $r = 0.74$, $p < 0.025$) and *Smelovskia calycina* ($y = 0.232x - 1.015$, $r = 0.91$, $p < 0.001$) are positively correlated with the volume of the *Sibbaldia* cushion. The other prevailing species (*Potentilla pamiro-alaica* and *Swertia* sp.) do not show significant relations to the cushion volume.

Species diversity (H') increases with cushion area ($r = 0.69$, $p < 0.05$, Figure 6b). The species evenness (J') (e.g., Crawley, 1986) ranges from 0.57 to 0.86, but without relation to cushion size (Table 2). A conclusion may thus be drawn: that the increase of species diversity with cushion size is caused mainly by species richness. No significant relationship was found for species diversity (H') plotted against the cushion volume. It thus appears likely that probability of successful establishment of further colonizing species is affected by the area available for colonization.

The log-linear relationship between the number of intruding species and cushion area is presented in Figure 7. There is a less obvious increase of species richness up to the cushion size of approximately 10 dm^2. The large cushions, however, generally host more intruding species.

Most of the species growing upon cushions were also recorded in the adjacent scree areas. Three species occurred within plot A (steep scree slope) exclusively upon the cushions: *Lloydia serotina, Draba altaica,* and *D. rosularis. Festuca alaica, Potentilla pamiro-alaica, Leontopodium ochroleucum, Dracocephalum oblongifolium, Leucopoa olgae,* and *Swertia* sp. occurred upon more than 15% of cushions present in plot A (Figure 8). Beyond cushions, the most common species were *Dracocephalum oblongifolium, Potentilla pamiro-alaica, Smelovskia calycina,* and *Allium platyspathum. Callianthemum alatavicum* was the only species found exclusively beyond cushions. However, the species occurrence values in and outside the cushions are comparable only approximately due to unequal areas involved in the calculation.

COMPARISON OF STEEP AND FLAT HABITATS

While the vegetation of plot A (steep scree slope) was formed by sparse populations of individual species scattered among *Sibbaldia* cushions of different size, the character of plot B (flat site) differed in the following features (Table 3):

TABLE 2

Quantitative characteristics of ten cushions of Sibbaldia tetrandra *invaded by other vascular plants and diversity and biomass (g) of intruding species*

	Cushion number										
	1	2	3	4	5	6	7	8	9	10	Total
Sibbaldia tetrandra											
Area (dm^2)	39.2	5.7	6.9	63.6	14.1	8.0	7.1	38.5	11.1	31.0	
Mean height (dm)	1.06	1.00	0.38	0.42	0.40	0.53	0.58	0.50	0.50	0.36	
Volume (dm^3)	41.6	5.7	2.6	26.5	5.7	4.3	4.1	19.2	5.6	11.4	
Biomass (g)	3303.8	452.6	206.5	2104.6	452.6	341.5	325.6	1524.8	444.7	905.3	
Other species (biomass, g)											
Potentilla pamiro-alaica	3.7	—	—	0.8	0.1		1.7	0.6	3.3	4.5	15.8
Festuca alaica	2.5	0.2	0.1	0.5	1.5	0.1	0.5	1.6	0.5	0.5	8.1
Swertia sp.	1.6	0.4	—	2.8	3.0	—	4.2	1.2	—	—	13.1
Smelovskia calycina	9.1	1.6	—	5.5	—	—	—	—	0.3	2.2	18.6
Botrychium lunaria	<0.1	—	—	—	—	—	—	<0.1	—	—	<0.1
Allium platyspathum	0.4	—	0.1	0.1	—	—	—	—	0.1	—	0.7
Astragallus sp.	0.7	—	<0.1	1.1	—	0.2	—	—	—	—	2.0
Leontopodium ochroleucum	—	1.2	—	0.4	—	0.3	—	0.9	—	0.9	3.7
Platytaenia sp.	—	—	<0.1	0.2	—	—	—	1.0	0.6	—	1.8
Taraxacum sp.	—	—	—	<0.1	—	—	—	<0.1	—	—	<0.1
Minuartia verna agg.	—	—	—	0.1	—	—	—	—	—	—	0.1
Leucopoa olgae	—	—	—	0.7	—	—	—	—	0.5	—	1.2
Taraxacum minutilobum	—	—	—	—	0.1	—	0.1	—	0.2	—	0.4
Dichodon cerastoides	—	—	—	—	—	—	0.5	—	—	—	0.5
Dracocephalum oblongifolium	—	—	—	—	—	—	—		<0.1	—	1.1
Draba altaica	—	—	—	—	—	—	—	—	—	0.1	0.1
Number of species	7	4	4	11	4	4	5	8	8	6	17
Total biomass	17.9	3.5	0.2	12.0	4.7	1.6	6.8	6.4	5.7	8.2	67.2
Species diversity H' ($\log_2$ base)	1.97	1.66	1.83	2.36	1.14	1.42	1.53	2.58	2.00	1.71	
Evenness J'	0.70	0.83	0.79	0.68	0.57	0.71	0.66	0.86	0.67	0.66	

(1) The individual plants of *Sibbaldia tetrandra* were not isolated and most could not be readily distinguished from each other. The cover of *Sibbaldia tetrandra* was approximately doubled.

(2) Total cover of other species was much higher, reaching a value similar to that of *Sibbaldia tetrandra.*

(3) Increase in the total number of species present in the plot.

Both the number of other species (Figure 9a) and their total cover (Figure 9b) in plots of 1 m² are negatively correlated with the cover of *Sibbaldia tetrandra.* Spearman rank correlation coefficient was calculated to com-

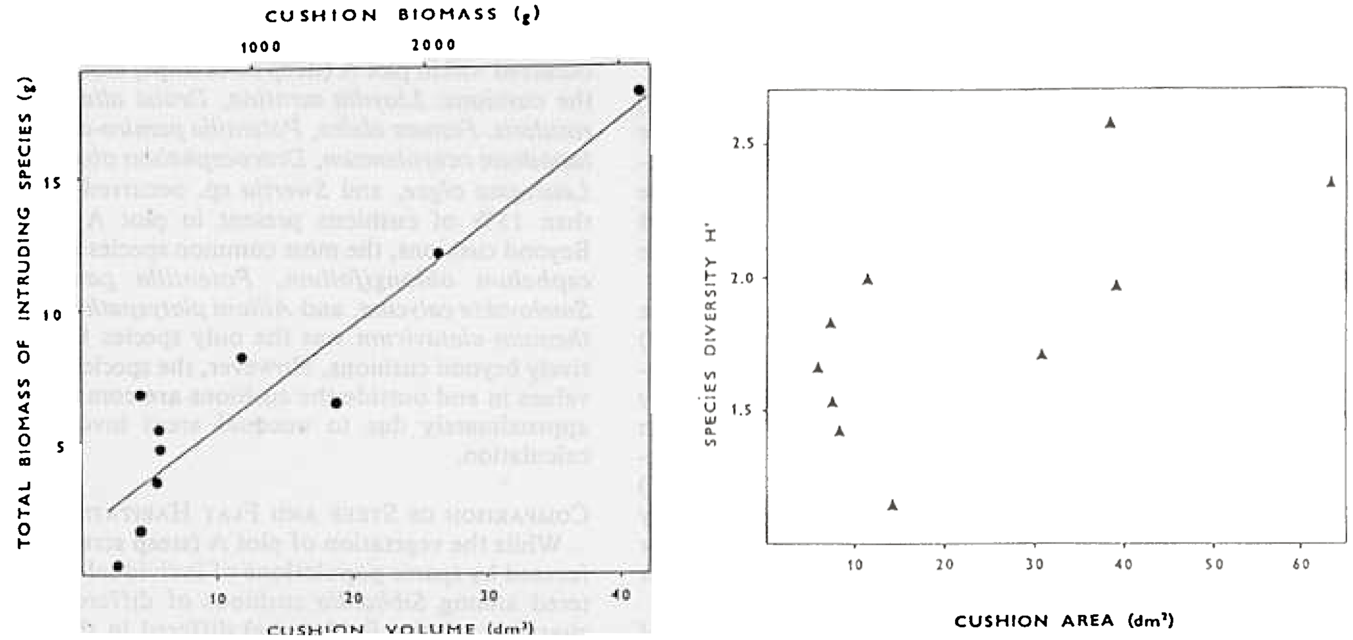

FIGURE 6. Total biomass of intruding species plotted against cushion volume. (a) The values of *Sibbaldia tetrandra* biomass indicated in the upper part of the diagram were calculated from the data on cushion volume. The fitted regression is $y = 0.372x + 2.002$, $r = 0.92$, $p < 0.001$. (b) Species diversity of intruding species plotted against cushion area ($r = 0.69$, $p < 0.05$).

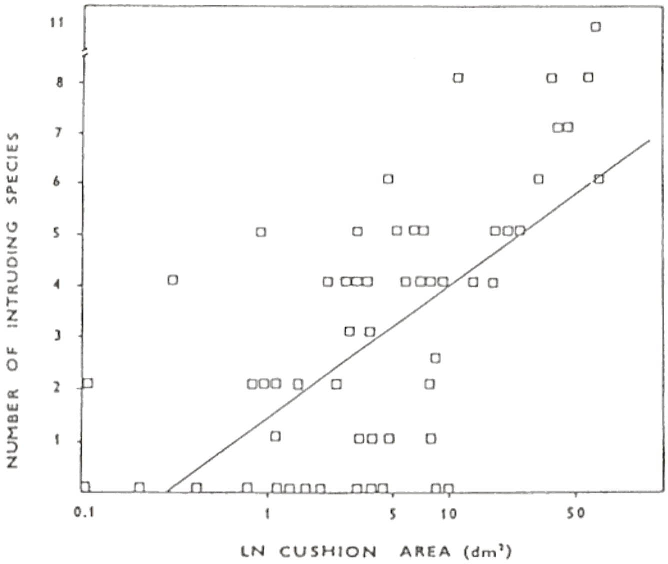

FIGURE 7. Number of intruding species plotted against area of *Sibbaldia tetrandra* cushions. Note the semilog scale. The fitted curve is $y = 1.1178 \ln x + 1.520$, $r = 0.66$, $p < 0.001$.

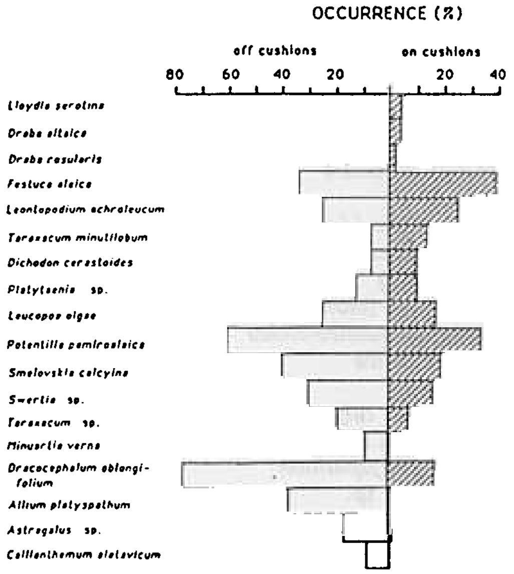

FIGURE 8. Species performance upon cushions (hatched bars) and beyond cushions (unshaded bars) in plot A. The occurrence upon cushions is expressed as a percentage of cushions ($n = 51$) on which the species occurred. The occurrence beyond cushions is expressed as a frequency in 25 subplots of 1 m².

TABLE 3

Comparison of vegetation characteristics in two Sibbaldia tetrandra *different habitats: steep scree slope (plot A) and flat site (plot B)*[a]

	Plot A	Plot B
Sibbaldia tetrandra cover (%)	15.9 (0–75)	32.0 (20–50)
Sibbaldia tetrandra biomass (g dm^{-2})	6.94	14.85
Spatial pattern	Contagious (isolated individuals)	Continuous cover
Total cover of other species (%)	4.8 (0–28)	35 (10–72)
Total number of species	15	21
Mean species number per 1 m^2	3.9 (0–8)	11.4 (5–17)

[a] Range of values are indicated in parentheses.

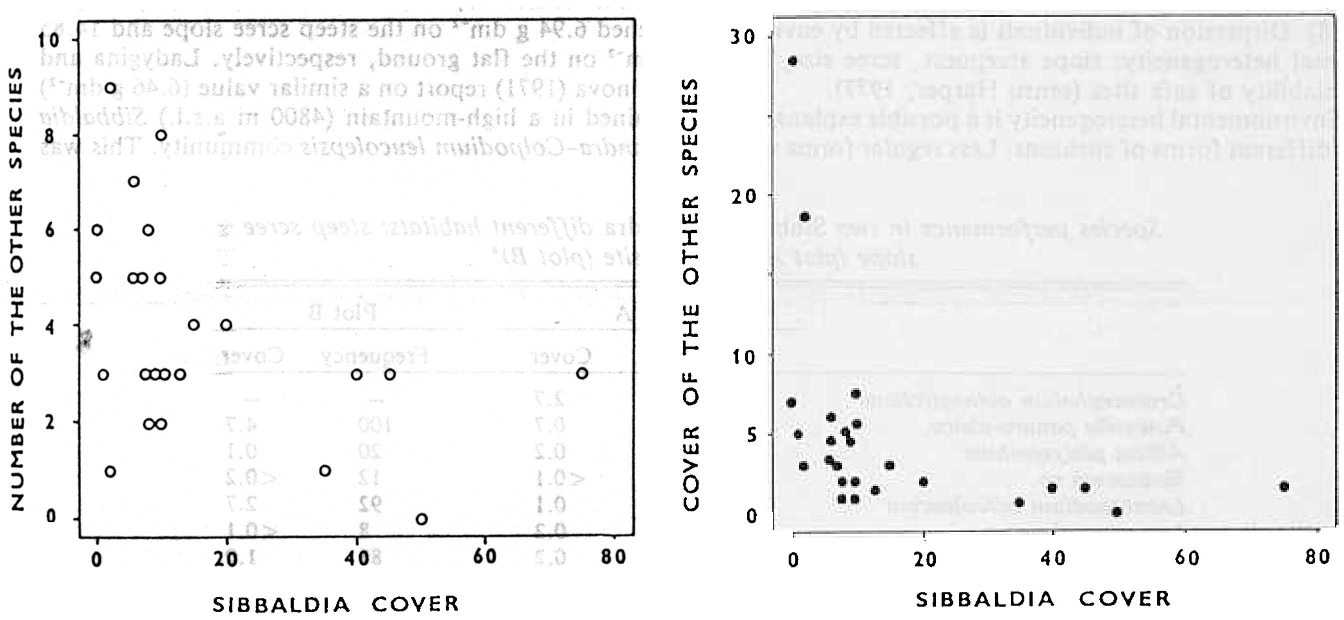

FIGURE 9. Number of species ($r_s = -0.46$, $p < 0.025$) occurring outside the cushions in the 1-m^2 subplots and (b) cover ($r_s = -0.71$, $p < 0.005$) of species occurring outside the cushions in the 1-m^2 subplots of plot A expressed against *Sibbaldia tetrandra* cover.

pare both relationships: closer correlation was found with the total cover of other species ($r_s = -0.71$, $p < 0.005$) than with the number of other species ($r_s = -0.46$, $p < 0.025$). It may be thus concluded that the cover of other species depends on the available space much more than does the number of the other species.

Table 4 shows the species performance in both habitats being compared. Species occurring with the highest frequency and/or cover on the flat ground are those capable of successfully colonizing *Sibbaldia tetrandra* cushions (compare with Figure 8): *Potentilla pamiroalaica, Festuca alaica, Leontopodium ochroleucum, Swertia* sp. Moreover, on the steep scree slope, the species preferring to grow outside the cushions were less frequent or even absent from the flat site (*Allium platyspathum, Leucopoa olgae, Callianthemum alatavicum*). A conspicuous example of this group is *Dracocephalum oblongifolium*, that had 76% frequency and by far the greatest mean cover (2.7%) of all species present on the steep scree slope but was not found on the flat site at all.

On the other hand, there are species which were present with low frequency and cover (*Astragalus* sp.) or even absent (*Polygonum nitens, Primula algida, Kobresia pamiroalaica*) upon cushions on the steep scree slope but occurred with high frequency and/or cover on the flat site.

DISCUSSION

In open habitats of arctic and alpine environments, sexual reproduction predominates and deterministic cushion growth forms are common (Callaghan, 1987). *Sibbaldia tetrandra* is a species reproducing by seed (Steshenko, 1963, 1973). Each cushion thus represents one genet.

One of the essential features of the size hierarchy is that the few large plants often make up most of the population biomass (Werner and Solbrig, 1984; Hutchings, 1986). The seven (out of 51) cushions analyzed in plot A, which exceeded an area of 10 dm^2, represented 63.7% of the total population biomass. A strongly skewed distribution can arise even in the absence of competition among individuals (Hara, 1984; Hutchings, 1986). In harsh environments where canopies are open, plant competition is probably less important than the physical environment in controlling the plant growth (Darwin, 1859; Harper, 1977; Callaghan and Emanuelsson, 1985).

Differences in size among individual *Sibbaldia tetrandra* cushions are thus caused mainly by (1) age of an individual, and (2) local site quality. Chance plays a large part in the colonization of scree slopes (Ellenberg, 1988). Dispersion of individuals is affected by environmental heterogeneity: slope steepness, scree size, and availability of safe sites (sensu Harper, 1977).

Environmental heterogeneity is a possible explanation for different forms of cushions. Less regular forms were recorded in larger cushions. The probability of unfavorable conditions (scree morphology, exposure to wind, space occupied by another cushion, presence of another species), which can locally reduce or even prevent the radial growth in a certain direction, is greater in large cushions.

Individual plants of *Sibbaldia tetrandra* are isolated and it can be supposed that no direct competitive contacts take place among them. Moreover, there is hardly competition for water. Natural population density can be very low in those environments with unpredictable and low supply of water, so that members of the population do not meet their requirements for resources (Harper, 1977). Certain cushion species can store up to several times their own weight in water (Walter and Breckle, 1989).

Slow growth of cushion plants of extreme high mountain habitats (Steshenko, 1963; Bliss and Mark, 1974; Walter, 1974; Crawley, 1986) is reflected by low biomass (Walter and Breckle, 1989). Total aboveground biomass of *Sibbaldia tetrandra* (estimated on the basis of the relation between cover, i.e., cushion area, and dry weight) reached 6.94 g dm^{-2} on the steep scree slope and 14.85 g dm^{-2} on the flat ground, respectively. Ladygina and Litvinova (1971) report on a similar value (6.46 g dm^{-2}) obtained in a high-mountain (4800 m a.s.l.) *Sibbaldia tetrandra-Colpodium leucolepsis* community. This was

TABLE 4

Species performance in two Sibbaldia tetrandra *different habitats: steep scree slope (plot A) and flat site (plot B)*[a]

	Plot A		Plot B	
	Frequency	Cover	Frequency	Cover
Dracocephalum oblongifolium	76	2.7	—	—
Potentilla pamiro-alaica	60	0.7	100	4.7
Allium platyspathum	36	0.2	20	0.1
Taraxacum sp.	16	<0.1	12	<0.2
Leontopodium ochroleucum	24	0.1	92	2.7
Leucopoa olgae	24	0.2	8	<0.1
Festuca alaica	32	0.2	88	1.0
Smelovskia calycina	40	0.2	40	0.4
Platytaenia sp.	12	<0.1	44	0.3
Swertia sp.	28	0.2	96	4.4
Taraxacum minutilobum	8	<0.1	—	—
Minuartia verna agg.	8	<0.1	—	—
Callianthemum alatavicum	8	<0.1	—	—
Astragallus sp.	16	0.1	100	14.7
Dichodon cerastoides	8	<0.1	48	0.3
Polygonum nitens	—	—	92	1.3
Primula algida	—	—	64	0.4
Saxifraga stenophylla	—	—	60	0.5
Kobresia pamiroalaica	—	—	84	1.1
Draba altaica	—	—	40	0.2
Lloydia serotina	—	—	64	0.4
Silene cf. *samarkandensis*	—	—	24	0.1
Carex alajica	—	—	32	2.8

[a]Species frequency and cover (values in %) estimated in 1 m^2 plots are given

the most productive among nine different communities which have been studied at the altitude of 3850 to 4800 m in the Pamirs (Walter and Breckle, 1989).

Our results suggest that those cushion features which provide the life conditions favorable for successful establishment and development of intruding species (water reservoir, accumulation of organic matter, reduction of extreme temperature) are related rather to the cushion volume, i.e., height (and biomass) than to its area.

The importance of niches provided by cushion plants to the intruding species have been discussed by Alliende and Hoffmann (1985) and Callaghan (1985). On the other hand, the growth of invading species may have negative impact on the cushion occupied. Cushion collapse due to colonization by intruding species was reported in some cushion species (Whitehead, 1951; Griggs, 1956; Lough et al., 1987). However, the compact form of a cushion may prevent intruding plants from attaining a larger size. Alliende and Hoffmann (1985) found no evidence of eventual replacement of *Laretia acaulis,* a high Andean cushion plant, by colonizing species, which is also the case with *Sibbaldia* tetrandra.

At an altitude of 3000 m, Alliende and Hoffmann (1985) recorded 19 species established on the cushions of *Laretia acaulis,* two of them occurring exclusively upon the cushions. In cushions of *Sibbaldia tetrandra,* we observed 17 species, three of them being absent from the adjacent area. However, if a large area on the steep scree slope is considered, the total number of species increases slightly. The size of *Laretia acaulis* cushions was positively correlated ($r = 0.37$, $n = 70$) with the number of intruding species. The closer correlation found in cushions of *Sibbaldia tetrandra* ($r = 0.65$, $n = 62$) may be due to the fact that *Laretia* differs from *Sibbaldia* in having greater variances both in density and size of rosettes, which also affects the performance of intruding species. The number and cover of intruding species in *Laretia* cushions were thus influenced not only by the cushion size but also by the compactness of the cushion.

Alliende and Hoffmann (1985) concluded that cushions cannot be considered as islands for their intruders since the same species occur also in the area beyond cushions. In the *Sibbaldia tetrandra* community, the "islandness" is more distinct since the substrate among cushions (large scree) is presumably less suitable for colonization than the fine material in *Laretia* habitats. However, on the basis of our data it is not possible to decide if *Sibbaldia tetrandra* cushions may be treated as islands in relation to the other species. The log-linear increase in number of invading species plotted against the area of *Sibbaldia tetrandra* cushions corresponds to the general species-area relationship (Begon et al., 1986; Lepš and Štursa, 1989).

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