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Populations of *Saxifraga oppositifolia* L., in Spitsbergen tundra in different ecological conditions

ABSTRACT: The paper deals with the structural variability and generative reproduction of *Saxifraga oppositifolia* populations in eight localities situated in Western Spitsbergen. The localities differed in terms of humidity, soil fertility, microclimate and frequency of disturbances. The population structure, the growth and development rate of individuals in the sea terrace and at the peat-bog prove that a dense plant cover influences positively the development of *S. oppositifolia.* The size of individuals, their biomass and population density is limited in most of the studied localities. Solifluction is the factor influencing the development of a population to the greatest extent. Of all the researched populations the weakest development was observed in the active structural grounds. Yearly changes in the structure of the populations as well as the yearly growth of the species studied are limited. The longevity, the development rate and size of the seedling recruitment are subject to modifications caused by the solifluction.

Key words: Arctic, Spitsbergen, *Saxifraga oppositifolia,* population structure.

Introduction

In the Arctic semi-desert zone, specimens of plant communities are separated from each other due to the low density of the plant cover. In those systems the competition for habitat is less important. Due to the limited accumulation of the organic matter in the ecosystem and lack of the competition caused by the separation of individuals — the whole ecosystem may be treated as a simple sum of the populations it is composed of (Svoboda 1977). Under Arctic semi-desert conditions reductionistic approach to the study of plant communities seems to be reasonable. Habitat conditions of every climatic zone modify the development rate and longevity of plant individuals. That also concerns Arctic, where due to the cool climate and short vegetation season, the production of biomass diminishes, as the growth rate and the longevity decrease (Bell and Bliss 1980).

The flora of Arctic semi-deserts is composed mainly of slowly growing dwarf shrubs and perennial plants (Ronning 1964, Callaghan and Emanuelson 1985).

The subject of this research was the structure and reproductivity of *Saxifraga oppositifolia* L. populations in Spitsbergen tundra. All types of habitats, occupied by *S. oppositifolia* in the area of Hornsund Fjord have been studied. The following components of the population structure were identified: density and congestion coefficient, spatial structure, size and age structure, the structure of development phases as well as fecundity, the size of seedling recruitment, but also the age, the rate of development and the yearly growth of individuals. The aim of this work is to compare the structure of the populations, fecundity and the seedlings' recruitment rate in eight *Saxifraga oppositifolia* populations in different habitats. The author comes out with the following hypothesis: population of *S. oppositifolia* are to greatest extent limited in their development in those habitats, where there is a risk of the strongest cooling and where individuals react to these difficult conditions by slowing down their ontogenetic development as well as increasing their longevity and decreasing the growth of shoots.

Methods

The research was carried out in seasons 1986 and 1988 in the south-western part of Spitsbergen in Hornsund fjord region (77°00'N, 15°00'E). All the habitats searched are fed by nutrients of sea origin via the colonies of Little Auk.

The research was conducted in typical ecosystems, in eight areas (Tab. I). Names of geomorphological forms are used after Pękala (1989) and the names of plant communities following Klekowski and Opaliński (1986) and Godzik (1987).

In order to evaluate the structure of a *S. oppositifolia* population in each locality, a small area of 5 × 10 m was chosen. The area was divided into 200 small fields, 0.25 m^2 each. Only at the ground moraine the surface was larger — 28 × 28 m. In order to define the density and the congestion coefficient (ecological density), all individuals in every field were counted and marked at the map in the scale of 1:10, taking into consideration their size and the micro-relief of the land. On the basis of this map, population aggregations were identified and their diameter as well as distance between these aggregations and those between individuals within a given aggregation were measured. To determine the type of individuals distribution we have used the dispersion coefficient for a basic surface of 0.25 m^2 (Kwiatkowska and Symonides 1980). In order to identify the structure of developmental stages all the individuals were counted taking into consideration following phases in individual development: seedling, juvenile, virginal, generative and senile phase. To describe the

Table I

Description of study surfaces overgrown with *S. oppositifolia* in the Hornsund region (Spitsbergen)

No of the surface	Geomorphological form	Plant community	Coverage of the soil by vegetation [%]
1	bottom moraine	Initial community with *S. oppositifolia*	1–2
2	ice-moraine ridge	–"–	5–10
3	sea terrace gravel with sand	Lichen tundra dominated by *Sphaerophorus globosus*	80–100
4	residual rocks	Lichen–moss tundra dominated by *Cladonia mitis, Cetraria nivalis* and *Rhacomitrium lanuginosum*	60–80
5	peat-bog	Mosses *Calliergon stramineum* — *Sanionia uncinata*	100
6	rock rubble on the Fugleberget slope	Lichen–moss tundra dominated by *Cladonia mitis, Cetraria nivalis* and *Rhacomitrium lanuginosum*	20–40
7	stabilized structural grounds	Initial lichen–moss community with *S. oppositifolia*	50–70
8	non-stabilized structural grounds	–"–	10–30

length of particular phase as well as the yearly growth rate in different phases of ontogenetic development, 50 individuals were taken at random from each population. The age, the yearly growth rate and the length of the long shoots were measured in living individuals. The age of an individual was determined by counting the number of segments of yearly growth of the longest non damaged shoot. Following the studies by Šilova (1988) we know that every year a new segment of yearly growth appears at the main axis of every living shoot. The limits between those sections can be identified from differences in colour and shape of the shoot axis. We measured separately the age of the living part — from the youngest segment to the main active root — as well as the age of the dead and living parts together. The size of individuals was estimated basing on the length of the long shoots. Yearly growth rate was estimated from the length of segments of the long shoots. The degree of branching was identified basing on the number of branches of the first order per every following segment of the yearly growth at the longest shoots. The age structure, the biomass, the number of branches and the length of yearly increment for different *S. oppositifolia* populations were defined basing on the sample of 30 individuals taken from each habitat at random.

In order to measure the biomass, plants were dried to the constant weight in the temperature of 80°C and weighed at the accuracy of 0.1 g. The form of growth of an individual was determined from the relation of biomass to the length of its longest shoot. The age structure and the yearly length increase were studied in eight populations and forms of growth were defined only for four populations (Nos 2, 3, 5 and 6). At the same time the number of branches was measured only in three populations (Nos 4, 5 and 6).

Fecundity was estimated basing on average number of fruits per individual in the generative phase. In order to identify the production of flowers and fruits they were counted in 50 individuals taken in each area at random and knowing the density of individuals in generative phase, those numbers were calculated per square meter.

The efficiency of flowering was estimated for particular populations basing on the proportion of the average number of flowers in a given vegetation season and the number of fruits from the former season.

The reproductivity of the population was defined basing on average number of seedlings per individual in generative phase.

In order to estimate the differences between average values of the above mentioned parameters, non parametric variance analysis was used — the Kruskal—Wallis test (Zar 1984) with the coefficient of 0.05.

Relation between the age and the length of yearly growth segment and the length of the shoot was defined with the use of the Spearman's rank correlation coefficient test.

Results

Age of individuals and the ontogenetic development rate. The average total age of an individual (the age of the living part and the age of the dead part) in the populations studied is highly diversified. It was highest on the sea terrace (9 years), at the peat-bog and the residual rocks, and lowest on the active and stabilized structural grounds. The differences between the average age of those populations are statistically important.

The longevity of individuals that was estimated basing on the total age was different at different localities. The individuals growing on the sea terrace reach even 22 years and those on the residual rocks 18 years. The shortest was the age in the initial community at the ground moraine Hansbreen (up to 10 years) and on the active structural grounds (up to 8 years).

The average age of some individuals, estimated only basing on their living parts, is lower than the total average age in some populations only. The difference in the population on the residual rocks, where mature individuals are composed of dead parts in 60—80%, is particularly conspicuous. Also at the peat-bog and on the sea terrace, large proportion of the individuals had dead

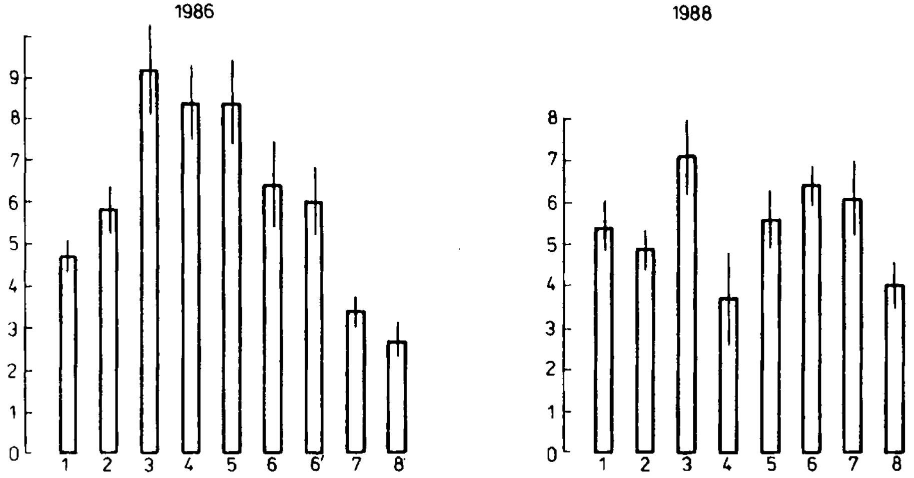

Fig. 1. Average age of individuals in *S. oppositifolia* populations of Spitsbergen tundra: 1 — bottom moraine, 2 — ice-moraine ridge, 3 — sea terrace, 4 — residual rocks, 5 — peat-bag, 6 — rock rubble on Fugleberget slope, 7 — stabilized structural grounds, 8 — non-stabilized structural grounds

main roots and the central part of the cushion. The average age of individuals in these populations is 2–4 years shorter than the total age. In the remaining populations the difference between the age of living part and total age was insignificant.

6, 7 or 8 years old individuals dominate in majority of the populations studied (Fig. 2). The specimens preserving living sprouts for the longest time come from the sea terrace (12 years) and from the stabilized structural grounds (13 years). The shapes of age pyramids show that specimens start dying off at the moraines in the age of six years at the stabilized structural grounds — seven,

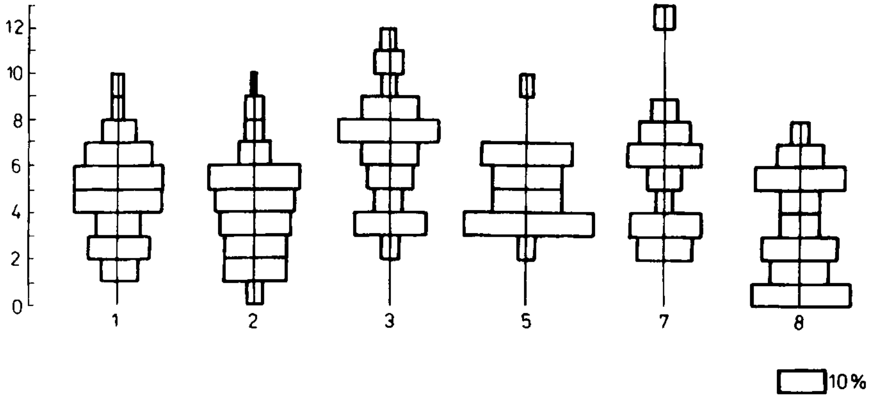

Fig. 2. Age structure of the *S. oppositifolia* populations estimated basing on the age of living parts of individuals. Numbers of populations as in Fig. 1

and at the sea terrace in the age of eight. The lack of one and two years old individuals in these populations evidence for the lack of an effective generative reproduction.

Individuals differ from each other in terms of the rate of ontogenetic development. In most of the populations studied the individuals remain in the juvenile phase until they are three years old (Tab. II). The juvenile phase lasts only until the second year at the ground moraine and until fourth year at the ice-moraine belt and on the active structural grounds. The length of the virginal phase differs also on the residual rocks, in the peat bog and at the mountain slope. Some of the individuals remain in this phase of development until they are 12—14 years old, and on the active structural grounds or at the ice moraine belt up to 8—10 year of age. The virgin phase is the shortest on the ground moraine and on active structural grounds (up to the 6—10 year of life). The flowering starts when individuals are four years old. This phase lasts sometimes till the end of life of a idividual. The oldest individuals, found on the residual rocks and at the sea terrace (22 years old) were in generative phase. Individuals enter their senile phase after the generative phase (around the age of 7) or omitting this phase (4—5 years old). They remain in this phase till 12—13 year of life. Not all specimens do ever reach the senile phase. In some populations (on the sea terrace, on the stabilized structural grounds, on the peat bog and on the ground moraine) there are no individuals in this phase. In the remaining populations the senile phase is reached by a limited percentage of individuals.

Table II

Total age ranges (in years) of *S. oppositifolia* individuals in successive ontogenetic development phases. Numbers of populations as in Fig. 1

No. of populations	1	2	3	4	5	6	7	8
Development phase								
juvenile	1—2	1—4	—	1—3	—	1—3	1—3	1—4
virginal	2—6	4—10	—	3—14	4—12	3—13	3—8	4—7
generative	3—10	3—15	4—22	4—18	4—14	3—13	3—9	4—8
senile	—	—	—	4—11	—	5—13	—	5—7

Two paths of the ontogenetic development of a individual may be identified. In the first case the virgin phase is reached by individuals three or four years old and lasts only 1 year. When these individuals are four of five they pass to generative phase that lasts till the end of their life or till the moment they reach the senile phase. We have compared the age distribution in the age categories of not flowering (in virginal and senile phase) and flowering individuals in those populations where flowering individual accounted for less than 70% of the total. The age range is the same for two groups in case of the population from the mountain side — flowering and non-flowering individuals are represented equally among the oldest individuals (Fig. 3). However the age distribution is

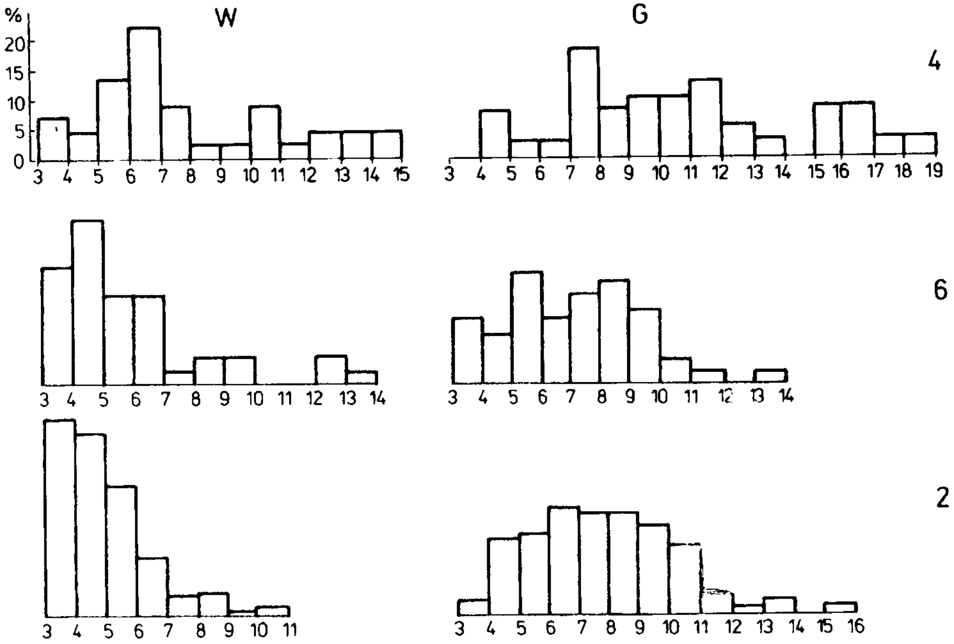

Fig. 3. Age distribution of flowering individuals (G) and mature non-fecund ones (W) in *S. oppositifolia* populations. Numbers of populations as in Fig. 1

different in the analysed groups. Among the flowering individuals, most of them are 5 – 9 years old, and among the non-flowering ones — majority is 3 or 4 years old. The distribution among age categories is similar in the groups of individuals originating from the residual rocks. The majority of flowering individuals are 7 – 11 years old and among the non-flowering ones most of them are 5 or 6 years old. The span of age is also different in these groups. The span is 4 years longer within the flowering group. Similar difference in the age span can be noticed in case of the populations settled on the side morain. The differences between the average age of individuals in the generative and virgin phase is statistically important, even if the span of age is similar for mature and flowering and non-flowering individuals.

Growth and branching of shoots. *Saxifraga oppositifolia* populations are statistically different in terms of the average length of segments of the yearly growth of stems. The growth of shoots within one vegetation season is the smallest on the see terrace (10 mm in average) and the biggest on the ground moraine (30 – 40 mm) (Fig. 4). Almost in all populations, the average size of the early growth is similar in successive vegetation seasons (Fig. 5). Only in case of the populations from the mountain side, the yearly growth segments were significantly longer in first few years of life of an individual (Fig. 5). In all the researched populations the length of yearly growth is positively correlated to the age of an individual.

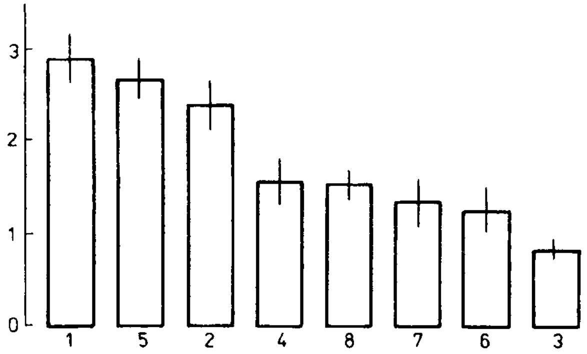

Fig. 4. Average and standard error for the length of yearly growth of long shoots in *S. oppositifolia* populations. Numbers of populations as in Fig. 1

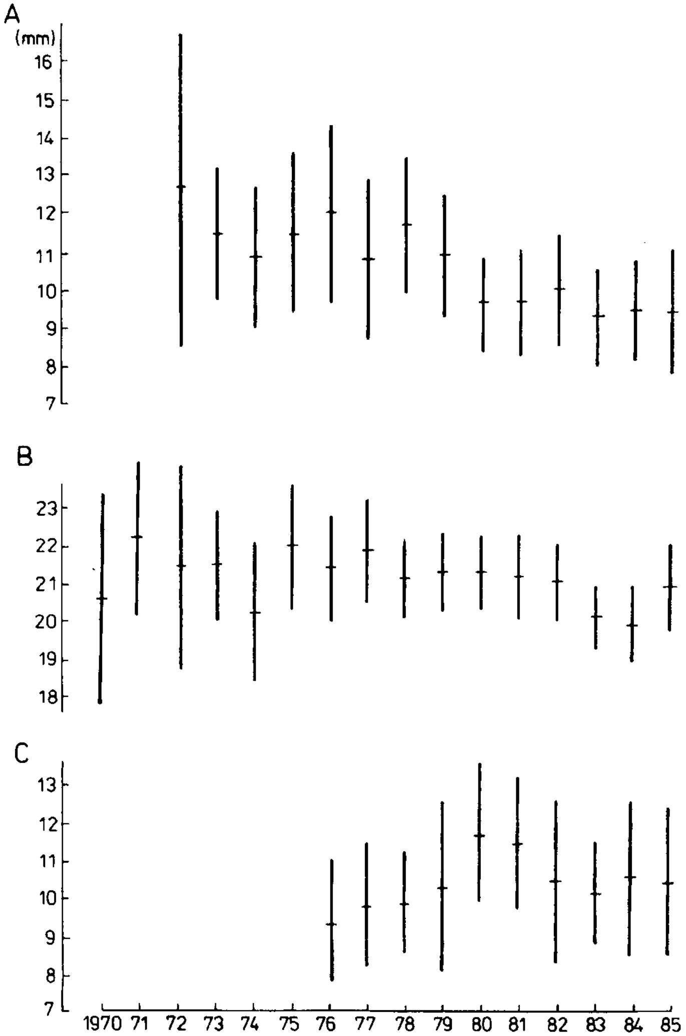

Fig. 5. Average and confidence limits for the length of yearly growth of long shoots in *S. oppositifolia* populations from residual rocks (A), peat bog (B) and sea terrace (C)

The differences in the length of yearly growth of individuals in different developmental phases are not statistically important for most of the researched populations. Only the groups of individuals being in the juvenile phase showed a noticeably smaller growth than the individuals being in the generative phase.

The branching of the main shoot begins after the juvenile phase. The first, unshortened branches of the main shoot appear already in the second year of life of an individual, at the last year's segment of the main shoot. The older is an individual, the higher is the number of branches. This continues till the fourth or fifth year. Afterwards, the oldest branches gradually die off and the total number diminishes. After two years every branch is able to generate the branches of the second and third order. The maximum number of branches remains at the three-four years old segments. The individuals from the residual rocks had the most branched sprouts of all the researched populations (on average 4 branches at every 5 years old segment of each shoot) and those living

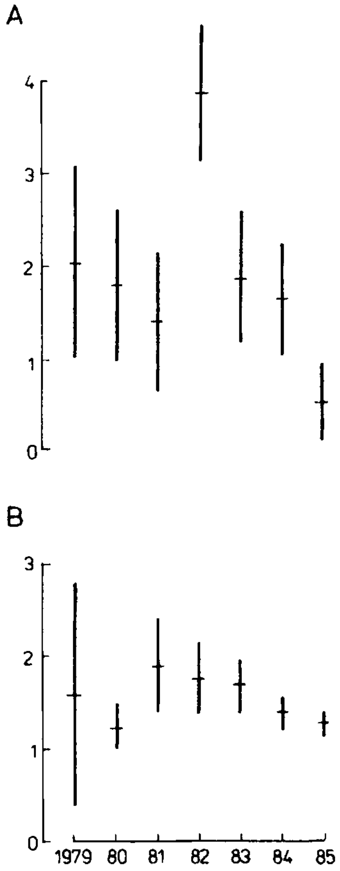

Fig. 6. Average and confidence limits for the number of I-order branchings falling on one segment of yearly growth on long shoots of *S. oppositifolia* populations on residual rocks (A) and mountain slope (B)

on the mountain side had the smallest number of branches (2 branches per each segment 5 or 6 years old (Fig. 6).

The form of individual growth. Not all individuals of *S. oppositifolia* are of a cushion form. Some of them have long creeping shoots. There are also individuals of intermediate morphological form, between cushion and creeping. The quotient of biomass and the length of the longest shoot have been accepted as a measure of the individual compactness. Those individuals for which this ratio was more than 0.5 were said to be of the cushion form. Many shoots with numerous branches of I, II and III order grow out from the main root. Individuals having the biomass to the sprout length ratio smaller than 0.1 were said to be creeping ones. In this case 1 or 2 long shoot with only a few branches of I and II order grow out of the main root. The populations studied differed in the share of these growth forms. On the mountain side the majority of individuals had the creeping form. In this population the cushion form did not exist, but among the individuals from the sea terrace population this form was the most common and the creeping form was not represented at all. In the remaining populations individuals in the intermediate form accounted for the biggest percentage of the total population. Creeping specimens were relatively numerous on the rocks and almost were absent on the peat bog and on the ice moraine belt.

Density and distribution of individuals. In the Hornsund region the density of the *Saxifraga oppositifolia* populations is highly diversified. The highest average density was observed in the population from the sea terrace area, while on the ground moraine Hansbreen the density was the smallest (2 individuals per 50 m^2, Fig. 7). The density did not change significantly in none of the populations within two years. In 1988, in the majority of the populations the density was a few per cent lower than in 1986 (Fig. 7).

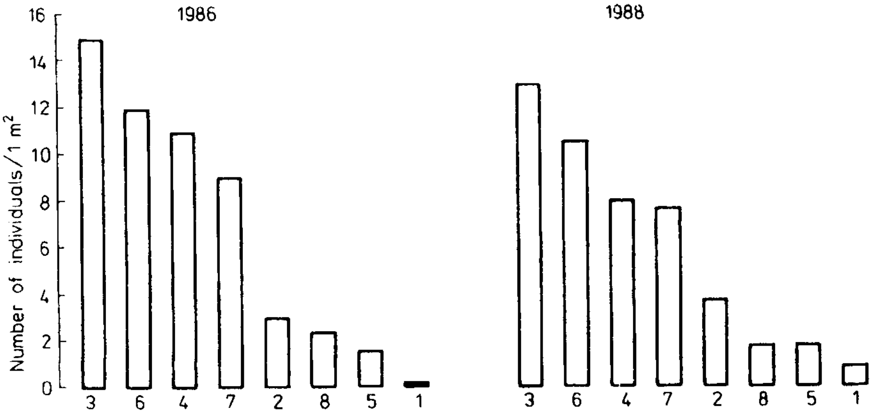

Fig. 7. Densities of *S. oppositifolia* populations in different habitats. Numbers of populations as in Fig. 1

Populations differed also in terms of distribution of individuals. The number of individuals per 0.25 m² field ranged from 1 to 10. The number of individuals was the highest at the sea terrace and the smallest on the ice moraine belt and on peat bog (Tab. III). Value of the dispersion quotient and the standard error for the 0.25 m² fields indicates, that individuals were distributed randomly on the ice moraine belt and on the residual rocks, and in the remaining populations their distribution was patchy. The frequency of individuals in the 0.25 m² fields was the highest on the sea terrace, and the lowest on the active structural grounds and on the ground moraine (Tab. III).

Table III

Maximal number of mature individuals (excluding seedlings and juvenile specimens), frequency and dispersion coefficient (d) with standard error (BS) in *S. oppositifolia* populations in different habitats. Numbers of populations as in Fig. 1. Frames denote the population with random distribution

Populations	2	3	4	5	6	7	8
Number of individuals per 0.25 m²	4	10	6	4	7	9	7
Frequency [%]	60	97	83	35	69	62	28
d	1.01	1.10	1.13	1.45	1.71	2.70	3.00
BS	0.28	0.28	0.28	0.28	0.28	0.28	0.28

In the populations of patchy distribution of individuals these patches were of various size. Populations differed in terms of the average diameter of patches (Tab. IV). In some communities patches are limited by the relief of the area. On the Hansbreen ice moraine belt the patches are elongated paralelly to the moraine edge and their shape is determined by a rock debris that is not occupied by any flowering plants. On the structural grounds the patches occurred on the fine grained material and they do not pass the borders of rock debris rings. In central parts of these rings most of the individuals grew along ground crevasses and at the inner circuit of the rings. On the stabilized grounds the individuals formed a dense collar along the rings. The smallest distance between neighbouring individuals was 5–10 cm in most of the populations and the longest distance equaled 15–30 cm. In the randomly distributed populations the individuals grow in similar distances (Tab. IV).

Table IV

Distribution of *S. oppositifolia* individuals on the surfaces studied in different habitats. Numbers of populations as in Fig. 1. Asterisk indicates the populations of random distribution

Populations	1	2	3	4	5	6	7	8
Patches diameter (m)	12–24	*	*	*	2–3	10	4–5	1–2
Distance between patches (m)	15–30	*	*	*	3–2	no data	1–3	1–4
Average distance between neighbouring individuals (m)	2	0.10	0.10	0.10	0.05	0.10	0.05	0.10
Maximal distance between neighbouring individuals (m)	8	0.30	0.20	0.30	0.15	0.30	0.20	0.20

Distribution of *S. oppositifolia* on the ground moraine is different than in other populations. Patches of individuals are significantly larger than in other populations and the distances between individuals ranged from 2 to 8 m (Tab. III).

The ecological density per 1 m^2 (the congestion quotient) of the populations on the ground moraine, on the peat bog and on both structural grounds was much higher than the density whereas in the remaining populations did not differ from the density value.

Size structure. The biggest individuals were found on the moraine and on the peat bog (Fig. 8). On the moraines, especially in the places positively influencing the growth of long shoots in the neighbourhood of big stones, cushions reached conspicuous size, the biggest ones produced sprouts 60 cm long. Individuals with the shortes shoots were present on the sea terrace and on the active structural grounds.

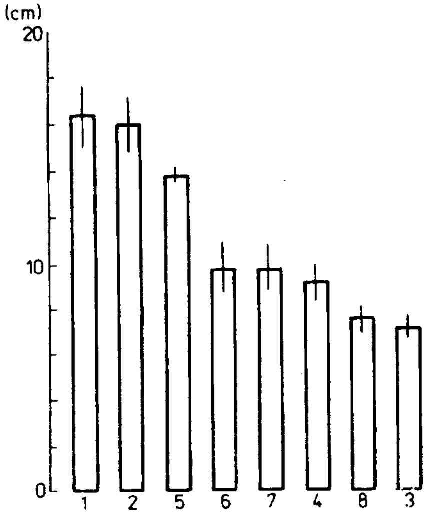

Fig. 8. Average length of long shoots with standard error in *S. oppositifolia* populations in different habitats. Numbers of populations as in Fig. 1

The average length of the longest sprout in majority of the populations differed significantly from those of the others. We did not detect statistically important differences between the average value of the longest shoots in none of the populations from the active grounds, from the mountain side and both moraines, the sea terrace and both moraines and between both moraines.

The described populations differed in terms of the share of individuals of different size (Fig. 9). On the side moraine individuals with longer shoots (15 – 30 cm) prevailed, on the peat bog shorter shoots (10 – 25 cm) dominated and on the residual rocks or on the sea terrace the shortest shoots (5 – 10 and 5 – 15 cm) prevailed.

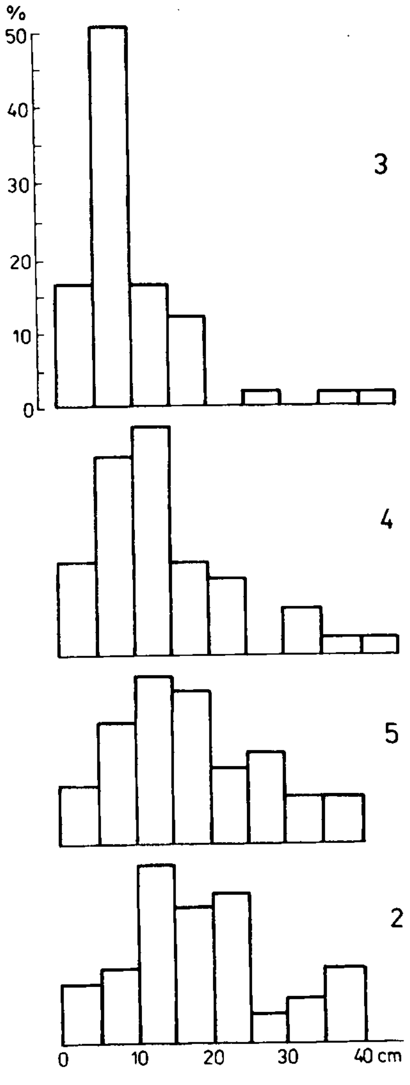

Fig. 9. Length distribution of long shoots in *S. oppositifolia* populations in different habitats. Numbers of populations as in Fig. 1

Biomass. Almost all of these researched populations differed significantly from each other in terms of the average biomass of an individual. The biggest average biomass was characteristic for the sea terrace population and the smallest biomass — for individuals growing on the mountain side (Fig. 10). The average biomass of a sea terrace individual is almost 30 times higher than the biomass of an average individual from the mountain side. The difference between the average biomass of the individuals from the moraine and from the ice moraine belt and the peat bog is not important statistically. Individuals with the highest

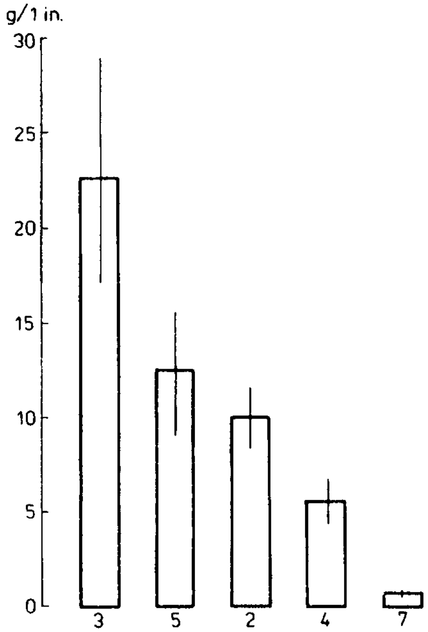

Fig. 10. Average biomass with standard error in *S. oppositifolia* populations in different habitats. Numbers of populations as in Fig. 1

biomass were present on the sea terrace (107.5 g), in the populations from the sea moraine, from the peat bog and the residual rocks the biggest individuals weighed 40 – 50 g and at the mountain side only 6 g.

In four out of five researched populations the distribution of the biomass deviates from the normal one (Fig. 11). In the populations from the sea terrace and the residual rocks there was the highest share of individuals, whose biomass was several times higher than the average. In populations from the mountain side and the peat bog the share of individuals in different classes of biomass was similar. Only in the population from the ice moraine belt the distribution was normal.

The structure of developmental phases. The researched populations differed mainly in terms of the share of individuals in the generative phase. Four types of the development structure can be identified in the populations studied.

(1) Individuals in the generative phase accounted for more than 70%, seedlings and juvenile individuals were not present or their share was limited. This type of the structure is characteristic of populations from the sea terrace and the ground moraine (Fig. 12).

(2) The majority of individuals were virginal. As in the first case, the share of juvenile and virginal specimens is very limited or none. This is characteristic of the peat bog and the stabilized structural grounds populations.

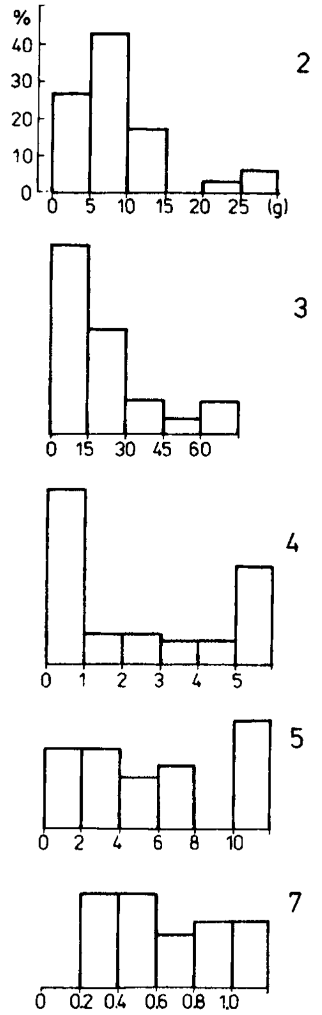

Fig. 11. Distribution of individual biomass in *S. oppositifolia* populations. Numbers of populations as in Fig. 1

(3) There was a similar share of virgin and juvenile individuals in a population. Between 1/10 and 1/4 of individuals were in the senile phase. This type of the structure can be identified on the residual rocks, mountain side and on the ice moraine belt.

(4) There was the highest share of individuals in virginal or juvenile phase. This structure of developmental phases was characteristic of the population from the structural grounds. The share of seedlings in this population was the most important from all the researched populations.

Within two years the shares of individuals in different developmental phases have changed in 5 out of 8 researched populations. The share of generative

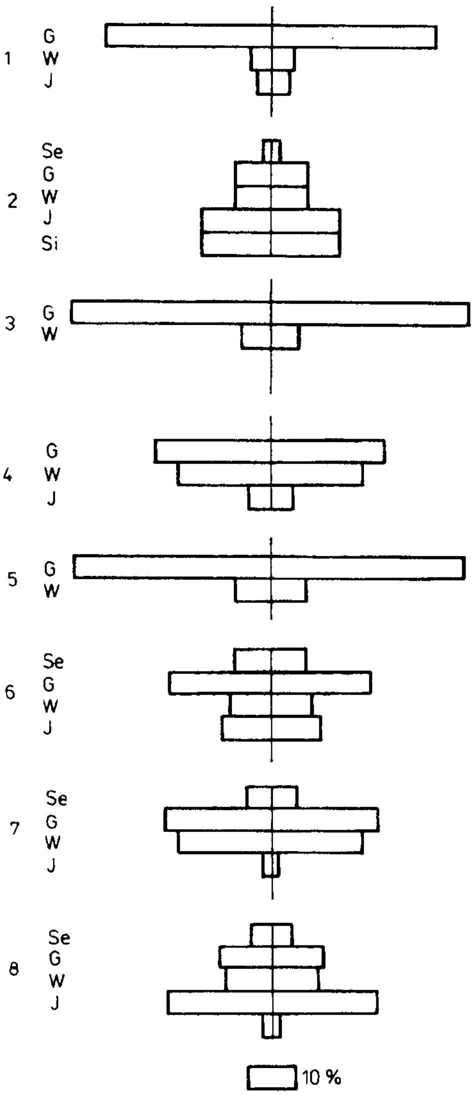

Fig. 12. Development phases in *S. oppositifolia* populations. Numbers of populations as in Fig. 1 Si — seedling phase, J — juvenile phase, W — virginal phase, G — generative phase, Se — senile phase

individuals in the populations of the peat bog and the stabilized structural grounds in 1988 increased noticeably in comparison to the 1986. On the mountain side and on the ice moraine belt the share of seedlings and the juvenile individuals increased in 1988 as compared to 1986. In case of the rocks, no senile individuals were found in 1988, and in 1986 they accounted for 24%. The average length of shoots in flowering individuals and in virginal individuals in some populations was significantly different (for instance on residual rocks or on the side moraine), whereas in other populations it was not.

The distribution of the length of shoots in flowering individuals and in non-flowering ones that have crossed their juvenile phase was different in particular populations (Fig. 13). On the mountain side the range of the length of sprouts in both analyzed groups is the same and small individuals are the majority (5 – 10 cm). On the ice moraine belt, shoots of the biggest flowering individuals reached 60 cm and those of the non-flowering ones — 10 – 20 cm. The distribution of the shoot length in the flowering and non-flowering individuals growing on the residual rocks is different: the longest shoots of the flowering individuals reached 55 cm, whereas shoots of the non-flowering ones — 40 cm. Among the flowering individuals, individuals measuring 5 – 15 cm are the most common and among mature but not-flowering ones, those of the length 3 – 10 cm.

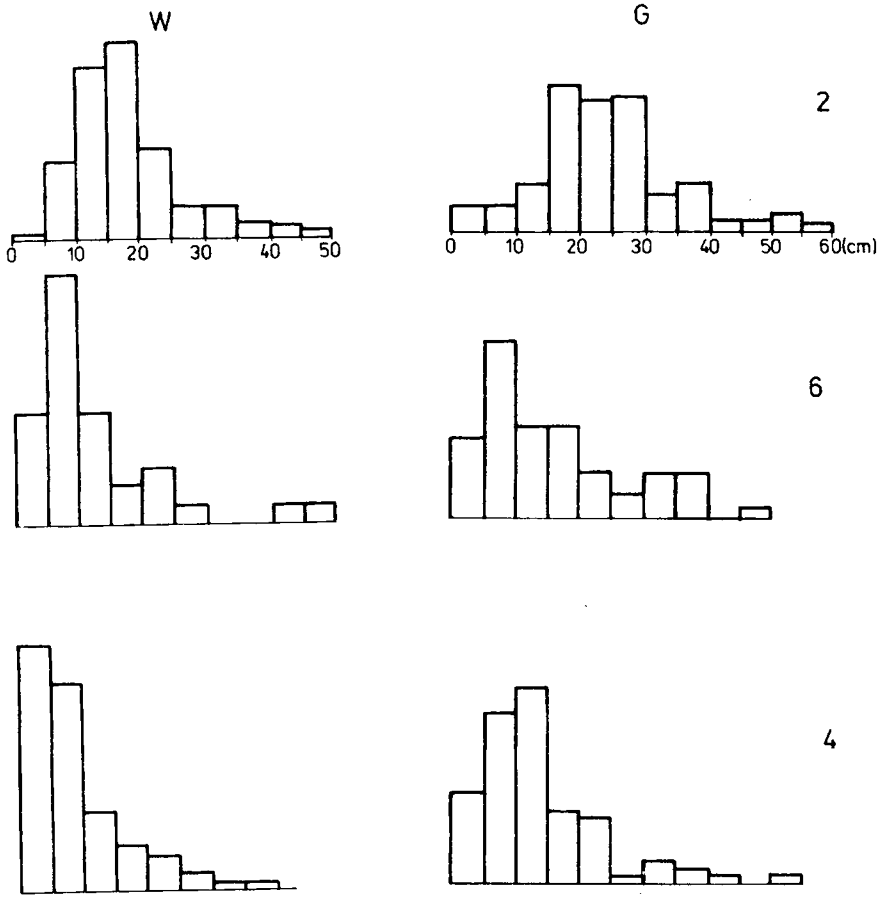

Fig. 13. Length distribution of long shoots of virginal individuals (W) and generative individuals (G) in *S. oppositifolia* populations in different habitats. Numbers of populations as in Fig. 1

Production of flowers and fruits. The average number of flowers per individual in generative phase in *Saxifraga oppositifolia* is highly differentiated. The highest amount of flowers (36 on average) was produced by individuals on the sea terrace. Slightly lower was the flower production in the individuals from the ground moraine and the ice moraine belt. The lowest number of flowers was produced by individuals on the active structural grounds. The difference in flower production between the two seasons was not significant.

The populations differed in the average number of fruits per individual in generative phase. Individuals living on the non-stabilized grounds and on the sea terrace were most fecund (Tab. V). Fecundity in most of the populations was different in different seasons.

Table V

Flowering efficiency in *S. oppositifolia* populations. Numbers of populations as in Fig. 1. Asterisk denotes lack of data

Populations	1	2	3	4	5	6	7	8
Average number of flowers from 1988 per 1 generative individual	30.28	19.55	23.75	7.31	20.71	9.09	4.50	3.94
Average number of fruits from 1987 per 1 generative individual	2.84	1.68	2.25	4.44	1.38	*	1.43	0.75
Flowering efficiency (%)	9.4	8.6	9.5	60.7	6.7	*	31.8	19.0
Average number of flowers from 1986 per 1 generative individual	21.33	18.19	36.58	9.06	8.84	13.03	3.00	2.00
Average number of fruits from 1985 per 1 generative individual	*	2.00	3.30	2.52	0.32	1.19	0	*
Flowering efficiency (%)	*	11.0	9.0	27.9	3.7	9.2	0	*

Production of fruits per individual in generative phase was small as compared to the production of flowers. The ratio of the number of flowers to the number of the last year's fruits was about 10%. Only in populations from the residual rocks and the stabilized structural grounds the flowering efficiency was higher (Tab. V). The ratio of average number of flowers per one generative individual to the number of last year's fruits was not significantly different in the two researched seasons.

Populations differed in terms of flower production per 1 m^2. The sea terrace population, where on average there are 460 flowers per squ.m. was especially conspicuous (Fig. 14). The population situated on the active structural grounds produced the lowest amount of flowers per area unit. In most of the researched populations the amount of flowers per squ.m differed in the two researched seasons (Fig. 14).

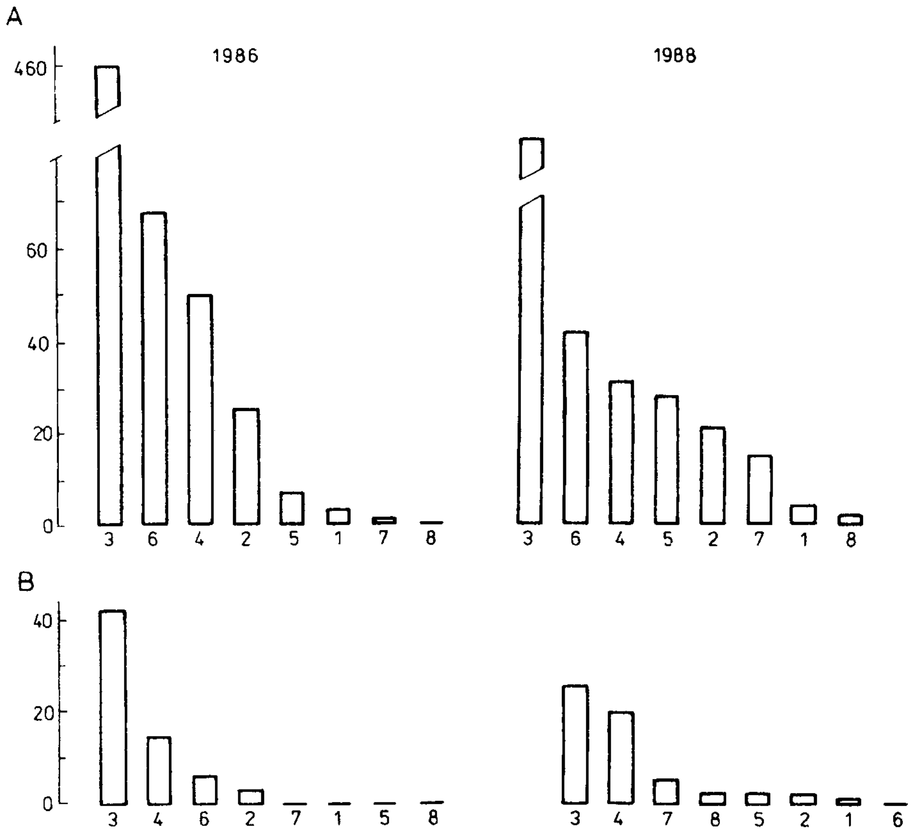

Fig. 14. Production of flowers (A) and fruits (B) per area unit in *S. oppositifolia* populations in different habitats. Numbers of populations as in Fig. 1

As far as the fruit production per squ.m is concerned, the differences between the researched populations were lower than in the case of lower production. The sea terrace population produced the highest amount of fruits (34 per squ.m) and the smallest number was produced by the population situated on the ground moraine. The differences between two seasons in flower production were not big (Fig. 14).

Recruitment of seedlings. The active generative reproduction did not take place in all the researched populations. Only in four out of eight populations studied seedlings appeared. Density of the seedlings was limited in the above mentioned populations; it was lower than the density of individuals in generative phase. In most cases there were on average 1—8 seedlings per 10 flowering individuals. Only in the case of the ice moraine population in 1988 there were twice as many seedlings as generative individuals.

Discussion

In the Arctic semi-desert zone most of the habitats are stressogenic, settled mostly by long living plants with the reproduction effectiveness at a low level (Grime 1977). Longevity of *Saxifraga oppositifolia* individuals in Spitsbergen in the Hornsund region is comparable to the longevity of other species of perennial plants occurring in tundra, i.e. *Lycopodium annotinum* and *Oxyria digyna* (Callaghan and Emanuelson 1985).

The calendar age is difficult to be estimated in case of plants, that keep on growing where their oldest parts die off and decay; then the normal procedure is to take into consideration the age of the living parts of a plant. The age of the living part may remain unchanged for many years in case of an individual, that is when these two processes: dying and growing are balanced. The method we used to estimate age of *S. oppositifolia* in this work, may be employed only in those stands, where the plants do not risk being crushed by animals. Reindeers do not occur in the Hornsund region and the geese feeding does not cause many disturbances in the growth of the *S. oppositifolia* shoots.

Longevity of Arctic plants is their adaptation to the short vegetation season. As soon as the snow cover melts, all plants begin intensive assimilation. The start of the vital functions takes place at the cost of the matter accumulated in the former season. Chapin et al. (1980) showed that the accumulation occurs in the oldest parts of plants. In the springtime the reserves of nitrogen, phosphorus and other nutrients are recirculated to the growing parts of plants. This possibility to recover nutrients from the old parts of plants allows to cross through the expansion obstacles, such as bands of completely barren rock debris in the areas with limited or hardly accessible resources.

Differences in the longevity of *S. oppositifolia* in the research region indicates to:

(1) the differences in the accessibility of nutrients and the richness of habitats — the less fertile the habitats are, the more years do individuals live,

(2) the frequency of disturbances in a habitat, i.e. rock debris sliding down the mountain side in time of de-freezing may rip the shoots and this in turn is the reason for their constant rejuvenation, also some cyclical movements and soil translocations in the structural grounds cause the shoots, sticking out of the ground, to resume their growth as 2—3 years old individuals,

(3) the desintegration age (vegetative reproduction).

The present research does not enable to determine precisely to which extent the above mentioned factors influence the age of individuals in a population. Low average age of *S. oppositifolia* individuals on the moraine, residual rocks and on active structural grounds might be a proof that these populations are in the settlement phase. Svoboda and Henry (1987) draw our attention to the fact that in the Arctic semi-desert zone there are many habitats, where the vegetation is still in the initial phase of succession. Periodical disturbances destroy the plants and the communities are never able to reach the structure typical of habitats of a certain fertility.

In the tundra zone the limited activity of soil microorganisms allows to preserve dead parts of plants and dead individuals in not disturbed habitats. Research held in Spitsbergen by Dziadowiec (1992) showed that 17% of the shoots and leaves necromass of *S. oppositifolia* decays in the first year and 1–3% in following years. Thanks to the long preserved dead parts of individuals it is possible to estimate more exactly the total age of an individual — calculated from the moment of appearance to the moment of death.

Age classes distribution may evidence for the dynamics of the population. Lack of gaps in the age pyramids of the described *Saxifraga oppositifolia* populations evidence for the systematic recruitment of new individuals every year. In the populations from the sea terrace and from the peat bog the youngest individuals (1 and 2 years old) did not occur. Similar phenomenon was noticed in populations of dwarf-shrubs from the families of Ericaceae and Salicaceae in tundra (Callaghan and Emanuelson 1985). This does not mean the extinction of the population, but the recruitment of the "old-born" individuals, that appear due to the disintegration of mature individuals. Slow decrease of the number of individuals older than 5 year in the *S. oppositifolia* populations proves that the disintegration of individuals starts at this age. Some of the individuals when five years old reach the balance between dying off and sprouting — as new shoot grow, the old ones die off and the age of the individual remains constant, in spite of the time that passes. At the same time the lack of dead individuals in the populations proves that the decreasing number of old individuals is the consequence of their disintegration rather, than their death. Similar age structure has been described as the result of the vegetative reproduction in a population of *Alchemilla glomerans* in Western Greenland (Lewilet et al. 1972 after Callaghan and Emanuelson 1985). The lack of individuals in the youngest age classes might be caused by an inefficient generative reproduction. It is easy to imagine that in the thick and dense moss in the peat bog seedlings do not develop and in the sea terrace community the lack of seedlings may be due to the allelopathy. The research of Fabiszewski (1975) proved that substances produced by bushy lichens, common in tundra can limit the germination of seeds of herbaceous plants.

It can be observed that the development of plants slows down in habitats poor in nutrients, where the individuals have low vitality (Rabotnow 1985). In the case of *S. oppositifolia* the length of phases in poor habitats was not extended as compared to the rich ones. In all of the researched habitats the youngest flowering individuals were at least 3–4 years old. The length of the virginal, generative and senile phases depended to the greatest extent on the rate of the disintegration of mature individuals and not on their condition. However the presence of individuals in the senile phase in the *S. oppositifolia* population may evidence for the tendency to the decreased vitality caused by unfavourable habitat conditions. In extreme climatic conditions many plant species reach their particular developmental phases in a wide range of age (Zaugolonova et al. 1988), which occurs also in the described *S. oppositifolia* populations.

Generally it is believed that in Arctic conditions the growth rate of plants depends on the length of vegetation season and thermic conditions in summer. Very limited differences in the length of *S. oppositifolia* yearly growth of long shoots in ten different vegetation seasons in the Hornsund region, where the weather conditions are far from being constant, indicate however that not the weather conditions determine this growth rate. Observations of the development of perennial plants held by the author within two vegetation seasons indicate that the growth of shoots in length occurs mainly in July after the snow has melted, when the moisture in the ground is sufficient. In August in spite of favourable thermic conditions, the shoots do not grow in length anymore. Similar phenomenon was observed by Chapin et al. (1980). According to them, summer precipitation do not limit the growth of plants; they have also observed, that in the second part of the vegetation season the increase of biomass slows down, whereas the reserves are laid down in order to enable the start up of assimilation and flower production in the next vegetation season.

Life forms of *Saxifraga oppositifolia* are facultatively described as cushion-like (Ronning 1964). In Hegi's Flora two forms of *S. oppositifolia* are described — the cushion form (f. pluvianta) in Alps, typical of sunny locations and the creeping form (f. reptans), typical of humid and shadow locations. In the Arctic the quantity of the effective photosynthetic radiation in the vegetation season in majority of habitats is not a limiting factor (Shaver et al. 1986), therefore other causes of morphological differentiation in *S. oppositifolia* must be searched for. Many studies on the variability of living forms of plants conclude that in poor habitats the most chances to survive has a "guerilla" form, where older individuals support the longest sprouts searching for new, favourable habitats to root themselves (Haper 1986). Other authors claim that the transition from the cushion form to a creeping form in far Arctic is caused by the micro-climatic conditions: shoots that lay on the ground in places where strong and cold winds are common, have more chances for the positive balance of the energy (on the surface cooling is much weaker) (Aleksandrova 1983). Such arguments would indicate that cushion forms should be met in rich locations (where plants grow fast), and in these habitats that are not endangered by winds and the lack of the snow cover. Since in most of the researched populations both creeping and cushion forms occurred, the thesis that only the habitat conditions determine the growth of the individuals studied is difficult to be maintained. This concerns especially poor habitats, i.e. residual rocks with barren initial soil (Melke et al. 1989), where it is difficult to suppose high heterogeneity. Probably the morphological diversity comes out from a genetic source. The important share of vegetative reproduction (in some populations this is the only reproduction form) is a reason for the limited genetic diversity, however in every population this diversity remains at a certain level.

There is no doubt that in more fertile habitats *S. oppositifolia* produces more side branches and that the cushion form is much more common than the creeping form. The present research supported the hypothesis that in less favourable habitat conditions the development of individuals is slower, but they did not support the assumption, that in the habitat extremely poor in nutrients plants attin a very gray age.

Plant population structure is modified by the intensity of stress (environmental factors, that limit the growth, development and reproduction of an individual) as well as of disturbances (factors that destroy plants or their parts) (Grime 1979). Spitsbergen habitats can be characterized by a high stress level and disturbances' intensity, but particular habitats differ in these terms. Habitats overgrown by the dense plant cover are different from those where the vegetation is never dense and individuals of different species never come into contact, i.e. the moraines mountain sides or solitary rocks.

The richness of a population measured by the density of individuals per area unit demonstrates both the capacity of a habitat and the effectiveness of the reproduction as well as the probability of the survival of an individual in its successive developmental phases. In undisturbed habitats the density of individuals reflects the density of ecological niches. In dense, multispecies community on the sea terrace, *S. oppositifolia* has the highest density of all eight studied sites in the Hornsund region, suggesting that the competition with other species in the conditions of Spitsbergen tundra does not limit the population density of the species under study.

Morphological features of *S. oppositifolia* cause that the individuals react in different ways to the habitat disturbances. Cooling winds coming from the glacier, solifluction in spring and in summer and sliding of the snow cover down the Fugleberget slope do not destroy the individuals but limit only the number of shoots branches and break them down. As a result some individuals never reach the size typical of this species in other habitats. Relatively high density of the *S. oppositifolia* population on the mountain side is due to the vegetative reproduction, effectuated by the disintegration of individuals. Low population density on the Hansbreen moraine may be due to the insufficient supply of seeds. These habitats are supplied with seeds originating from a far transport, whereas the seeds produced on the moraine are blown by winds coming from the glacier towards the sea (Svoboda and Henry 1987). The study by Grulke and Bliss (1985) on seven different *Saxifraga* species in Canadian Arctic revealed that the seed germination power of these species is very low and equals not more that 1%. Vegetative and generative reproduction on the moraines is not very effective. Probably the solifluction, which is pretty intensive on the side moraine destroys young plants. For similar reasons on the non-stabilized structural grounds the number of individuals is low. Within one year the surface of the ground in Revdalen rises nearly 5 cm and then falls down back to the original level (Migała 1989). Year after year, new portions of fine grained material from the interior of the stone rings come up and flood *S. oppositifolia* individuals. On structural grounds in the narrow valley snow cover lasts for at least two weeks more than in other locations (Migała 1989). Many authors indicate to the influence of the snow cover on vegetation (Aleksandrowa 1983). Vegetation season shortened by 2 weeks on average, causes the limitation of growth of individuals and the survival of seedlings. Both phenomena imply low density of the *S. oppositifolia* population on the structural grounds.

Individual size, the biomass and the size of flower production may be used as a measure of vitality of a population. These characters are modified mainly by the fertility of the habitat and by interactions between species. Characters of the population of *S. oppositifolia* linked with the vitality are realized in different way than those hitherto discussed. The biggest and the most flowering individuals occurred on the moraines. Richness and humidity of the ground favoured their intensive growth. It is worth mentioning that other species of vascular plants in this environment (on the moraines) are small and have low production of flowers. Therefore one can suggest that among all plants occurring on Spitsbergen *Saxifraga oppositifolia* is a species withstanding the best the unfavourable low temperatures in the neighbourhood of the glacier and the solifluction. Many authors indicate that in the Arctic local micro-climatic and water conditions influence the vegetation equally as soil fertility (Klimowicz and Uziak 1987). The biggest *S. oppositifolia* individuals on the moraines, grow in the neighbourhood of big stones. According to Aleksandrova (1983) in summer in the Arctic stones usually absorb more heat than fine grain material in their environment. Therefore in the neighbourhood of such stones the most favourable conditions do occur positively influencing luxuriant growth of *Saxifraga oppositifolia* individuals. The development of plants is greatly influenced by the presence of other plant species. Among plants of a low growth rate it can be observed that along with the increasing severity of environmental conditions and the decreasing number of competitors, the development of a population is more luxuriant (Svoboda and Henry 1987). This may be an explanation for the very large size of the oldest *S. oppositifolia* individuals on the moraines. However such individuals are most numerous in communities of a dense plant cover — on the sea terrace and on the peat bog among other plant species, where *S. oppositifolia* reach the maximum of its biological possibilities. In extreme climatic conditions the development of plants can be supported by some positive interaction between individuals of different species such as wind and cool screening, protection against the eolic erosion or drainage. The more dense is the plant cover, the more important are these interactions for the individual development (Callaghan and Emanuelson 1985). In the far Arctic conditions dense plant cover develops in those locations that are intensively fed with organic matter of sea origin, that is on the peat bog absorbing material coming from colonies of auks and on the sea terrace on old storm ridges with decaying layers of algae (Klekowski and Opaliński 1986).

Positive interactions between plants in the Arctic semi-desert zone are one of the reasons of the patchy distribution of individuals (Callaghan and Emanuelson 1985). In most of the populations of *S. oppositifolia* the minimum distance between individuals was 5 cm, which may be caused byu insufficient nutrient resources in the soil. In populations growing in extreme conditions it is common that individuals are small poorly developed (i.e. with smaller number of branches) and their growth rate is slower than in communities living in optimal conditions. Unfavourable life conditions tend to level the structure of the population (Andrzejewski and Falińska 1986). Population of *S. oppositifolia* from the Fugleberget mountain side has the most leveled structure. Individuals in this population are very small and they produce few flowers. In this habitat the development of plants is limited mainy by the lack of water. After the snow melting (since mid July) practically all water flood down the hill and the initial soil retains only limited part of rainfalls. Moreover the fertility of initial soils on the sides of the mountains that are not inhabited by auks is very limited (Melke et al. 1989). It is believed that the main reason for the different size of the plants within one population is the heterogeneity of the habitat (Andrzejewski and Falińska 1986). The highest biomass and size diversity of individuals existed in case of the most luxuriant populations — on the sea terrace, despite the little diversified micro-relief there in comparison with other habitats. Sea terraces in the region of Hornsund are free of ice for the longest period of time and these habitats are the least disturbed ones. Fertile brown soil occurs there (Melke et al. 1989).

A chance to survive is for plants a direct function of their biomass (Falińska 1990). A given energy input is required for the reproduction process. Only those individuals that have managed to reach a given biomass and size start the reproduction process. It is important to point out, that only in few populations of *S. oppositifolia* flowering individuals are bigger than the mature but sterile ones. This seems to indicate the lack of correlation between the number of flowers and the size of an individual (length of shoots and biomass). It is possible that some individuals of this species never produce flowers, but they participate in a vegetative reproduction, after attaining big size.

Saxifraga oppositifolia prolongs to the perrenials which individual growth is connected with vegetative reproduction (Silova 1988). This species begins late its vegetative reproduction in the period of optimal development of generative phase. After the maximum size is reached in a given habitat conditions, the cushion starts to divide into descendant ones. *S. oppositifolia* reproduces also by rooting of young, single shoots, that have been separated from the cushion.

The functioning of a population depends on the proportion of individuals in different developmental phases. The structure of the developmental phases can be modified by the competition with other species. *S. oppositifolia* populations from the dense plant communities are distinguished by the high proportion of individuals in generative phase and by the lack of seedlings and juvenile individuals. This structure of developmental phases is typical of many perennial plants of the temperate climatic zone, living in communities of heavy competition pressure. The non-complete spectrum of developmental phases indicates to the lack of generative reproduction (Zaugolonova et al. 1988). In the populations described above, vegetative reproduction has been observed, effectuated by the disintegration of old individuals, without significant signs of rejuvenation. This type of reproduction implies low risk of death and is very common in the temperate climatic zone, in phytocoenose of very dense turf of competitions, which makes the survival of seedlings and juvenile individuals impossible (Zaugolonova et al. 1988). Studies on many species of perennial plants and dwarf-shrubs in the Arctic have shown low effectiveness of generative reproduction (Callaghan and Emanuelson 1985). In the communities with dense vegetation the vegetative reproduction is the most common, whereas in the initial communities or in some marginal habitats — generative reproduction is the most common one. However, this is not an absolute rule. It appears that along with the increasing severity of climate and in Arctic habitats unfavourable for plant settling the vegetative and not the generative reproduction plays the major role in renovation of population and also in its settling down (Johnson 1969 after Callaghan and Emanuelson 1985). In the case of *Saxifraga oppositifolia* in Spitsbergen tundra conditions enabling the generative reproduction do not occur in all the localities. Very limited recruitment of seedlings in the population is striking. If a generative individual leaves only one progeny (seedling) per vegetation season, the chance to keep the number of individuals in the population at the same level is very limited.

Low effectiveness of flowering in the majority of the populations of *S. oppositifolia* may be caused by the insufficient number of pollinating insects (Aleksandrova 1983) and by geese feeding. Geese prefer *S. oppositifolia* fruits. Only in the area inaccessible for geese chicks — on the slopes of Fugleberget and on the residual rocks the effectiveness of flowering is high. However, in both above mentioned habitats, the conditions of germination and development of seedlings are unvafourable.

The abundance of a population at a given habitat is determined by the production and the loss rate of individuals. In Arctic conditions the lack of competition with other species favors the stabilization of the population (Svoboda and Henry 1987). The conditions occurring in the researched habitats in the Hornsund region influence population processes in *Saxifraga oppositifolia* in many different ways. Generative reproduction measured by the share of juvenile individuals and seedlings in the populations studied is the most intense in often disturbed habitats covered with poor vegetation: on the ice moraine belt Hansbreen and on the structural grounds. This process, as it has already been mentioned, practically does not exist in the habitats covered with dense vegetation due to allelopathy.

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Streszczenie

Badania prowadzono na Spitsbergenie w rejonie fiordu Hornsund w 1986 i 1988 r. Obiektem badań była *Saxifraga oppositifolia* — bylina o największej amplitudzie ekologicznej w tym rejonie.

W pracy przedstawiono struturę i rozrodczość populacji oraz tempo rozwoju osobnikow *Saxifraga oppositifolia* na ośmiu stanowiskach różniących się wilgotnością i żyznością gleby, sytuacją geomorfologiczną oraz mikroklimatem.

Badane populacje różnią się długowiecznością, długością rocznego przyrostu (Rys. 4), tempem rozwoju ontogenetycznego, a także architekturą osobnika (Rys. 6). Wielkość rocznego przyrostu w poszczególnych populacjach niewiele zmienia się w okresie 10-ciu lat (Rys. 5). Najwolniej przebiega rozwój osobników na nieustabilizowanych gruntach strukturalnych, a najszybciej na morenie dennej (Tab. II).

Maksimum możliwości biologicznych badany gatunek realizuje na terasie morskiej. Rozmiary osobników, ich biomasa, a na niektórych stanowiskach zagęszczenie populacji i współczynnik zatłoczenia są modyfikowane przez żyzność gleby oraz interakcje między gatunkami wchodzącymi w skład zbiorowiska. Niekorzystne warunki siedliskowe na zboczu góry, np. ruchy gruntu, wychładzające wiatry, nie zmniejszają zagęszczenia populacji, lecz ograniczają biomasę i liczbę rozgałęzień pędów. Intensywne ruchy gleby na gruntach strukturalnych ograniczają nie tylko rozmiary osobników i biomasę, ale i wpływają na zagęszczenie populacji.

W większości populacji osobniki rozmieszczone są skupiskowo (Tab. III). Sposób rozmieszczenia związany jest z mikromorfologią siedlisk. W zbiorowiskach inicjalnych obserwuje się *S. oppositifolia* tylko w sąsiedztwie dużych kamieni, które nagrzewają się szybciej i stygną wolniej niż drobnoziarnisty materiał.

Struktura faz rozwojowych jest silnie modyfikowana przez siedlisko. Największym udziałem osobników w fazie generatywnej charakteryzuje się populacja z najżyźniejszego i najmniej zakłóconego siedliska (Rys. 12). Na siedliskach silnie zakłóconych w populacjach jest większy udział siewek i osobników juwenilnych niż na pozostałych siedliskach. Produkcja kwiatów i owoców jest największa na siedlisku najżyźniejszym i najmniej zakłóconym, zaś najmniejsza w siedlisku silnie zakłóconym (Rys. 14). Efektywność kwitnienia w większości populacji nie przekracza 10%. W populacjach niedostępnych dla żerujących gęsi dochodzi do 60% (Tab. V). Na siedliskach, na których jest największa produkcja owoców, nie ma odpowiednich warunków do rozwoju siewek. Rekrutacja siewek zachodzi tylko w czterech z ośmiu badanych populacji, rekrutacja siewek jest największa w populacjach bytujących na siedliskach podlegających zakłóceniom. We wszystkich populacjach *S. oppositifolia* liczebność osobników jest utrzymywana dzięki reprodukcji wegetatywnej.