

## LIFE HISTORY OF *Plantago coronopus* L. AT THE LIMIT OF ITS RANGE

ZOFIA SOTEK

Department of Botany and Nature Conservation, University of Szczecin, ul. Felczaka 3a, 71-412 Szczecin, Poland; e-mail: sotek@univ.szczecin.pl

### Abstract

Sotek Z.: Life history of *Plantago coronopus* L. at the limit of its range. Ekologia (Bratislava), Vol. 26, No. 1, p. 14–29, 2007.

The main aim of the study was to recognise the life history of individuals growing in a marginal population of *Plantago coronopus* L., at the eastern limit of the range of the species (NW Poland). It has been established that the population was mainly composed of perennial plants with a significant contribution of biennial and a small contribution of annual plants. The shorter cycle was characteristic of the individuals growing in the conditions of the lack of competition or strongly limited competition of the co-existing plants. Relationship was found between the length of life of *P. coronopus*, the density of its rosettes and the time of recruitment of new individuals. A correlation was also found between the age of reaching the reproductive phase and the rosettes' size. Irrespectively of the life history all individuals were characterised by a long vegetation period.

Changes in the habitat conditions caused by increased moisture content of the ground and cessation of agricultural use of the majority of the land had little effect on the character of the population but significantly reduced its area.

*Key words:* life cycle, fertility, recruitment of individuals, seedlings mortality, seasonal rhythm

### Introduction

It is known that the life history of individual plants often differs from the pattern characteristic of a given species. Some individuals of the species classified as annuals sometimes realise their cycle over two years, e.g. *Poa annua* (Law, 1981). Among the biennials one can distinguish two groups of species that is “strict biennials” (Kelly, 1985) and “facultative biennials” (Kelly, 1989). The first group comprises the plants which really do flower in the second year of life, irrespective of the conditions of growth (Verkaar, Schenkeveld, 1984; Kelly, 1985), while the second are the plants frequently requiring three or four years to flower, especially under crowded conditions (e.g. Werner, 1975; Harper, 1977; Symonides, 1979; Falińska, 1997). However, in the optimum conditions some individuals belonging to “biennials” can shorten their life cycle to 1.5 year, as for example *Geranium robertianum* (Falińska,

Pirożnikow, 1983), or *Cirsium palustre* (Falińska, 1997). The tendency towards the lifetime shortening in certain conditions is also shown by some perennials, e.g. *Puccinellia distans*, in the process of colonisation of anthropogenic localities (Lembicz, 1998). A very interesting group comprises the species whose life cycle can vary from one to two or even a few years. This group includes *Plantago coronopus* L., which has been established in a study of a population in an area in the central part of its range (Waite, Hutchings, 1982).

The main factors affecting the length of the life cycle of the individuals, apart from their biological properties, are the environmental conditions (e.g. Grime, 1977; Harper, 1977; Jong, Klinkhamer, 1988; Kelly, 1989). Their role is particularly pronounced for marginal populations growing at the range limits, where the conditions of life favoured by the species are gradually deteriorated and the individuals are under a strong effect of abiotic stress and competition. Often the ability of marginal populations to survive is determined by the climate (e.g. Woodward, Williams, 1987; García et al., 2000 and references therein). The factors that can significantly restrict development of such populations are low temperature (Loik, Nobel, 1993) and water deficiency (García et al., 2000). These abiotic factors can cause a significant increase in the death rate of individuals, especially those in the juvenile stage, and a significant decrease in the reproduction ability (García et al., 2000). Under restricting conditions the marginal populations often reveal life history pattern different than that established for the plants of central range populations (Johansson, 1994).

In the above aspects it seemed interesting to study a marginal population of *P. coronopus*, growing at the eastern limit of the range of the species on the island Karsiborska Kępa (NW Poland). The morphological and developmental characterisation of *P. coronopus* and the conditions of this population have been the subject of an earlier paper (Sotek, 2002a). The aim of this study is to recognise the life history pattern of individuals from this marginal population and determination of factors affecting its modification. To accomplish the aim I have been trying to answer the following questions: (i) which life history pattern is developed by *P. coronopus* in a marginal population and if it is consistent with that found in the central populations of this species, (ii) what is the effect of environmental conditions on the life history pattern actually realised, (iii) which intra-population factors have significant effect on the growth and fertility of individuals studied, (iv) does the time of recruitment affect the rate of their development, and (v) what is the seasonal rhythmicity of *P. coronopus* in the marginal population.

## Study area and methods

The island Karsiborska Kępa is localised on the west part of the Polish Baltic coast in the Świna reverse delta, near the village Karsibór. The Old Świna river and its tributaries surround it. During the backflow marine water together with the river water gets into the drainage ditches and floods the low land causing weak salinity of the ground. The island Karsiborska Kępa is one of a few localities of halophilous species on the Polish coast. Its wet meadows grow for example: *Plantago coronopus*, *P. maritima* L., *Glaux maritima* L., *Triglochin maritimum* L., *Juncus gerardi* L o i s, *Spergularia salina* J. P r e s l & C. P r e s l, *Aster tripolium* L., *Blysmus rufus* (H u d s.) Link, and the ditches are grown with tolerating salination *Bulboschoenus maritimus* (L.) P a l l a and *Schoenoplectus tabernaemontani* (C. C. G m e l.) P a l l a.

From the mid, 90s the ground water level has elevated mainly because of partly destroyed drainage system. The habitat conditions, especially in the low-lying land where water is often stagnant for a long time, have changed. Moreover, intense grazing of the majority of the meadows has stopped at about this time.

The study of the marginal population of *Plantago coronopus* on the island Karsiborska Keпа was conducted in the years 1987–1992 and then after the change of the habitat conditions in 2001. The observations of development of the individuals were performed on 6 study plots of 1 m<sup>2</sup> selected at random in different parts of the population area. In the autumn of 1987 all the seedlings in the study plots were labelled. The new individuals appearing over the two subsequent years were also taken into account in the study. In the spring of 1989 additional 200 seedlings, growing outside the study plots at the sites covered with the soil taken from the drainage ditches on their deepening, were labelled. In the first three vegetation seasons the developmental observations were accompanied with biometric measurements and phenological observations, at 6–10 day intervals. Over the next two years the degree of development of the individuals was noted once a month. In total the history of 1232 individuals was followed over the period of 5 years.

Observations of the seasonal rhythm of the population were carried out for the plants from the above-mentioned 6 study plots. In the years 1988–1990 phenological observations were conducted and the number of individuals in the following phases was counted: 1 – seedling, 2 – vegetative growth, 3 – production of immature inflorescences, 4 – blossoming, 5 – unripe fruits (transformation of flowers into capsules), 6 – ripe fruits and seed dispersal (the majority of capsules in the fructifications), 7 – the end of seed dispersal, 8 – dormancy (inhibited development and growth, withering of bottom leaves of the rosettes, reddening of the base and margin of the leaf blade). When two phases occurred simultaneously the dominant one was taken into account. Results are presented graphically in the form of the so-called phenological spectra. The numbers in parentheses are the maximum numbers of individuals in the plots, assumed as 100%. The meteorological conditions in the years 1988–1990 were taken into regard. The mean monthly values of temperatures and precipitations were calculated on the basis of the data collected at the Meteorological Station in Świnoujście.

In order to characterise the population, a pilot study was undertaken including a mapping of *P. coronopus* aggregations occurring in the south-western part of the island and biometric measurement of 30 individuals randomly chosen from each aggregation. On the basis of the pilot study results two representative plots of 40 m<sup>2</sup> and 18 m<sup>2</sup> were sorted out. On the basis of the observations in these plots and taking into account the data from the 6 study plots the spatial structure of the population was described, the size structure of the population and rate of the vegetative growth were estimated. The spatial structure of the population was described using the aggregation coefficient known as the Leksis index

$$I = s^2 : \bar{x},$$

where  $s$  – standard deviation (S.D.) and  $\bar{x}$  – the mean density. The description of the size structure of the population was made using the diameter of the rosette the length of the longest leaf in a rosette and the number of leaves.

In 2001 the aggregations of *P. coronopus* growing in the south-western part of the island were mapped again. The largest two taking an area of 24 m<sup>2</sup> and 48 m<sup>2</sup> were selected for detail observations performed at the level of an individual (fertility, vegetative reproduction) and a population (spatial structure and size structure).

Statistical analysis of the significance of differences between the mean values of the selected traits of *P. coronopus* individuals growing in different habitats was performed by Kruskal-Wallis non-parametric ANOVA. Having rejected the zero hypothesis (H<sub>0</sub>) the groups between which significant differences occurred at  $p < 0.01$  were found. The groups were identified by a procedure similar to the Tukey's range test, but based on a comparison of the modules of differences between the mean ranges of the samples. Statistical analyses were conducted using "STATISTICA 6.0" software.

## Results

### *Recruitment of Plantago coronopus and seedlings mortality*

In the *P. coronopus* population on the island Karsiborska Keпа only ~ 5% of individuals showed vegetative type of reproduction. This process was noted in individuals not earlier

than after the first blossoming and occurred most often in plants growing in great density. The underground bases of *P. coronopus* shoots branched in a plagiotropic mode and in the above-ground part produced a few ramets (2–9) in the form of the so-called sister rosettes, developing into a monocentric clone with the oldest rosette at its centre. In time the aboveground parts of the oldest rosette died but its underground shoot and root remained. At the next stage the branched underground shoots grew in length and adventitious roots developed. In the main root a process of centrifugal atrophy of the eldest tissues took place (Fig. 1).

In *P. coronopus* the generative reproduction is dominant. In the population studied seedlings appeared throughout the vegetation season, often with two (spring, autumn) and less frequently with three (spring, summer and autumn) periods of increased intensity of appearance. In the times of rain deficiency the number of germinating diaspores was significantly reduced. The mean density of seedlings was 93 per m<sup>2</sup>. The greatest number of new individuals (~ 295 seedlings per m<sup>2</sup>) occurred in patches of a high density of *P. coronopus* rosettes, while the least (~ 4 seedlings per m<sup>2</sup>) appeared in the neighbourhood of perennials higher than 15 cm, e.g. *Holcus lanatus* L., *Agrostis stolonifera* L. and *Poa pratensis* L., hence-forth referred to as tall perennials.

The seedlings were characterised by high mortality, especially in the first four weeks of life, then the death rate decreased to slightly increase again between 8 and 10 week of age (Fig. 2).

The seedlings were characterised by high mortality, especially in the first four weeks of life, then the death rate decreased to slightly increase again between 8 and 10 week of age (Fig. 2).

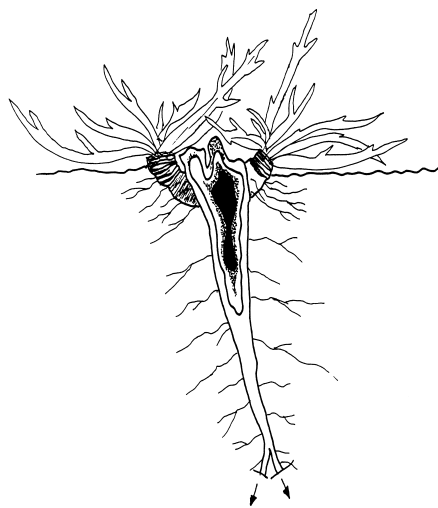


Fig. 1. Clone of *Plantago coronopus*. In the rhizome cut-set visible the dead central part, which surrounded the ring of living layers.

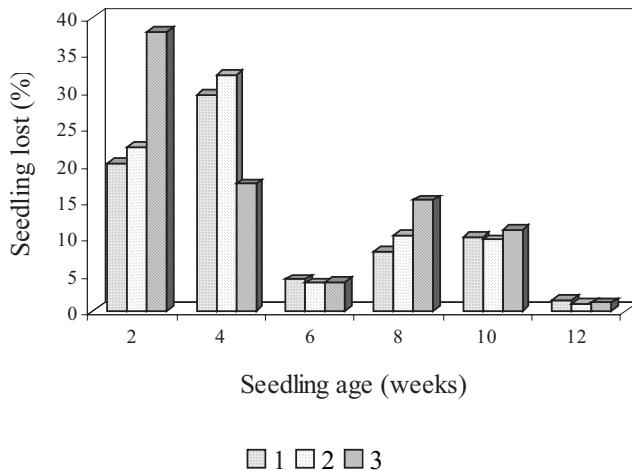


Fig. 2. Mortality of *Plantago coronopus* seedlings. 1 – spring cohort, 2 – summer cohort, 3 – autumn cohort.

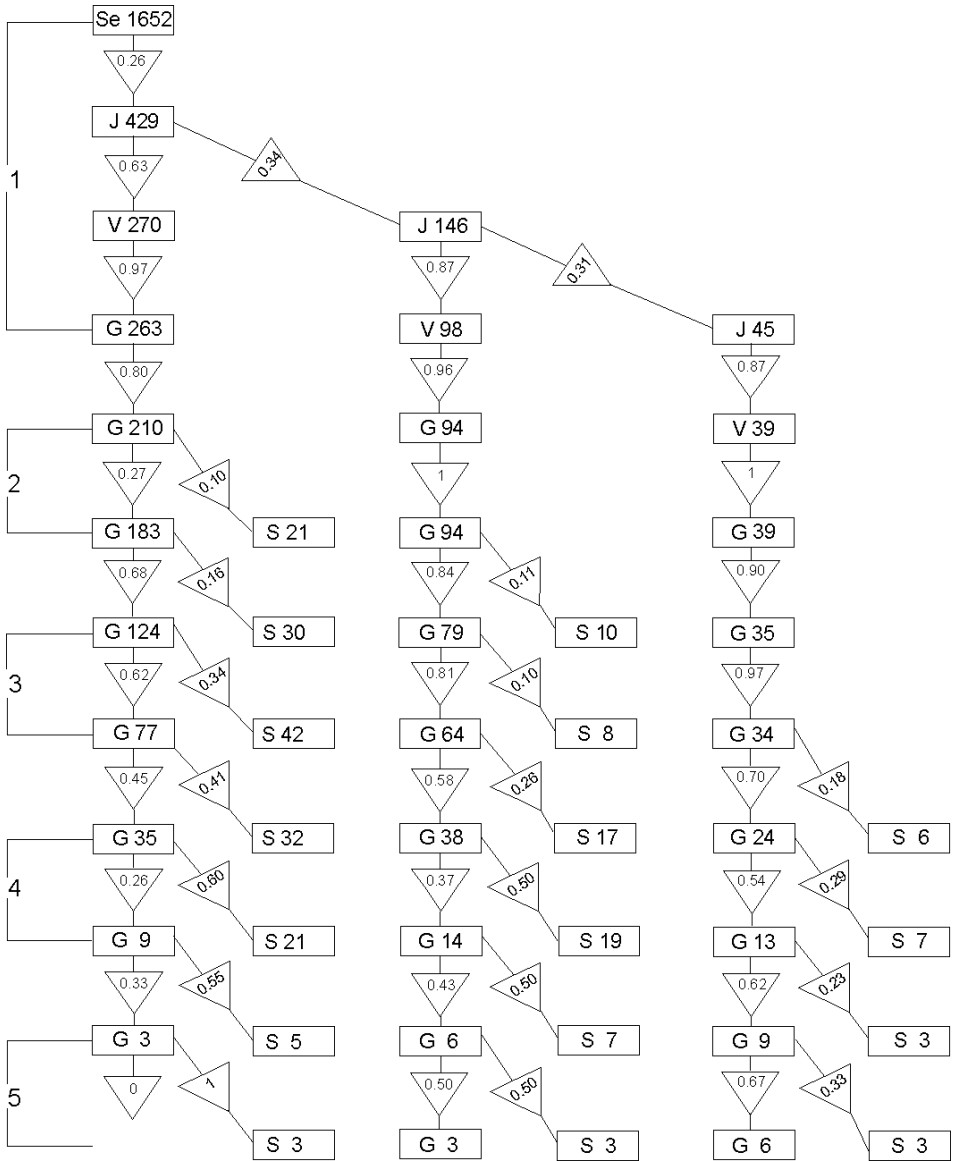


Fig. 3. Diagrammatic life-table of *Plantago coronopus* spring cohort. 1–5 consecutive years, Se – seedlings, J – juveniles, V – vegetative stage, G – flowering individuals, S – senile individuals; triangles – survivability index, rectangles – numbers of individuals at different stages.

The survivability of young individuals was significantly related to the time of their recruitment – the lowest survivability index of 0.13 was noted for autumn seedlings. For summer seedlings this index was 0.21 and for spring ones it was about twice that of the autumn ones reaching 0.26. The lowest death rate was observed in patches of high density of *P. coronopus* individuals and the highest in the neighbourhood of tall perennials.

### *The life cycle of Plantago coronopus individuals in a marginal population*

The life cycle of *P. coronopus* in the population on the island Karsiborska Kepa lasted for from 1 to over 5 years (Fig. 3). A great majority of individuals – 74.4% revealed a few years cycle the biennials made 22.8% and the annuals only 2.8% of the population. The pattern of blossoming also varied from that of semelparous annuals, through that of biennial plants flowering in the first and second year of life, biennial plants flowering only in the second year to that of perennials flowering for the first time in the first year of life to that of perennials flowering for the first time in the second or third year of life.

The life cycle of individuals was definitely related to the time of their recruitment. The seedlings of the spring cohort appearing in April at the earliest, reached the juvenile stage after 1–1.5 month. For the majority of them (63%) this stage lasted from 1 to 2 months, while for the others this period lasted longer from 4 to 10 months. The individuals characterised by a short time juvenile stage reached the generative stage in the same season producing a maximum number of 11 spikes on a single plant. The first generative shoots were noted to develop already in July. In the first season these *P. coronopus* individuals produced mature seeds able to germinate directly after dispersal. Only a few individuals completed their life cycle in one year. The plants of extended in time juvenile stage reached the generative stage in the second year of life and then produced a maximum number of 19 spikes on a plant.

Having reached the generative stage the plants flowered in each subsequent season producing inflorescences from spring to late autumn. At the end of the vegetation period the generative shoots died out, the plants became postgenerative and wintered in this form. In certain individuals the senile stage was noted at the end of the second year of life (Fig. 3). This stage was well seen only in late autumn and early spring when the rosettes died out. In the fourth year after germination about 60% of *P. coronopus* individuals were at the senile stage and died in the autumn of that year or in spring of the next year. At the end of the fifth year of life only a few individuals remained in the generative stage.

The individuals from the summer and autumn cohorts the early developmental stages often lasted for a longer time; also for them the death rate in the stage of seedling was higher, whereas in the other developmental stages the survivability indices were similar for all cohorts. The individuals appearing in summer or autumn wintered while being in the stage of seedling, in the juvenile stage, rarely in the virginal stage. In the next year at the earliest in June and at the latest in August the majority of the individuals produced the first generative shoots, in the maximum number of 15 per an individual. Later their life cycle was similar to that of the spring cohort individuals.

### *The life cycle of Plantago coronopus in the process of recolonisation*

The first plants colonising the sites covered with the soil dug out from the drainage ditches were *P. coronopus* individuals. In the conditions of no competition their early developmental stages were shortened. The stage of seedling and the juvenile stage lasted for 2–3 weeks. The virginal stage ended at the earliest after 4 weeks. The plants produced large rosettes (the maximum diameter 21.0 cm) and numerous (over 40) creeping generative shoots with peduncles ascending only near the spikes. After the seed dispersal at the end of the first year of life, in autumn or in early spring 22.7% of the rosettes died out. The other individuals blossomed in the next season, in the autumn the majority of them died out and only 7% survived.

### *Spatial structure of the population and density of Plantago coronopus individuals*

The individuals of *P. coronopus* show the aggregation type of distribution as indicated by a high value of the Leksis index. In the years 1987–1990 the value of the index increased from 72.78 to 330.89. The largest aggregations were found in the pastures, along the drainage ditches and along the ground road shoulders, especially on the pieces of land slightly elevated with respect to the surrounding area (Fig. 4). The habitat conditions changing from the mid, 90s did not affect the type of distribution in the population. In 2001 the value of the Leksis index was 297.83. The majority of current aggregations grow on the margins of the meadows on the pieces of land subjected to most intense treading. In the area of large meadows the plants were met in disperse small groups of a few or a few ten individuals.

An important role plays the seed dispersal as on germinating the seeds are glued forming aggregations, thanks to production of mucilage. The largest number of seeds was accumulated near individual parent plants and along the margins of groups of individuals. The most abundant aggregations of rosettes were found in the patches with the co-existing plants not higher than 10 cm. In these aggregations the density of plants was very high and sometimes reached even 696 individuals (seedlings included) per m<sup>2</sup>. In such conditions *P. coronopus* individuals were characterised by a slower rate of development, especially when compared to that individually growing plants. The plants in the densely packed aggregations reached the generative stage at different age. In the first year only 30% produced inflorescence, in the second year 64% flowered for the first time and in the third the remaining ones flowered. In the group of *P. coronopus* plants of delayed reproduction phase the most extended was the juvenile stage, which could last up to 1.5 year. Some individuals in the generative stage produced young sister rosettes from the underground base of the shoot, apart from the parent one. The new rosettes appearing in the clone, reached the reproduction phase in the following season at the earliest. At the end of the 5-year life cycle the aggregations contained still 18.3% plants in the generative stage.

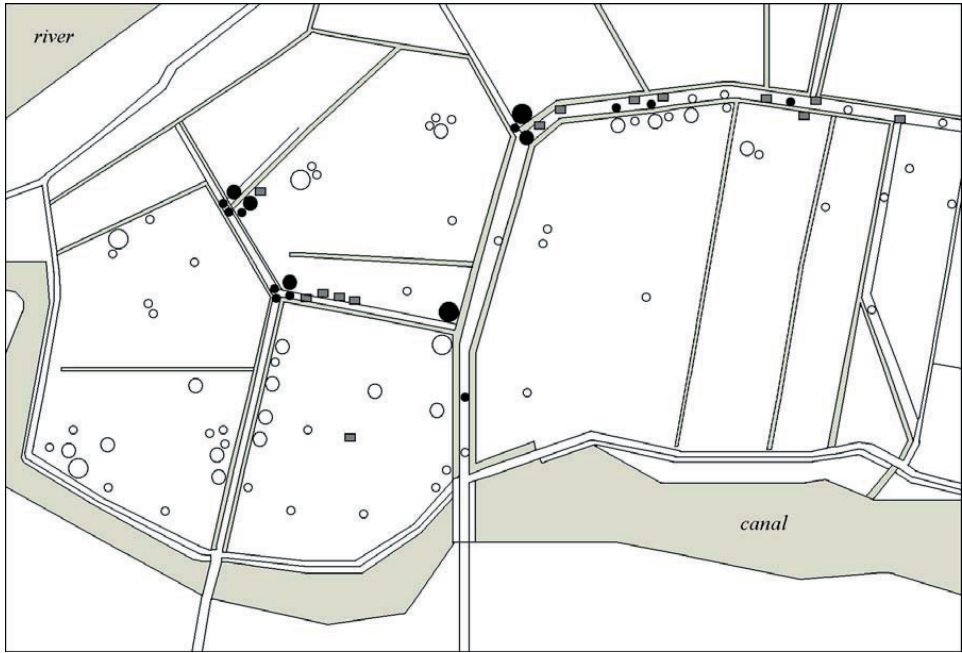


Fig. 4. Distribution of *Plantago coronopus* L. on the Karsiborska Kępa island. ○ – locality, not existing at present, ● – locality, permanently existing, ■ – new locality.

#### *The size structure of plants in the population*

The mean diameters of rosettes of *P. coronopus* in the virginal stage were 4.5–9.6 cm, and in the generative stage 5.8–14.5 cm (Table 1). In the period of observation the diameters of the flowering individuals were always greater than 3.6 cm, and the number of leaves was always greater than 11.

Differences in the size of individuals growing in different conditions were significant (Table 1), while the analogous differences for the plants growing in the same conditions in subsequent years were insignificant. Significant differences were observed in particular in individuals growing in the conditions with no or limited competition, e.g. in the process of colonisation of the sites covered with the soil dug out from the drainage ditches, in these conditions *P. coronopus* produced the largest rosettes of the most numerous leaves. Also the individuals growing among tall perennials reached large size, these individuals produced the long ascending leaves rarely pinnatifid. The individuals growing in the patches subjected to treading, in the virginal phase were also characterised by high mean values of the traits analysed (Table 1).



Table 1. Effects of habitat on plant size and fertility of *Plantago coronopus* in 1990 year.

| Type of patch                    | I                   | II                | III               | IV                | V                 | VI                | TEST K-W       |
|----------------------------------|---------------------|-------------------|-------------------|-------------------|-------------------|-------------------|----------------|
| Virginal stage                   |                     |                   |                   |                   |                   |                   |                |
| n                                | 70                  | 82                | 68                | 60                | 66                | 68                | H P            |
| Rosette diameter [cm]            | $9.4 \pm 1.4$       | $9.6 \pm 3.3$     | $4.9 \pm 1.1$     | $4.5 \pm 0.6$     | $4.9 \pm 1.7$     | $7.9 \pm 1.5$     | 234.059 < 0.01 |
| Number of leaves in a rosette    | $20.8 \pm 4.7$      | $17.0 \pm 2.7$    | $16.6 \pm 3.1$    | $15.0 \pm 1.5$    | $17.8 \pm 3.5$    | $21.5 \pm 4.5$    | 107.032 < 0.01 |
| Leaf length [cm]                 | $5.0 \pm 1.4$       | $7.1 \pm 3.1$     | $3.5 \pm 0.7$     | $3.0 \pm 0.4$     | $3.0 \pm 1.1$     | $5.0 \pm 0.7$     | 191.316 < 0.01 |
| Generative stage                 |                     |                   |                   |                   |                   |                   |                |
| n                                | 72                  | 72                | 72                | 72                | 72                | 72                |                |
| Rosette diameter [cm]            | $14.5 \pm 2.9$      | $10.5 \pm 2.4$    | $6.5 \pm 1.5$     | $5.8 \pm 1.2$     | $6.2 \pm 1.4$     | $9.3 \pm 0.9$     | 315.178 < 0.01 |
| Number of leaves in a rosette    | $45.6 \pm 9.5$      | $22.4 \pm 3.8$    | $21.6 \pm 5.1$    | $20.0 \pm 4.0$    | $23.3 \pm 5.4$    | $24.5 \pm 6.4$    | 193.358 < 0.01 |
| Leaf length [cm]                 | $7.4 \pm 1.3$       | $7.4 \pm 2.2$     | $3.9 \pm 0.8$     | $3.5 \pm 0.7$     | $3.6 \pm 0.9$     | $5.5 \pm 0.5$     | 305.181 < 0.01 |
| Height of generative shoots [cm] | $8.8 \pm 3.0$       | $12.2 \pm 1.8$    | $5.5 \pm 1.4$     | $5.1 \pm 1.1$     | $6.4 \pm 1.8$     | $8.2 \pm 2.2$     | 246.107 < 0.01 |
| n                                | 100                 | 100               | 100               | 100               | 100               | 100               |                |
| Number of generative shoots      | $19.3 \pm 11.1$     | $4.1 \pm 2.0$     | $6.0 \pm 3.5$     | $6.8 \pm 4.3$     | $5.9 \pm 4.2$     | $5.9 \pm 3.7$     | 226.028 < 0.01 |
| Spike length [cm]                | $1.7 \pm 0.8$       | $2.4 \pm 0.7$     | $0.9 \pm 0.3$     | $0.8 \pm 0.2$     | $1.0 \pm 0.4$     | $1.4 \pm 0.4$     | 326.501 < 0.01 |
| Number of seeds / in individuals | $1935.3 \pm 1360.9$ | $580.6 \pm 296.6$ | $318.5 \pm 207.7$ | $321.0 \pm 159.7$ | $348.1 \pm 250.6$ | $487.3 \pm 327.5$ | 270.577 < 0.01 |

Key: I – patches in the process of colonisation, II – patches with tall perennials, III – patches with *P. coronopus* growing in aggregations of high density, IV – patches frequently flooded, V – patches subjected to grazing, VI – patches subjected to treading

### Fertility of individuals

The fruit bearing shoots produced capsules containing 3–5 seeds. 500 capsules collected from individuals from different parts of the area were analysed; 79.1% of them contained 5 seeds, 18.5% contained 4 seeds and 2.4% contained 3 seeds. The differences in the seed production were related to the length of the life cycle and the conditions of occurrence. *P. coronopus* individuals growing in the conditions of no or strongly limited competition of co-existing species often completed their life cycle in 1 or 2 years and revealed the greatest fertility on average about 3000 seeds per plant. The plants of many-year cycle produced on average about 2000 seeds per plant in its lifetime.

No significant variation in the number of seeds produced, number of generative shoots and length of spikes was found in subsequent years, although significant differences in these parameters were observed

between different parts of the population area (Table 1). The numbers of generative shoots and seeds produced by the individuals growing in the conditions of limited competition were significantly different than the corresponding numbers in individuals growing in the other parts of the population area. The lowest number of generative shoots but characterised by the longest spikes were produced by the individuals growing in the neighbourhood of high perennials.

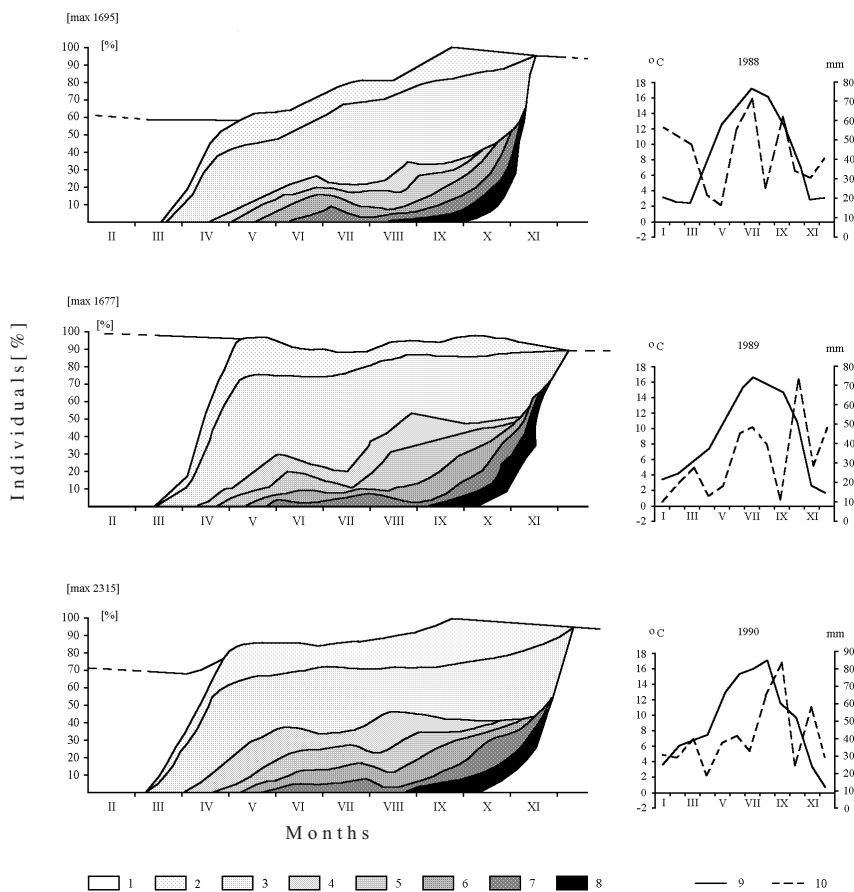


Fig. 5. The seasonal rhythmicity of the marginal population of *Plantago coronopus*. 1 – the rest state of plants, 2 – seedling, 3 – vegetative growth, 4 – production of immature florescence, 5 – blooming, 6 – unripe fruits, 7 – ripe fruits and dissemination of seeds, 8 – the end of dissemination of seeds, 9 – the mean monthly temperatures of the air, 10 – the mean monthly precipitation.

### *Seasonal rhythm of Plantago coronopus*

*P. coronopus* is characterised by a long period of vegetation starting in March or April and ending in November (Fig. 5). In the first 3 years of observations the vegetation was the longest in 1990 – 270 days and the shortest in 1988 – 225 days. Each year the individuals growing in marshes were the last to begin vegetation. The reproduction phase started in early spring between the first decade of April and the first decade of May and lasted till late autumn. The first inflorescences produced in early spring had the top fragments of the spikes of purple colour. Production of generative shoots at different times led to the superposition of particular phenophases. The spectra revealed two maxima in the curves illustrating the percent contribution of plants in the reproduction phase. The first maximum occurred at the turn of May and June, while the second (always greater) in July or August. The blossoming started from the third decade of April till the second decade of May, and ended usually in October. The phase of diaspores dispersal was long, the number of individuals in this phase decreased in July or August and increased again in the end of August or September.

In the autumn, before winter, the plants ceased their development and entered the dormancy. The lower leaves and the bases, margins and top parts of all the other leaves went purple. This process occurred earlier and with greater intensity in the individuals growing on the margins of the drainage ditches and in wet grounds (almost all leaf surfaces went purple). The least intensity of the colour change was noted in individuals growing among tall perennials.

The weather had little effect on the phenological phenomena. The warm springs in the years 1989 and 1990 caused an early start of the reproduction phase. The meteorological conditions also influenced the process of *P. coronopus* getting into the dormancy. The process went smoothly when there were no sudden and significant drops in temperature below zero Celsius, but when such a sudden drop occurred e.g. to  $-5^{\circ}\text{C}$  in 1988, or after early snowfalls the process was rapid.

### **Discussion**

The marginal population of *P. coronopus* on the island Karsiborska Kępa, similarly as the populations of this species in the central part of its range (Hutchings, Waite, 1985), was composed of individuals of different life cycle: annual, biennial and perennial, and showing different pattern of flowering. According to Hutchings and Waite (1985), the *P. coronopus* individuals of different life history are distributed at random and are not concentrated over specific areas. The observations of the Karsiborska Kępa population lead to slightly different conclusions. The semelparous annual individuals were found to grow mainly on the disturbed and recolonised areas at limited competition of co-existing species, which were most favourable for them. Such plants grew individually and developed the largest rosettes and in the reproduction phase produced the greatest number of generative shoots. At the end of the first year of life, in late autumn or early spring they died out. Their life pattern

illustrates the mechanism of the trade-offs rule. The production of many spikes demanded the use of all resources and the plant could not survive after the reproduction phase. These observations mean that in the favourable conditions the life cycle of the plants can get shortened.

The biennial plants were also met more often in the disturbed areas. Over half of the individuals flowered in the first and the second year of life, and the other half only in the second year of life. The individuals of such a type of life history could be treated as an intermediate group between the annuals and perennials. The plants flowering only in the second year of life can be treated as semelparous annuals of prolonged life history with a delayed reproduction phase. The plants flowering in the first and in the second year of life could be treated as iteroparity perennials of a shortened life history with an early reproduction phase.

In the deteriorating environmental conditions the individuals of the species showing plasticity of the developmental cycle often prolong the time of life (e.g. Grime, 1977; Harper, 1977; Waite, Hutchings, 1982; Jong, Klinkhamer, 1988; Kelly, 1989; Falińska, 1997). In the marginal population studied, especially in the conditions of strong intra- and interspecies competition, the majority of *P. coronopus* individuals were characterised by a few year life cycle. They spent relatively little energy for early reproduction and stored the resources. Reaching the generative stage in the first year of life they produced fewer inflorescences than those flowering for the first time in the second year of life. In this way, in agreement with the trade-offs rule they enhanced their chances of survival. As follows from the above observations, the competition of co-existing plants is a factor significantly affecting the life history of *P. coronopus*. The competition restricts the area occupied by an individual plant that reduces the access to water and other nutrients from the soil. This restriction affects the chances of survival and leads to an extension of the pre-reproduction period. According to Hutchings and Waite (1985), the *P. coronopus* individuals of different individual areas often revealed much different life histories.

It is known that the generative stage can only be reached after the plant's rosette has a certain size (Gross, 1981; Mitka, Tumidajowicz, 1993; Bullock et al., 1994; Falińska, 1997). For instance the rosette of *Cirsium palustre* must be at least about 20 cm in diameter when reach the generative stage (Falińska, 1997). The plants of *Verbascum thapsus* produce flowers when they have rosettes of diameters above 41 cm (Gross, 1981), whereas the plants of *V. chaixii* subsp. *austriacum* do not produce flowers when they have fewer than 10 leaves (Mitka, Tumidajowicz, 1993). The *Plantago coronopus* individuals producing generative shoots had rosettes of diameters equal to at least 3.6 cm and greater than 11 leaves. The compact vegetation cover restricted the size of rosettes and often delayed their development. The negative effect of the compact vegetation cover on the growth and development of plants has been noted earlier, e.g. by Collins, Pinder (1990); Falińska (1997).

The size of the rosettes was also affected by the density of plants. When the density of plants was high some individuals attained the size needed for inflorescence production only in the second or even third season of growth, which extended their life cycle. Growing in aggregations, *P. coronopus* individuals much differed in size and the degree of develop-

ment. In the plants growing in aggregations the vegetative reproduction was more frequent. New seedlings developed on the margins of the aggregations or among the leaves of older individuals. The dying plants leaving empty space and releasing nutrients helped their offspring. In aggregations the individuals of different size and age set up a certain mechanism controlling demographic processes of *P. coronopus*, the so-called rosette mechanism (Falińska, 1991).

The life history of a plant was also found to be related to the term of its recruitment. In the marginal population on the island Karsiborska Kępa, just like in the central populations, new seedlings appear in the whole vegetation period. The time model of the growth of the number of individuals can be modified by environmental conditions. In autumn in the populations in the central parts of the species range a significant maximum of seedling appearance was observed. In spring another increase in the seedling appearance from the seed bank was observed, but lower than that noted in autumn. In summer the seedling recruitment was much limited, most probably due to moisture deficiency in the soil (Blom, 1976; Waite, Hutchings, 1979; Waite, 1984). In the marginal population, increased intensity of seedling appearance was observed in spring, autumn and sometimes in summer. In spring and autumn the number of new individuals recruited from seeds was similar. In some seasons in summer the number of germinating diaspores was significantly smaller, which is also interpreted as a consequence of moisture deficiency in the upper layer of the soil.

The majority of individuals from the autumn cohort winters in the seedling stage, which considerably decreases their survivability and the rate of development. The individuals appearing earlier spend winter in the juvenile or virginal stage, or in the secondary vegetative stage. The later stage of wintering gives the greater the chances of survival and faster development in the next season. The greater pace of development and higher survivability of individuals appearing at the earlier phenological season has been suggested many times, e.g. by Cook (1980); Falińska, Pirożnikow (1983).

The phenological study has shown that *P. coronopus* begins vegetation relatively early. The fast growth in early spring gives it an advantage over the co-existing plants which have not started their development yet, similarly as it happens for other rosette plants e.g. *Cirsium palustre* (L.) Scop. (Falińska, 1997). The individuals of *Plantago coronopus* are characterised by a long generative phase. The length of the spike flowering is affected by the clearly earlier appearance of the style. The style with featherly stigma is produced about two weeks earlier than stamens. The long generative phase is not a consequence of a long time of flowering or fructification of a single spike, but is a result of not simultaneous production of inflorescences. Therefore one and the same individual can have continuously produced generative shoots, flowering shoots, fructifying shoots or seed dispersing shoots. The production of generative shoots extended in time enables creation of a generative generation even in difficult conditions such as periodical drought, mowing or grazing.

My results have confirmed the earlier reports of e.g. Falińska (1973) or Bac (1970), that the weather conditions can modify the time of the beginning or duration of particular

phenophases, however, the sequence and general character of the phenophases remain the same. It seems that the delay in vegetation of *P. coronopus* is related not only to low temperatures but also to stagnant cold water and infiltrating ground waters. These conditions are responsible for the delayed seedling appearance in spring and the delay of the generative phase. In similar conditions a delayed germination of *Salicornia patula* Duval-Jouve was observed in a saline area in Maławy (Wilkoń-Michalska, 1976).

The production of purple discoloration of leaves in winter and top parts of young inflorescences in early spring most probably protects the plants against the effect of low temperatures. The discoloration of rosettes in winter was also observed in some individuals of *P. coronopus* growing in north-eastern Scotland (Dodds, 1953).

It has been established that the populations of the same species growing in different environmental conditions often show differences in the course of phenological phases (e.g. Korpelainen, 1993). The differences are particularly notable between the central and marginal populations growing in different climatic conditions. Comparative analysis of the available data on the phenology of a *P. coronopus* population in Great Britain in the central part of the species range (Dodds, 1953) and the data obtained for the marginal population on the Karsiborska Kępa revealed the extension of the flowering phase in the latter by about 1–1.5 month. The greatest differences were noted in the phase of seed dispersal. In the marginal population this phenophase started at the turn of May and June and lasted till late autumn, while in the central population this phase started only in the end of August. The earlier beginning of this phase increases the chances of seed germination and survival of new individuals at the limits of the range.

Increased moisture content of the soil on the island Karsiborska Kępa and cessation of agricultural use of the majority of the meadows on the island in general did not cause changes in the population parameters but significantly reduced the area it occupied. The majority of individuals withdrew from the meadows and at present the largest aggregations are found in the areas subjected to some form of use, which is related to the species resistance to grazing and the light trampling (Sotek, 1999). Of importance in this aspect is the rosette type of structure of the plants, the presence of contractile roots pulling the apical meristem slightly below the ground level (Soekarjo, 1992) and the plant ability to regenerate from the dormant axillary buds on the shoot (Dodds, 1953; Blom, 1977). The results of the observations have confirmed that *P. coronopus* is not strongly competitive, especially towards tall perennials. The absence of the factors limiting the competition from the co-existing species, such as grazing or mowing, leads to a reduction of the population area. *P. coronopus* is a species poorly developing in wet habitats and is sensitive to long water stagnation. According to Schat (1982) the reason for mortality of individuals of this species remaining under water for a long time is the deficiency of oxygen.

Each species has its own life strategy allowing its reproduction and survival (e.g. Grime, 1977; Taylor et al., 1990; Czarnecka, 1995; Falińska, 1997). The fact that the population of this species still remains on the island Karsiborska Kępa is related to such traits of the life strategy as production of numerous anemophilous seeds, formation of seed bank, appear-

ance of seedlings throughout the whole vegetation season, production of generative shoots from spring to autumn, resistance to mechanical stress (treading and grazing), resistance to salination (Dodds, 1953; Blom, 1977; Sotek, 1999, 2002b). In general high plasticity of the life history pattern is one of the most important features allowing survival and development of this species population on the island.

Translated by M. Spsychalska

#### Acknowledgements

I would like to thank to K. Falińska for valuable remarks concerning the research and K. Wawrzyniak (the University of Szczecin) for performing statistical analyses and help in result interpretation.

#### References

- Bac, S., 1970: The first annual phenological phenomena in certain wild plants under geophysical conditions of Poland (in Polish). PWN, Warszawa, 116 pp.
- Blom, C.W.P.M., 1976: Effects of trampling and soil compaction on the occurrence of some *Plantago* species in coastal sand-dunes. I. Soil compaction, soil moisture and seedling emergence. *Oecologica Plantarum*, 11: 225–241.
- Blom, C.W.P.M., 1977: Effects of trampling and soil compaction on the occurrence of some *Plantago* species in coastal sand-dunes. II. Trampling and seedling establishment. *Oecologica Plantarum*, 12: 363–381.
- Bullock, J.M., Clear H.B., Silvertown, J., 1994: Demography of *Cirsium vulgare* in a grazing experiment. *J. Ecol.*, 82: 101–111.
- Collins, B.S., Pinder, J.E., 1990: Spatial distribution of forbs and grasses in a south Carolina old field. *J. Ecol.*, 78: 66–76.
- Cook, R.E., 1980: Germination and size-dependent mortality in *Viola blanda*. *Oecologia*, 47: 115–117.
- Czarnecka, B., 1995: Biology and ecology of the isolated populations of *Senecio rivularis* (Waldst. et Kit.) DC. and *Senecio umbrosus* W a l d s t. et K i t. (in Polish). Wyd. Uniw. M. Curie-Skłodowskiej, Lublin, 263 pp.
- Dodds, J.G., 1953: Biological flora of the British Isles *Plantago coronopus* L. *J. Ecol.*, 41: 467–478.
- Falińska, K., 1973: Flowering rhythms in forest communities in the Białowieża National Park in relation to seasonal changes. *Ekol. Pol.*, 21: 828–867.
- Falińska, K., Pirożnikow, E., 1983: Ecological structure of *Geranium robertianum* L. populations under natural conditions and in the garden. *Ekol. Pol.*, 31: 93–121.
- Falińska, K., 1991: Plant demography in vegetation succession. In Lieth, H., Mooney, H.A. (ed.), *Task for vegetation science*. Kluwer Academic Publishers, Dordrecht/Boston/Lancaster, 26, 210 pp.
- Falińska, K., 1997: Life history variation in *Cirsium palustre* and its consequences for the population demography in vegetation succession. *Acta Soc. Bot. Pol.*, 66, 2: 207–220.
- García, D., Zamora, R., Gómez, J.M., Jordano, P., Hódar, J.A., 2000: Geographical variation in seed production, predation and abortion in *Juniperus communis* throughout its range in Europe. *J. Ecol.*, 88: 436–446.
- Grime, J.P., 1977: Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am. Nat.*, 111: 1169–1194.
- Gross, K.L., 1981: Predictions of fate from rosette size in four biennial species: *Verbascum thapsus*, *Oenothera biennis*, *Daucus carota* and *Tragopogon dubius*. *Oecologia*, 48: 209–213.
- Harper, J.L., 1977: *Population biology of plants*. Academic Press, London, New York, San Francisco, 857 pp.
- Hutchings, M.J., Waite, S., 1985: Cohort behaviour and environmental determination of life histories within a natural population of *Plantago coronopus* L. In Haec J, Woldendorp J.W. (ed.), *Structure and functioning of plant populations 2*. North-Holland Publishing Company, Amsterdam, p. 171–184.
- Johansson, M.E., 1994: Life history differences between central and marginal populations of the clonal aquatic plant *Ranunculus lingua*: a reciprocal transplant experiment. *Oikos*, 70: 65–72.

- Jong, T.J., Klinkhamer, P.G.L., 1988: Population ecology of the biennials *Cirsium vulgare* and *Cynoglossum officinale* in a coastal sand dune area. *J. Ecol.*, 76: 366–382.
- Kelly, D., 1985: On strict and facultative biennials. *Oecologia*, 67: 292–294.
- Kelly, D., 1989: Demography of short-lived plants in chalk grassland. I. Life cycle variation in annuals and strict biennials. *J. Ecol.*, 77: 747–769.
- Korpelainen, H., 1993: Phenological differentiation in *Rumex*. *Acta Ecologica*, 14, 2: 287–297.
- Law, R., 1981: The dynamics of a colonizing population of *Poa annua*. *Ecology*, 62: 1267–1277.
- Lembicz, M., 1998: Life history of *Puccinellia distans* (L.) P a r l. (*Poaceae*) in the colonisation of antropogenic habitats. *Phytocoenosis* 10 (N.S.) *Arch. Geobot.*, 7: 1–32.
- Loik, M.E., Nobel, P.S., 1993: Freezing tolerance and water relations of *Opuntia fragilis* from Canada and the United States. *Ecology*, 74: 1722–1732.
- Mitka, J., Tumidajowicz, D., 1993: Programme of protection of endangered plant species (in Polish). In Biderman, A.W., Wiśniowski, B. (eds), Maintenance and restitution of plant and animal species threatened with extinction in national parks and nature reserves. Records and Materials of the Władysław Szafer Museum, Ojców, p. 27–37.
- Schat, H., 1982: On the ecology of some Dutch dune slack plants. Ph. D. Thesis, Free Univ. Amsterdam, NL.
- Soekarjo, R., 1992: General Morphology. In Kuiper, P.J.C., Bos, M. (eds), *Plantago: A multidisciplinary study*. Springer-Verlag, Berlin, Heidelberg, New York, p. 6–12.
- Sotek, Z., 1999: The effect of grazing on the population of *Plantago coronopus* L. *Folia Universitatis Agriculturae Stetinensis*, 203, 80: 83–89.
- Sotek, Z., 2002a: Morphological and developmental characteristics and ecological conditions of occurrence of *Plantago coronopus* L. on the island of Karsiborska Kępa (in Polish). *Bad. Fizj. Pol. Zach.*, 51: 117–128.
- Sotek, Z., 2002b: The present situation of *Plantago coronopus* L. population on the Karsiborska Kępa island (NW Poland). In Fock, T., Hergarden, K., Repasi, D. (eds), Salt grasslands and coastal meadows in the Baltic region. Proceedings of the 1<sup>st</sup> Conference. Schriftenreihe der Fachhochschule Neubrandenburg, 18: 313–317.
- Symonides, E., 1979: The structure and population dynamics of psammophytes on inland dunes. III. Populations of compact psammophyte communities. *Ekol. Pol.*, 27, 2: 235–257.
- Taylor, D.R., Aarssen, L.W., Loehle, C., 1990: On the relationship between r/K selection and environmental carrying capacity: a new habitat templet for plant life history strategies. *Oikos*, 58: 239–250.
- Verkaar, H.J., Schenkeveld, A.J., 1984: On the ecology of short-lived forbs in chalk grasslands: life history characteristics. *New Phytol.*, 98: 659–672.
- Waite, S., Hutchings, M.J., 1979: A comparative study of establishment of *Plantago coronopus* L. from seeds sown randomly and in clumps. *New Phytol.* 82: 575–583.
- Waite, S., Hutchings, M.J., 1982: Plastic energy allocation patterns in *Plantago coronopus* L. *Oikos*, 38: 333–342.
- Waite, S., 1984: Changes in the demography of *Plantago coronopus* at two coastal sites. *J. Ecol.*, 72: 809–826.
- Werner, P.A., 1975: Predictions of fate from rosette size in teasel (*Dipsacus fullonum* L.). *Oecologia*, 20, p. 197–201.
- Wilkoń-Michalska, J., 1976: Structure and dynamics of the populations of *Salicornia patula* Duval-Jouve (in Polish). *Rozprawy UMK, Toruń*, 156 pp.
- Woodward, F.J., Williams, B.G., 1987: Climate and plant distribution at global and local scales. *Vegetatio*, 69: 189–197.

Received 15. 11. 2004