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Changes in population structure of *Carex cespitosa* during 10 years of secondary succession in an abandoned meadow in Białowieża, Poland

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Changes in the structure of a *Carex cespitosa* population were studied during secondary succession on abandoned meadows near Białowieża National Park (NE Poland) over a period of ten years (1987–1997). During succession the spatial relations between dominants (*C. cespitosa*, *C. acutiformis*, *Filipendula ulmaria,* and *Salix* spp.) changed. *Carex cespitosa* is one of the species playing a major role in the transformation of vegetation on abandoned meadows in Białowieża. In the initial stage of the terminal phase of succession, which starts with the appearance of willows, the population of *C. cespitosa* begins to regress. The beginning of regression is manifested by changes in age structure of the population. The size of tussocks (diameter and height) still increased during the study, but the rate of growth was lower in patches dominated by *C. acutiformis* or willows than in meadows dominated by *C. cespitosa*.

Key words: abandoned meadows, *Carex cespitosa*, colonisation, plant ecology, population dynamics, succession

Introduction

According to the theory of population structure of vegetation, the course of succession is determined by the processes taking place on the population level, thus succession is considered the effect of demographic processes (Peet & Christensen 1980, Huston & Smith 1987, Mortimer 1987, Pickett *et al*. 1987, Falińska 1989a, 1989b, 1991). In terms of this theory, succession can be interpreted as a process of replacing individuals of one species by those of another. Particular species play specific roles in transformation of vegetation undergoing succession. According to Falińska (1991), species whose subsequent phases of development coincide with particular stages of succession are most important in the process of succession on abandoned meadows.

In the present study, I attempt to identify the factors that determine the retreat of one species and its replacement by others, when the succession starts in a species-rich community. Observations of *Carex cespitosa* behaviour in abandoned meadows provided grounds for explication of the mechanisms of succession on the basis of demographic processes and biological properties of the species (Brzosko 1999a, 1999b, 1999c, 1999d, 1999e).

A feature determining the life history of a population is the stage of its development in the phase of colonisation. Olsson (1987) claims that the colonisation success, which can be interpreted as survival of individuals of a given species, their growth and reproduction in the microsite where its seeds fell (Peart 1989a, 1989b, 1989c), depends on 'who comes when'. This is consistent with the inhibition model of Connell and Slatyer (1977) where the first colonisers maintain their positions despite the arrival of newcomers, which are inhibited. It is also confirmed by the initial floristic model (Egler 1954), according to which species dominant in later stages of succession are early colonisers. Thus, the success of colonisation depends to a significant degree on the priority of colonisation.

Almost all species taking part in succession on abandoned meadows have occurred there prior to abandonment. Mowing is known to favour development of certain species while restricting some others (Falińska 1996). Some of the species reveal colonising abilities only after cessation of mowing, which is a disturbance factor in the structure of semi-natural meadow communities, whose existence was determined by management. A rapid population increase of many species whose contribution was small under the mowing regime, e.g. *Carex cespitosa*, was observed after its cessation. The sure colonisation success and a significant role of *C. cespitosa* population in the process of succession, especially in the transitory stage can be attributed to the type of growth of its individuals, vitality of perennial organs and high fertility of individuals ensuring permanent recruitment. These characteristics are particularly important when *C. cespitosa* is the first colonist not accompanied by competitors. However, later the life strategy of *C. cespitosa* proves insufficient to cope with other factors appearing in subsequent stages of succession.

In this study, I attempt to answer the following questions: (1) When does regression of the population start and what are the reasons initiating it; and (2) Which features of a population indicate regression?

Materials and methods

The area where the populations of *Carex cespitosa* were studied lies in the NW part of Polana Białowieska, in the Narewka river valley (NE Poland). On one side it is bounded by the riverbed, on the other by the slopes of the Białowieża National Park. The study area, commonly known as Uroczysko Reski, covers about 15 hectares and lies at a height of 170 m above sea level. The area is characterized by a subboreal-continental climate, with an annual snow cover of 90 to 150 days and a relatively short growing season. (Olszewski 1986).

Uroczysko Reski was deforested about 200 years ago (Faliński 1966). Meadows in this part were mown only once a year, and not every year due to the high water level in some years. Difficulty of access and poor fodder value (large quantities of sedge) caused their gradual abandonment at different times between 1960 and 1978 (Falińska 1991). After 15 years without mowing the result was a mosaic of 16 phytocoenoses, of which the initial phase of willow thicket and a *Lysimachio vulgaris–Filipenduletum* herb community and *Salicetum pentandro-cinerea* occupied the largest area, accompanied by aggregations of such species as *Filipendula ulmaria, Salix cinerea, S. pentandra, Carex cespitosa, C. acutiformis, Lysimachia vulgaris* and small fragments of thistle meadow (Falińska 1991).

Observations on the 2600 m^2 area were carried out in 1987 and 1997. They concerned the relationships among the major components of vegetation, the spatial organization of the *Carex cespitosa* population, and its age and size.

In order to define the size of individuals in the *Carex cespitosa* population the diameter of tussocks was measured (the diameter was considered to be that of the closely packed material forming the tussock base, measured at ground level) as well as their height (the closely packed part of the tussock protruding above the ground). In order to determine the age structure, each tussock was attributed a biological age (developmental phase). The age of particular individuals was determined on the basis of biological criteria (Gatsuk *et al*. 1980), including the following developmental phases:

— seedling (s): a one-shoot individual, maximum height 1 cm, with one rolled leaf, seed still attached,
— juvenile (j): an individual of one to several shoots and at least two leaves, but not assuming a tussock form,
— virginal (v): an individual in the form of a tussock, characteristic for the species, not flowering,
— generative, without signs of ageing (g1): a tussock forming flowering shoots, but lacking senile parts,
— generative, senile (g2): a tussock forming flowering shoots, with senile parts or a clearly decreasing density of shoots,
— subsenile (ss): an individual not in bloom, with large senile parts but retaining vegetative shoots,
— senile (s): a tussock on which shoots do not appear.

It was assumed that the population of *Carex cespitosa* consisted of all tussocks of this species growing in the area of Uroczysko Reski, while the limit of the population was taken to be the border of the range itself. The vegetation of Uroczysko Reski was, among others, composed of the following patches: (a) Meadow containing a number of species, with *C. cespitosa* dominant (frequently with another tussock species, *C. appropinquata*); (b) Meadow dominated by *C. acutiformis*; (c) Dominated by *Filipendula ulmaria*; (d) Patches dominated by two willow species, *Salix pentandra* and *S. cinerea* (Falińska 1991). Tussocks of *C. cespitosa* occurred in all these patches. To study the impact of the other species on the demographic processes of *C. cespitosa*, four subpopulations were selected within the total sample area of 2600 m^2, depending on the species dominant in the particular patch where the groups of *C. cespitosa* tussocks occurred:

1. A meadow subpopulation of *Carex cespitosa*, formed of tussocks growing in a species-rich meadow. Tussocks of *C. cespitosa* dominated some patches of the meadow (together with *C. appropinquata*) or more rarely occurred fragmentarily as in the surviving thistle meadows (*Cirsietum rivularis*).
2. A swamp subpopulation, made up of tussocks occurring in areas dominated by *Carex acutiformis*.
3. A *Filipendula* subpopulation, formed of tussocks occurring in patches dominated by *Filipendula ulmaria*.
4. A willow subpopulation, formed of tussocks occurring in willow thicket (*Salix pentandra* and *S. cinerea*).

Results

Spatial relations between dominants

In 1987, the area of 2600 m^2 hosted 69 species of vascular plants, only four of them forming large patches: *Filipendula ulmaria*, *Carex acutiformis*, *C. cespitosa*, and *Salix cinerea* (Fig. 1). The greatest area (1144 m^2) was occupied by *Carex acutiformis*. A substantial area was also occupied by the tussock-forming sedges *C. cespitosa* and *C. appropinquata* (868 m^2). *Filipendula ulmaria* occupied 296 m^2, whereas willows with dominant *Salix cinerea* covered 292 m^2 (11.2% of the total area). In 1997, covers of the species had considerably changed (Fig. 1). Willows became dominant and occupied four times greater an area than before (988 m^2, or 38% of the total area). Expanding willows eliminated

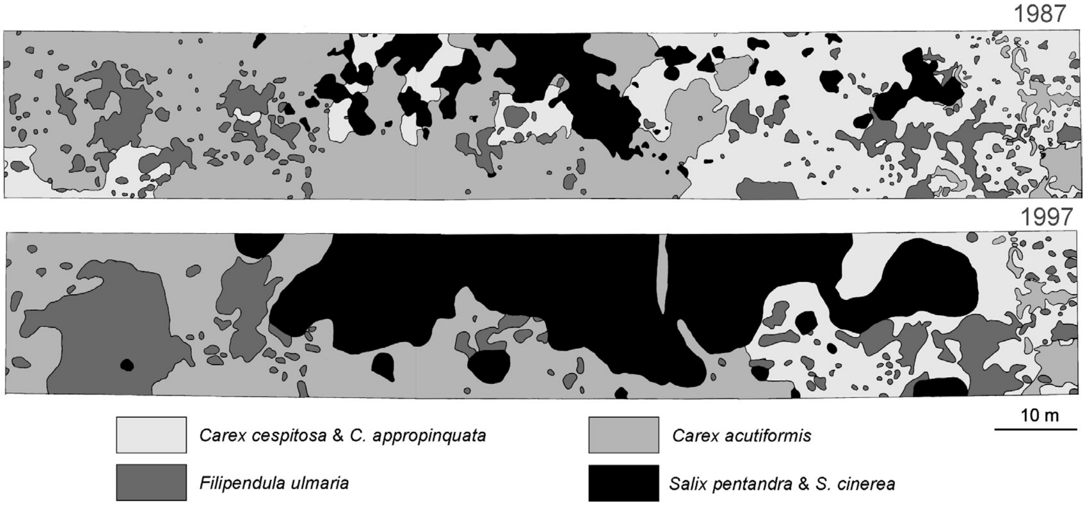

Fig. 1. Changes in cover and spatial relations between dominants on abandoned meadows within a period of 10 years.

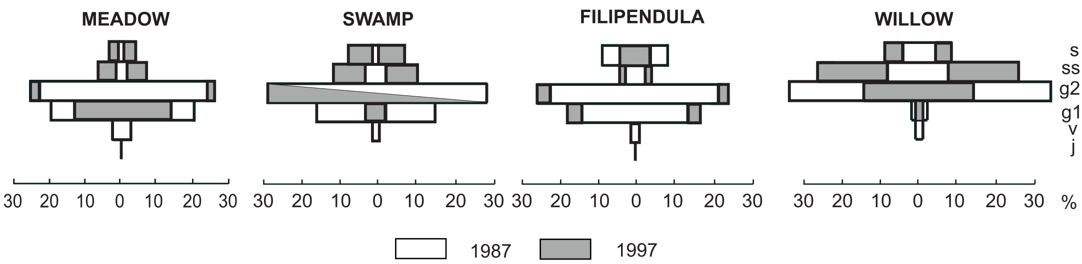

Fig. 2. Changes of age structure of *Carex cespitosa* subpopulations in patches dominated by different species (j = juvenile, v = virginal, g1 = generative, without signs of ageing, g2 = generative, senile, ss = subsenile, s = senile).

meadow species and, consequently, many tussocks of *C. cespitosa* grew in their vicinity. Expanding willows reduced the area occupied by *C. cespitosa* and *C. appropinquata* by half and caused a 35% reduction in the area occupied by *C. acutiformis*. They did not affect *F. ulmaria,* which occupied an area almost twice as large as in 1987 (486 m^2).

Number of *Carex cespitosa* tussocks

With the altered spatial relations among the four species, the population structure of *Carex cespitosa* changed. In 1987, 1146 tussocks of this species were recorded. Within the 10-year period of the study, the size of the *C. cespitosa* population changed relatively little: 5% of the tussocks died, and no new were found.

Changes in age structure of *Carex cespitosa* population

In the meadow subpopulation the number of senile individuals increased as a natural consequence of tussock ageing and a lack of recruitment of young individuals (Fig. 2). Ten years from the first observation there were no individuals in preproductive age in this habitat. The contribution of the generative tussocks without senile parts (g1) decreased by 15%, while the tussocks with senile parts (g2, ss, s) made up about 72.6%, i.e. 20% more than the total

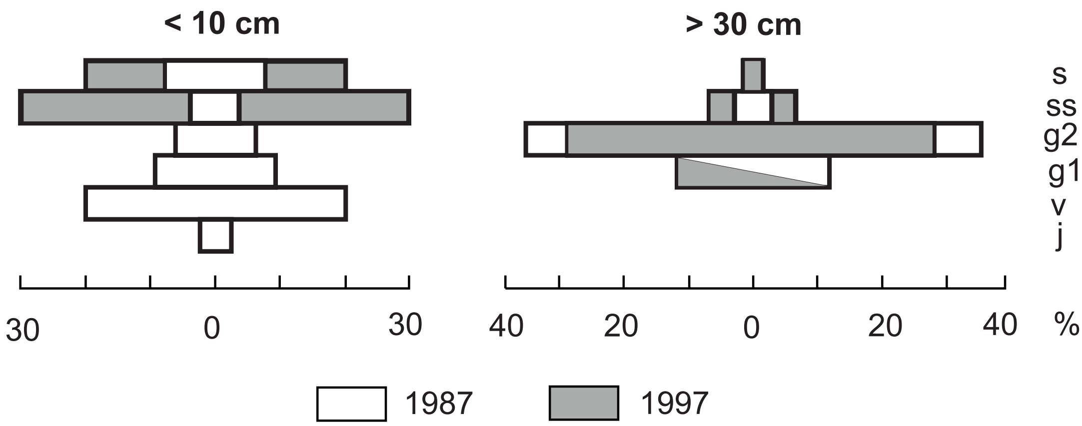

Fig. 3. Age structure of *Carex cespitosa* tussocks of different size (j = juvenile, v = virginal, g1 = generative, without signs of ageing, g2 = generative, senile, ss = subsenile, s = senile).

number of tussocks 10 years earlier. The proportion of senile and subsenile tussocks in the population increased considerably (Fig. 2).

Similar changes in the age structure occurred in the *Carex cespitosa* swamp and willow subpopulations, however, the increase in number of senile tussocks was greater than in the meadow subpopulation (Fig. 2). In the swamp in 1997, the percent of tussocks with senile parts had increased by 30%. In the willow subpopulation, only 2% of the tussocks did not have senile parts. These 2% included the tussocks which had grown beyond the willow canopy and presently grew at the margin of the canopies, thus their development was less affected by *Salix*. Many of the tussocks growing among the willows in 1997 had begun their development on the meadow and were in a very good condition. The tussocks growing among the willows for few years did not age so much as tussocks growing in the central part of willows for many years.

The changes in the age structure of the *Carex cespitosa* growing in the patch with *Filipendula ulmaria* as the dominant species were different in character. After 10 years the proportion of individuals in reproductive age increased while that of subsenile and senile ones decreased (Fig. 2). In this patch, 13% of the tussocks of *C. cespitosa* which were in the senile phase in 1987 died before 1997, while the corresponding number for the meadow was only 2.4%, among willows 7% and in swamp 7.9%. In 1997 in the patches with *F. ulmaria* there were many tussocks in good condition. These were the ones which in 1987 grew among the meadow species, in conditions favourable for their development. These tussocks grew in the patches with *Filipendula* for a relatively short time and could remain in good condition. Moreover, the influence of *F. ulmaria* on the tussocks of *C. cespitosa* was different than 10 years before as the structure of the patch became thinner due to ageing of the genets of the former. In 1997 the tussocks of *C. cespitosa* were much bigger and more distinct than 10 years earlier. In addition, the frequency of *F. ulmaria* in the tussocks of *C. cespitosa* was reduced by half when compared to that in 1987.

Changes of the size-age population structure

Regression of the *Carex cespitosa* population was also indicated by a change in the size of the tussocks and the process of their ageing. In 1987, there were 53 tussocks (5%) of a diameter less than 10 cm, and they represented all developmental stages (small tussocks can be either young or aged, Fig. 3), with the majority in the virginal phase. In 1997 there were only ten tussocks (1.5%) of less than 10 cm in diameter, and all of them were subsenile or senile (Fig. 3). The biggest tussocks over 30 cm in diameter made up 8.1% of the total population in 1987 (86 tussocks), while in 1997, their contribution

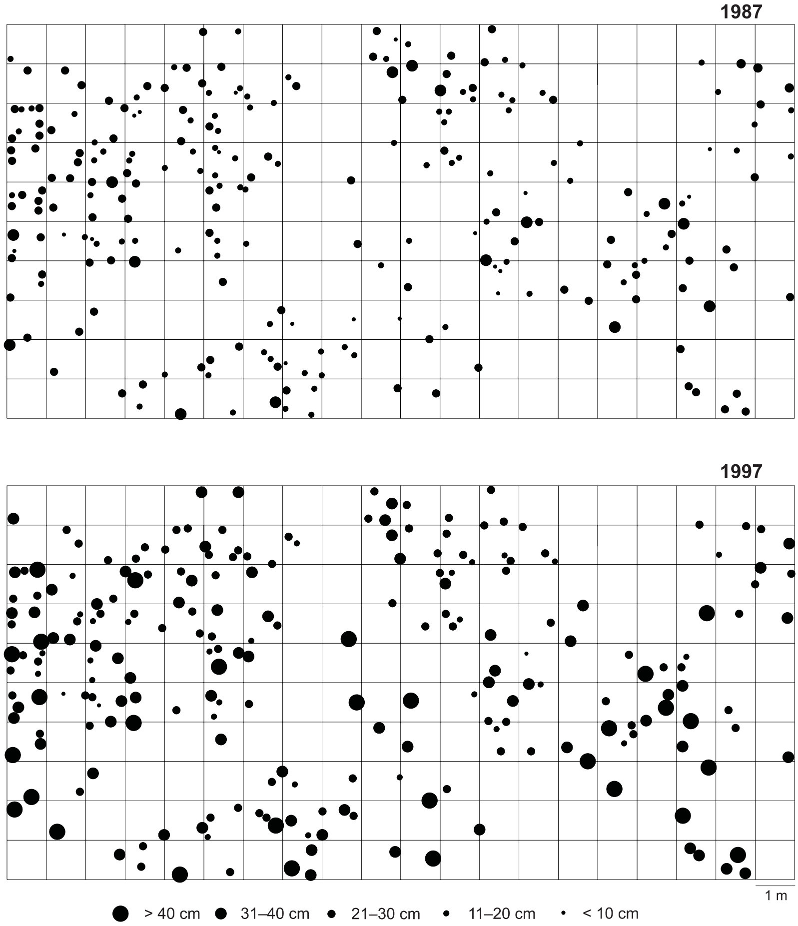

Fig. 4. Spatial organization of *Carex cespitosa* population and changes of tussock diameter during 10 years.

was 4.5-fold increased, making up 37%. The age structure in this group of tussocks changed little in comparison with the smallest tussocks (Fig. 3). This observation may be accounted for by the fact that the ageing *C. cespitosa* tussocks (with enlarging senile parts) continued to expand vertically and horizontally.

Changes of the tussock size structure of population

During ten years, the sizes of *Carex cespitosa* tussocks changed (Figs. 4 and 5). In the meadow community the tussock diameter increased on average by 9 cm and height on average by 8 cm. Similar changes in subpopulation Filipendula were observed — both diameter and height increased in significantly (Fig. 5). Some tussocks increased their diameter to more than 30 cm and thus multiplied their size (Fig. 4). The difference in tussock sizes in the other patches was smaller (Fig. 5). In the swamp, the diameter of *C. cespitosa* tussocks increased only by 4 cm and height by 3 cm. Among willows, the corresponding values were 6 cm and 2.5 cm, respectively. Differences in diameter and height between 1987 and 1997 were statistically significant. F-value for diameter ranged from 21.707 in willow subpopulation to 211.648 for meadow subpopulation ($p < 0.05$). For the tussock height, F-value ranged from 9.165 to 273.911 ($p < 0.05$).

Discussion

The species involved in the process of succession have different influences on the rate of

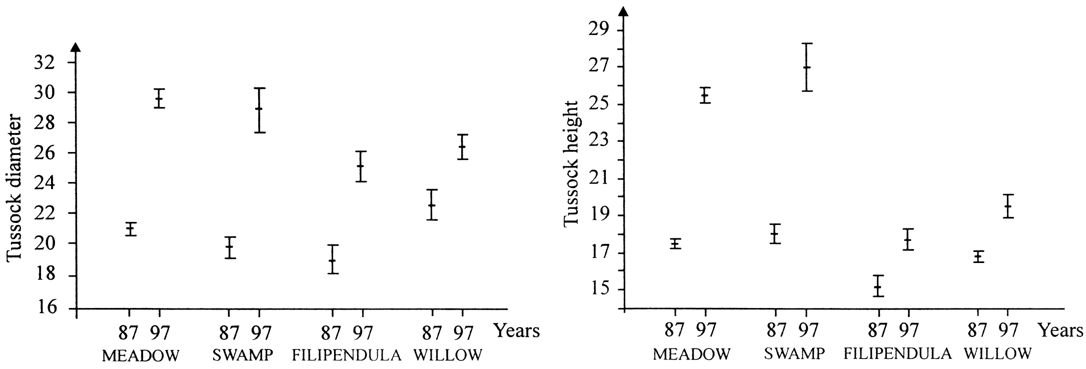

Fig. 5. Changes of tussock size (diameter and height) in patches dominated by different species. Vertical bars indicate ± SE.

vegetation transformations, first of all simply because of different sizes of the occupied areas. Different species can be either inhibitors or promoters of the return of forest onto abandoned meadows. When *Carex cespitosa* is in transitory stage of succession, the tussocks are characterised by a compact system of rhizomes and because of that they effectively inhibit colonisation by other species and thus they also inhibit succession. On the other hand, the tussocks of *C. cespitosa* support development of many meadow species. Over ten years, the meadow species withdrew from the tussocks or reduced their frequencies and were replaced by other species, predominantly forest species. In the later stages of succession, when the tussocks age, they can promote species turnover (Brzosko 1999d, 1999e).

The presence of *Carex cespitosa* during succession from meadow to forest and the variable contribution of this species in the vegetation structure is a consequence of certain biological properties of the individuals which determine the population processes (Brzosko 1991, 1999a, 1999b, 1999c). These properties are:

1. *Type of growth*. Compactness of perennial organs frequently leads to their persistence which effectively prevents other species from colonising the area occupied by the tussocks, and longevity of the tussocks ensures their persistence.
2. *Pattern of growth*. Multiplication of the number of shoots in the first stages of development permits a fast expansion over the area and enlargement of the size.
3. *Great vitality of rhizomes and roots*. Considerable storage of resources in the permanent organs of *C. cespitosa* is favourable for the tussocks' longevity and persistence in deteriorating conditions.
4. *High individual fertility*. Constant inflow of a large number of seeds is the fundamental factor for permanent recruitment (Brzosko 1999c).
5. *Phenology*. *Carex cespitosa* begins its growth in spring as one of the first meadow species, and early flowering and fruit production favours seed germination before the appearance of other species (Brzosko 1999a).
6. *Pattern of ageing and dying*. The ageing process does not affect the whole tussock at the same time; enlargement of senile parts leads to disintegration of the tussock, and separation of younger fragments of the genet which prolongs its life (Brzosko 1999a).

The above-mentioned properties of *Carex cespitosa* allow effective colonisation and long time persistence at a given site. Many authors have pointed out that the maintenance and colonization success of plant populations depend on biological properties, especially clonal form of growth (Cook 1983, Callaghan *et al.* 1990, Eriksson & Jerling 1990, Eriksson 1992, Fagerström 1992, Jonasson 1992). The importance of vegetative reproduction by clonal growth for population dynamics has been reported for *Carex rostrata* (Salonen *et al.* 1992), *Calamagrostis* spp. (Soukupova 1992), and

Brachypodium pinnatum and *Carex flacca* (de Kroon & Kwant 1991). The increase of cover of a *Molinia coerulea* population during 24 years of succession on a Danish mire was a result of increase of tussock size (Hansen & Madsen 1984).

However, already in the initial stage of the terminal phase of succession, which starts with the appearance of willows, the population of *Carex cespitosa* begins to regress. Only the longevity and vitality of tussocks maintained a subpopulation in the study area. Such species survive for only a limited time until they become shaded out by tall plants (David & Kelsey 1985). Thus willows may be considered to be the species which would effectively eliminate the *C. cespitosa* population. Thus, the appearance and expansion of willows, which substantially affect spatial relations between the components of a plant community, is the main cause of regression of this population. Individual willows grew in abandoned meadows already in the initial stage of succession, and the *Salix* species are particularly expansive, rapidly enlarging the occupied area and eliminating other species (Brzosko 1999b). Tussocks of *Carex cespitosa* growing between the willows suffer from this: for example, the tussocks produce only a small number of flowering and fruiting shoots and signs of ageing were evident from the appearance of senile parts in more than 90% of the tussocks, while in other sites the corresponding percentage was 53%–67% (Brzosko 1999b). A relation between reproduction parameters and the stages of succession was also found by Barkham (1980a, 1980b), Hester *et al*. (1991), Kollman (1995), and Kollman and Reiner (1996).

Initially it was assumed that a significant increase of the diameter of *Carex cespitosa* tussocks growing among willows was the consequence of the fact that they had earlier grown in favourable conditions in the meadow. However, analysis of the size of the tussocks which grew already in 1987 under the canopy of willows showed that the tussocks ageing among willows increased their size despite deteriorating conditions of development (shadow, greater density, more litter).

The regression is not only caused by the appearance of willows. The maximum space filling by *Carex cespitosa* and accumulation of necromass finally lead to the conditions in which the appearance of progeny is impossible. It is known that dense swards of other species and the previous years' shoots, especially of *Carex* spp., closely covering the soil, inhibits germination and limits survival of seedlings (Petersen 1981, Gross & Werner 1982, Van den Berg *et al*. 1985, Olson & Richards 1989, Jonasson 1992). Predominance of *C. cespitosa* seedlings in the experiment in which plant cover was removed emphasizes the importance of open space for colonization (Brzosko 1999c). Peart (1989a, 1989b, 1989c) claimed that the colonizing rate for *Anthoxantum odoratum* and *Holcus lanatus* even increased by 2500 times in cases when gaps occurred, while Silvertown and Smith (1989) showed that many more seedlings of *Cirsium vulgare* appeared in gaps of 10–20 cm diameter than in those of 5 cm diameter, or on control plots without gaps. Gaps in plant cover also increased the probability of seedlings emergence in *Prosopis glandulosa* (van Auken & Bush 1987, 1990).

The above-mentioned phenomena are accompanied by an increased mortality of *Carex cespitosa* tussocks, which gradually leads to a decrease in the population size and recession of the species enabling the return of forest. The beginning of regression manifested by a growing proportion of senile individuals was a consequence of the following processes:

- a natural senescence of tussocks,
- a lack of recruitment; this a direct consequence of the decreasing number of safe sites for germination (among other reasons due to accumulation of necromass) and lower reproducing potential (older tussocks produce a smaller number of generative shoots) (Brzosko 1999c, 1999e),
- increasing rate of senescence and mortality of tussocks as a result of the development and expansion of willows leading to a shortening of ontogenesis in unfavourable conditions.

The question arises, which of these characteristic features are most reliable and characterize the vitality of the subpopulation most adequately? They are closely related to one another, exert mutual influences and depend primarily on the biological properties of the species, developmental phase of the population, and, finally, they are modified by habitat conditions. Age structure is considered to be one of the most basic features of a population, as it has a major role in the shaping of the various processes going on within it, particularly on reproduction and mortality.

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