Plant population processes in the course of forest succession in abandoned meadows. I. Variability and diversity of floristic compositions, and biological mechanisms of species turnover

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Abstract

Within Białowieża Forest the studies on the rate and nature of changes in meadow vegetation on the sites no longer mown were conducted for 15 years (1974-1988). The successional processes were analysed at various organizational levels by applying hierarchical system of study areas, varying in size (Figs. 1, 2). Changes in plant landscape were studied on 15 ha, those in phytocoenoses — 4×1 ha, populations — 24×200 m², and those in the individual development — 6×25 m². Forest re-colonized abandoned meadows at a various rate through: a) gradual transformation of meadow phytocoenoses into tall-herb, and later brushwood communities, which went on for c. 15 years; b) formation of the mosaic of monospecific aggregations of a few, among 124, components of meadow communities, such aggregations persisted for 5-15 years; c) the development of tree biogroups (forest outpost) directly in the meadow sod. This diversity resulted from the habitat heterogeneity (microrelief, water level) and variety of colonization strategies among the species present prior to the succession. They vary in their role in the successional process and can: 1) stimulate the changes in the structure of meadow phytocoenoses and lead to the formation of new communities (promoters), 2) limit species turnover due to their long-lived aggregations (inhibitors), 3) play no crucial role in the vegetation transformation (indifferents).

Key words: succession, species-turnover mechanisms, colonization strategies

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INTRODUCTION

Vegetation dynamics is mainly the dynamics of phytocoenoses and populations as the elements of ecosystems, hence liable to the rules and principles of their functioning. Therefore the studies on vegetation dynamics attempt to explain the fate of a given phytocoenose from its formation till its stability, or the fates of successive phytocoenoses. The elucidation of successional processes comes from the analysis on the mechanisms of plant grouping. Because of the success of populational genetics and plant demography such problems are being solved from the point of view of reductionism (Harper 1977, Grime 1979, Begon et al. 1986). Then, a succession is a process of species turnover under actual conditions, while their role is determined on the grounds of their life-strategies (Horn 1974, Connell and Slatyer 1977). The formation, development and persistence of phytocoenoses result from the phenomena ongoing in and between plant populations (Rabotnov 1985a, b). The range of interrelations between populations as phytocoenose components can be explained, to a large extent, by various life-strategies of species expressed in their life forms, morphological types and reproductive modes. In order to determine a species role in the phytocoenose properties of individuals during their life-cycles should be analysed, especially: architecture, life-span, longevity of underground organs and reproductive modes (Falińska 1985, 1986, 1988). Those properties shape demographic processes, hence determine the rank of a species in the phytocoenose (cf. White 1985, van der Maarel 1980), e.g. whether it is a component of only one or a few phytocoenose types, whether it is a dominant and constant component in the whole successional process, or only complementary and ephemeral component of some of the consecutive phytocoenoses.

The studies aim to determine:

1. The rate and nature of vegetation transformation in the successional process of rich meadow re-colonization by forest.
2. The fates of consecutive phytocoenoses in the course of succession, and how they form, persist in time, and become transient.
3. Biological mechanisms of species turnover.

METHODS

STUDY AREAS

The studies were conducted in 1974-1988 in the centre of Białowieża Forest, in the Uroczysko Reski, on 15 ha of meadows, abandoned at different, but known, time (1960-1974). The study areas were located in the Narewka valley deforested for the last 200 years, close to the Białowieża National Park (Fig. 1).

<i>Cirsietum salisburgensis</i>	<i>Circaeο-Alnetum</i>
<i>Lysimachio vulgaris-Filipenduletum</i>	<i>Carici elongatae-Alnetum</i>
<i>Caricetum acutiformis</i>
non-facial community	<i>Salicetum pentandro-cinereae</i>
facies with <i>Lythrum salicaria</i>	brushwood of <i>Alnus glutinosa</i>
facies with <i>Iris pseudacorus</i>	clumps of <i>Alnus glutinosa</i>
<i>Caricetum vesicariae</i>
non-facial community	clumps of <i>Salix pentandra</i> & <i>S. cinerea</i>
facies with <i>Lythrum salicaria</i>	singular trees of <i>Alnus glutinosa</i>
<i>Iridetum pseudacori</i>	singular trees of <i>Betula pendula</i> , <i>Sorbus aucuparia</i>
aggregation of <i>Phragmites australis</i>	

Fig. 1. Changes in the vegetation of the Reski Uroczysko on 15 ha of abandoned meadows

The transformation of vegetation was analysed at different organizational levels i.e. those of: landscape, phytocoenose, population, and individual, on the hierarchical system of study areas varying in size (Fig. 2). In order to observe changes in plant landscape 15 ha were investigated, those in phytocoenoses — 4×1 ha, in populations — 24×200 m², and those concerning individuals 6×25 m². Due to the abandonment date four 1 ha meadow sectors were distinguished: A — meadows abandoned at the beginning of the study (1974), B — meadows unmown for 5 years i.e. since 1970 (tall-herb communities), C — meadows unmown for 10 years, i.e. since 1965 (willow brushwood) (Fig. 3), D — meadows unmown for 15 years, i.e. since 1960 (initial forest phase).

In each sector six 200 m² study areas were selected and divided into 25 m² plots. In each study area one of the plots was divided into 25 1 m² quadrats (Fig. 2).

OBSERVATIONS

1. Community dynamics. In order to follow the transformations of vegetation in unmown meadows the map of communities was constructed every 4th years for the whole 15 ha area. on the grounds of the grid of 10×10 m square areas.

2. Population spatial structure. Every season (1974-1988), in each study area the distributions of all populations were mapped at 1:100 scale (Fig. 2), whereas on every plot (25 m²) flowering and vegetative shoots of all species were counted.

3. The number of individuals and shoots. Every season on each plot individuals of all species were mapped at 1:10 scale. Also following parameters were determined: the individual area size, the number of vegetative and generative shoots, their distribution within the individual area, and the bare ground size (Fig. 2): Necromass layer was also measured.

RESULTS

THE RATE AND NATURE OF CHANGES IN MEADOW VEGETATION

The forest re-colonization of moist rich meadows close to the forest complex is characterized by the rapid rate of changes in vegetation, reflected in short-lived, consecutive species combinations and early development of forest initial phase (after 15-20 years of abandonment). It is worth noting that the analysed forest comeback is associated with floristic richness in the whole successional series regarding both the species number and their diversity (cf. Figs. 3-6). This has been determined by a specific character of a preliminary situation of the process: a) *Cirsietum salsburgensis* (*C. rivularis*), the first community in the successional series consisted of 124 species among which

Distribution of plant communities in Reski Range (15 ha)

Distribution of populations (200 m²)

Distribution of individuals (25 m²)

Plan of study plots in communities (4 x 1 ha)

Distribution of offspring (1 m²)

Fig. 2. Hierarchical system of areas to study changes in: landscape (15 ha), phytocoenoses (4 x 1 ha), populations (24 x 200 m²), individuals (6 x 25 m²), seed bank (100 x 100 cm²)

Fig. 3. Vegetation succession in abandoned meadows. 0 — preliminary phase — mown meadow;

A — meadow unmown for 3 years; B — for 8 years, C — for 13 years (Phot. J. B. Faliński, J. J. Faliński)

20% were the components of forest phytocoenoses; b) the habitat of *Cirsium* meadows was differentiated into microsites, which favoured the patchiness of vegetation; c) close vicinity of a forest (the Białowieża National Park) explains the constant presence, even in a mown meadow, of seedlings of forest species.

The changes in the vegetation studied were diversified, especially they started and terminated at different time. Hence the meadows unmown for 15 years were the mosaic of various phytocoenose types and aggregations of a few plant species (Fig. 4), the most abundant being *Lysimachio vulgaris-Filipenduletum* (40%), and initial phase of *Salicetum pentandro-cinereae* (30%). The remained area was occupied by aggregation mosaic of such species as: *Filipendula ulmaria*, *Carex cespitosa*, *C. acutiformis*, *Lysimachia vulgaris*, *Salix cinerea*, *S. pentandra*, and small fragments of *Cirsium* meadow.

Succession of phytocoenoses. Successional series from floristically rich *Cirsietum salisburgensis* meadow towards flood-plain forest (*Circaeo-Alnetum*) was initiated and affected by diversified preliminary situation. Consecutive phytocoenoses, such as: *Lysimachio vulgaris-Filipenduletum*, *Filipendulo-Geraniatum* (tall-herb communities), and *Salicetum pentandro-cinereae* (willow brushwood), had many species in common, although their proportions and frequencies changed with the succession.

Community sequence characteristic of flood-plain forest successional series was observed twice: 1) soon after hay-harvest abandonment some species increased rapidly in number which caused fast (5-6 years) formation of polydominant meadow, or 2) when various parts of *Cirsium* meadow were dominated by one or two different species resulting in the replacement of a homogeneous phytocoenose by some of its facies.

1. Changes in the quantitative relations between flood-plain forest components took place. The transformations lay in the domination of species which in a mown meadow community had been represented by only a few individuals. Their percentage cover in mown meadows did not exceed 5-10% while afterwards increased to 30-50% (Fig. 5). Such species include: *Filipendula ulmaria*, *Lysimachia vulgaris*, *Geum rivulare*, *Carex cespitosa* and *C. acutiformis*. If two first species became dominants while other subdominants, then in 7-8 years a meadow was replaced by tall-herb communities, *Lysimachio vulgaris-Filipenduletum* or *Filipendulo-Geraniatum*. In reality these communities formed during the period of increasing domination of *Filipendula ulmaria*, i.e. in the first five years of the meadow abandonment. Well-formed tall-herb community usually developed in 9-11-year-old unmown meadows. However it could persist for various periods of time. If during the period of *Filipendula* domination no individuals of *Salix cinerea* and *S. pentandra* appeared, then tall-herb communities, with practically unchanged spatial structure, could persist on a single site for 15, or more, years. On the other hand, when numerous willow clumps accompanied increasing *Filipendula* domination, then tall-herb community did not form, but initial phase of

Fig. 4. Mosaic of communities and monospecific aggregations formed in the course of 15 years' succession in unmown meadows (0.98 ha)

Salicetum pentandro-cinereae with large proportion of *F. ulmaria* developed. The willow brushwood was well-formed already in 10-12 years, just as, in other meadow parts, *Lysimachio vulgaris-Filipenduletum*. Often both phytocoenose types developed simultaneously in close vicinity, hence their demarcation in space and time was difficult due to the formation of mosaic systems (Fig. 4).

Fig. 5. Proportions of dominants and subdominants in consecutive successional phases: I – meadow unmown for 5 years; II – for 10 years, tall-herb communities; III – for 15 years, tall-herb communities with willows; IV – for 20 years, willow brushwood

2. When various meadow parts were dominated by different species, then some facies of meadow phytocoenose developed. They occupied small, 0.2 to 0.5 ha, areas. After a number of years each facies evolved towards different phytocoenose type, e.g. facies with *Carex acutiformis* – into *Caricetum acutiformis*, facies with *Polygonum bistorta* – into *Polygono-Cirsietum palustris*, facies with *Lysimachia vulgaris* – into *Lysimachio vulgaris-Filipenduletum*, facies with *Geranium palustre* – into *Filipendulo-Geraniatum*. However, only the last two communities led in a relatively short time (9-10 years) to willow brushwood (Fig. 6). Other went through series of indirect transformations, e.g. *Polygono-Cirsietum palustris* was often replaced by aggregations of *Carex cespitosa* or *Filipendula ulmaria*, and only after 9-10 years single individuals of *Salix cinerea* developed between groups of dominants. The facies with *Carex*

after 5 years

(a)

after 8 years

(b)

Description on page 451.

Fig. 6. Transformations of meadow vegetation (a) for 15 years; development of tall-herb communities (b, c) and brushwood (d); e) legend: key symbols of main components of communities

acutiformis persisted the longest, even when willow brushwood grew all around.

Succession of populations. In some parts of *Cirsium* meadow one or two species among 124 components rapidly increased in number. The process commenced almost in the second season of abandonment, and in 4-5 years large monospecific aggregations developed, with their area of 500-2000 m². This concerns following species: *Filipendula ulmaria*, *Carex acutiformis*, *C. cespitosa*, *Lysimachia vulgaris* and *Scirpus sylvaticus*. In few years in various meadow parts these species eliminated, totally or partially, characteristic species combination or *Cirsietum salisburgensis*. Aggregations differed in their further fate, e.g. they could occupy the site even for 5-9 years, surrounded by new phytocoenoses.

The areas of monospecific aggregations and of the phytocoenoses that establish in the course of the succession were comparable (0.2-0.5 ha). Some

aggregations were replaced in a few years by those of another species. Following sequences of dominant populations from meadow to forest species were observed:

- a. *Filipendula ulmaria*, *Carex acutiformis*, *C. cespitosa*, *Salix cinerea*;
- b. *Carex acutiformis*, *Lysimachia vulgaris*, *Salix cinerea*;
- c. *Carex acutiformis*, *Lythrum salicaria*, *Alnus glutinosa*;
- d. *Filipendula ulmaria*, *Salix cinerea*, *S. pentandra*;
- e. *Cirsium palustre*, *Polygonum bistorta*, *Scirpus sylvaticus*, *Filipendula ulmaria*, *Salix cinerea*.

When aggregations of dominants formed a mosaic which preceded forest initiation, and some dominants were replaced by others, then short-lived 2-5 species combinations developed, which could not be classified to any known phytocoenose type. They lasted 8-12 years and were built by: e.g. *Filipendula ulmaria*, *Carex cespitosa* and *Salix cinerea* (Fig. 7), or *Lysimachia vulgaris*, *Carex acutiformis* and *Salix cinerea*.

Fig. 7. Population mosaic of *Filipendula ulmaria* (spots), *Salix cinerea* (checks) and *Carex cespitosa* (circles), with a small proportion of other species. Explanations in Fig. 6e

Biogroup role in the forest succession. In some fragments of mown meadows single individuals of *Salix pentandra*, *S. cinerea*, and *Alnus glutinosa* were left untouched. In some years they formed large clumps composed of a number of tree species (*Salix*, *Betula* and *Alnus*), surrounded by forest herbs like *Anemone*

nemorosa, *Lycopus europaeus*, *Solanum dulcamara*, *Peucedanum palustre*, *Impatiens noli-tangere* and *Cardamine amara*. Such groups grew rapidly due to the emergence of new individuals and vegetative propagation of willows, which in 10-12 years led to the linkage of neighbour biogroups and initiated forest development.

DOMINATION VERSUS FLORISTIC DIVERSITY

It is crucial to the course of forest succession in moist rich meadows that: a) even though an increase in the domination caused some decrease in the species number, floristic richness accompanied the whole successional process; species number ranged from 66 to 124, reaching in patchy vegetation 175 species; b) 12 species (among 124), that became dominant are usually common to meadow, brushwood and forest communities; c) diversity regarding biological form (biennials, perennials), ecological amplitude (forest, meadow, reed-swamp and other species), and various systematic group, has been maintained in the course of the succession.

In spite of the domination of some species in the course of the analysed succession, a considerable decrease in floristic richness (to ten or so species) was observed only locally and ephemerally. Usually, domination of one species eliminated only a fragment of a given phytocoenose type, almost simultaneously initiating the development of another type.

THE ROLE OF INDIVIDUAL SPECIES IN THE TRANSFORMATION OF VEGETATION

The presence of a number of forest species in *Cirsietum salisburgensis* was characteristic of the analysed successional process. Many such species were also present in the course of the whole succession, although their roles in this process and in the structure of consecutive phytocoenoses differed and varied.

In the succession from meadow to *Salicetum pentandro-cinereae* brushwood communities 170 species of vascular plants were present. Among them 28 occurred solely in meadow communities, while 37 — only in forest phytocoenoses. Remaining species were present in consecutive successional phases and formed various floristic combinations.

Only 24 species (12%) play a crucial role in the course of the analysed succession. They can be divided into following groups regarding the nature of their influence:

1. Promotors that stimulate transformations of meadow vegetation and initiate new floristic combinations. They include the species that dominate in the first (1-6) years, hence significantly change quantitative relations between meadow components and, after 8-9 years, by losing their domination enable further development of forest species in the sites now free. These are: *Filipendula ulmaria*, *Lythrum salicaria* and *Lysimachia vulgaris* (Fig. 8).

Fig. 8. Dynamics of spatial structure of *Filipendula ulmaria* population and its effect on the changes in meadow phytocoenose (200 m²). Explanations as in Fig. 6c

Fig. 9. Dynamics of spatial structure of *Carex cespitosa* population and its effect on the changes in meadow phytocoenose. Explanations as in Fig. 6c

2. Inhibitors that hamper species turnover due to the formation of their large long-lived aggregations with high individual density. They include *Carex acutiformis* and *C. cespitosa* (Fig. 9).

3. Conservatives that stabilize phytocoenose structure, like *Salix pentandra*, *S. cinerea* and *Alnus glutinosa*. However, any of the species of two previous groups, being a component of consecutive phytocoenoses, can be conservative at some successional stage, e.g. *Filipendula ulmaria* in brushwood or *C. acutiformis* in reedswamp.

4. Indifferent that are present in the whole course of succession, but do not play any essential role in species turnover. They enclose: *Myosotis scorpioides*, *Caltha palustris*, *Cirsium palustre* and *Galium palustre*.

BIOLOGICAL MECHANISMS OF SPECIES TURNOVER

The role of promoters has been attributed to these species which significantly affect transformation of successive phytocoenoses. They: a) are present in mown meadows; b) exhibit rapid rate of colonization and occupation of abandoned meadows; c) they affect changes in habitat, like water conditions, due to the accumulation of necromass on the ground (*Filipendula ulmaria*, *Lythrum salicaria* and *Lysimachia vulgaris*). Their role is determined by specific individual properties: longevity, dual reproductive mode, capability of forming polycormones, and ability to survive under adverse conditions in the form of dormant subterranean organs.

Due to these properties species turnover is characterized by following processes:

1. Large monospecific aggregations replace rich multispecific meadow.
2. Gaps are formed within aggregations due to their gradual fragmentation.
3. Free microsites within aggregations are colonized by individuals of various species, usually different from those prior to the formation of aggregation.
4. The number of individuals and species in gaps gradually increases causing total or partial elimination of the dominant from the area.
5. Species diversity increases, in the site previously occupied by a dominant there simultaneously grow forest and meadow species, and those common to both phytocoenose types.

Processes of organism rejuvenation and senescence. The individuals of succession promoters are able to multiply the number of their rooted shoots in the multiyear life-cycle. The populations of these species consist of monocormones and diversifies polycormones that comprise from a few to almost a hundred of shoots, while the clones can be composed of several hundred.

In mown meadows individuals of such species like *Filipendula ulmaria*, *Lysimachia vulgaris* and *Lythrum salicaria* are distributed at random and consist of a few (1-6) shoots. In the first 1-7 years on abandoned meadows the

shoot number per individual increases three- to fivefold. Polycormones form large shoot groups with blurred margins, such process leads to the formation of large aggregations and elimination of big fragments of floristically rich meadow (Fig. 8).

The geometric growth of polycormones during the first 5-6 years of their life is crucial to the transformations of meadow communities, especially causes a decrease in the floristic richness. On the other hand, gradual intensification of senescence processes in the polycormone centre leads to the increase in species diversity due to the establishment of individuals of other species in gaps (Fig. 10).

In several-year-old polycormones the processes of rejuvenation and senescence are simultaneous. Their roles in the species turnover are opposite. Rejuvenation, due to the formation of new shoots and rhizome parts, results in polycormone growth. The process favours establishment of monospecific aggregations and eliminates previous species. On the other hand, senescence leads to the desintegration and death of polycormones, giving free space open to the development of individuals of different species, either those already present or new-comers, e.g. forest plants. This process increases floristic richness, as one polycormone, which covered e.g. the area of 0.5 to 2 m², is replaced by many individuals of up to 20 species (Fig. 10).

Architecture of individuals. The structure of individuals, and especially their underground organs, determine whether the site is occupied solely by one individual or shared with many individuals of one or several species. Polycormones as ecological community of rooted shoots favour the former situation, which, regarding morphological properties of polycormone, can be short- or long-term. It is the longest when distances between shoots within a polycormone are small (2-5 cm), while space near the ground is occupied by leaves or rosettes, as in *Filipendula ulmaria*. Also tussock forms, of *Carex cespitosa* and *C. appropinquata* for a long time solely occupy the space. In *F. ulmaria* only senescence of polycormone may loose its structure and enable the other species to enter its area (Fig. 11). In tussock forms of *C. cespitosa* such opportunity increases when their height amounts to 20-50 cm. Then at the tussock base individuals of other species develop, as well as between shoots on its surface. The tussocks of *Carex cespitosa* and *C. appropinquata* are overgrown by individuals of various species (Fig. 9). The individual tussocks form microphytocoenoses with a specific structure and longevity. They desintegrate usually through the growth of *Salix cinerea* individuals, which appear first between the tussocks, and later on their surface.

Species with polycormones loosely-structured, even if their proportion in the phytocoenose is high, do not form monospecific aggregations. Between polycormone shoots numerous individuals of various species develop. These are the properties of species either with linear structure of polycormones (*Carex acutiformis*), or with new shoots growing far from the mother plant centre (e.g. *Lysimachia vulgaris*).

Fig. 10. Desintegration of *Iris pseudacorus* polycormones and senescence of *Filipendula ulmaria* polycormones as biological mechanism of species turnover

Fig. 11. Architecture of 8-year-old polycormone of *Filipendula ulmaria*. Loose structure enables individuals of other species to enter its area

SUCCESSION PHASES FROM *CIRSIIETUM SALIBURGENSIS* TO WILLOW BRUSHWOOD

The formation of monospecific aggregations by some plant components in various sites is a crucial stage in forest succession in abandoned meadows (Fig. 12). This precedes establishment of forest, herb and tree, species. Following periods can be distinguished in the transformation of vegetation in abandoned meadows:

1. The first period lasts 5 years. Changes in vegetation are quantitative. The number of some species, already present in mown meadows, increases rapidly or consecutively. In various meadow parts aggregation with 1-3 species develop. Their domination raises, while floristic richness is still maintained. The meadow so far homogeneous transforms into a mosaic, becomes polydominant.

2. The second period lasts 6-9 years. The changes are qualitative. Species turnover continues, floristic richness decreases. Tall-herb communities, *Filipenduleto-Geranietum* and *Lysimachio vulgaris-Filipenduletum*, develop.

3. The third period lasts 10-15 years. Qualitative changes become more intense. Forest species appear. Species diversity increases. Willow brushwood forms. The development of *Salicetum pentandro-cinerae* is initiated.

communities and in unmown meadows their cover rarely exceeds 5%, in the period of the development of tall-herb communities it increases to 50-70%, locally to 90% (Falińska 1985).

To the species playing an important role in the succession the term "succession promotor" has been applied, first proposed by Piotrowska (1984) for the trees (forest outpost) that initiated the development of biogroups in dune succession.

In the earlier author's studies on populational properties of one of the promotors, *Filipendula ulmaria*, it was suggested that the species formed distinct ecotone populations in the forest-meadow margin with their high density associated with ecotone effect (Falińska 1979, 1986). Only has following the fate of labeled individuals indicated that this resulted from the phase of maximum *F. ulmaria* population size characteristic of the initial stage of willow brushwood, a typical phytocoenose of forest margins. The transient nature of tall-herb communities is caused by short growth phase of promotors (9-11 years) followed by a considerable decrease in their number. However, monospecific *F. ulmaria* aggregations may also persist longer, e.g. for 15 years (Wolf 1979). In the studies on this species its big population size is rather associated with habitat fertility and weak competition than with the phase of population development (Wolf 1979, Balsberg 1982a, b). *Filipendula ulmaria* is one of the species present in natural flood-plain forests (*Circaeo-Alnetum*), being at the same time constant, even though not always essential, meadow component. It considerably increases in number in unmown meadows, forms luxuriant tall-herb communities, and is still present both in the phase of willow brushwood and in spontaneous secondary flood-plain forests (Falińska 1985). The time of regeneration succession of flood-plain forest in abandoned moist and rich meadows has been estimated for 120 years (Faliński 1986a, b).

The process of initiation, development and decline of phytocoenoses undoubtedly results from the processes in and between the populations analysed against their environment, considered broadly.

From the studies on promotors, especially *Filipendula ulmaria*, it may be inferred that consecutive developmental phases of the population are attained in consecutive phytocoenoses of the forest succession in abandoned meadows, i.e.: 1) establishment and increase in population size — in unmown meadows, 2) maximum population size — in tall-herb communities, 3) a decrease in population size — in willow brushwood phytocoenose, 4) dynamic equilibrium of population size — in flood-plain forest.

It has been shown that *Filipendula ulmaria*, and later *Salix cinerea*, in the course flood-plain forest succession in moist, rich meadows play similar role as juniper, and later aspen, in pine forest succession in old fields (Faliński 1980a, b, 1986a, b).

High reproductive effectiveness, i.e. large production of well germinating

seeds, and considerable survival of individuals to reproductive phase enable promotor to colonize unmown meadows rapidly. However, the crucial in the colonization and establishment of promotor is their specific, clonal growth (Harper 1977, Noble et al. 1979). Geometric increase in the shoot number and longevity of underground organs determine the role of polycormonal species in the dynamics of populations and phytocoenoses, and govern their competitive ability. Only do senescence and desintegration of polycormones give the chance to other species to appear within their area. Senescent polycormones are replaced by willows that initiate the development of brushwood. This indicates that competitive ability is closely related to individual age, also confirmed by Kershaw (1962) for *Carex bigelowii*. From the hitherto studies on promotor populations it can be inferred that this is the age structure which is responsible for the course of many populational phenomena and determines the species role in the structure and dynamics of vegetation. Clumped spatial structure is mostly interpreted as population response to habitat microstructure and the effect of uneven dissemination (Harper 1977, Connell and Slatyer 1977). However, an increase in the clumping degree in populations results mainly from the growth of individuals into multishoot polycormones and clone formation. The division of polycormones and senescence of their oldest parts leads to the comeback of random spatial structure of the population, associated with the decreasing proportions of these species in the structure of consecutive phytocoenoses.

The observations conducted so far on the dynamics of populations against the phytocoenose transformations in dunes (Symonides 1979a, b, c), meadows (Falińska 1979, 1985, 1986) and fallows (Faliński 1980a, b, 1986a, b) indicate that only some species affect the successional process. It has been found that in forest succession in meadows long-term role of one species is reflected in the relation: consecutive phytocoenose — consecutive phase of population development. If the promotor domination (maximum population size) continues, it restricts the development of other species. On the other hand, a decrease in the size of promotor population creates favourable conditions for the growth of other components or newcomers. For example, the species with individuals capable of forming multishoot polycormones, occupying large areas, can rapidly colonize the space and considerably limit the development of other plant populations. Such individuals can persist for a long time on the colonized sites due to the rejuvenation of senile structures. For instance, the expansion of *Carex arenaria* population changed specific composition of *Spergulo-Corynephorum*. This process was accompanied by changes in the habitat which resulted in the regresion of most species from the phytocoenose, and made their comeback impossible (Symonides 1979a, b, c). Cryptogams can also inhibit the rate of vegetation transformation through forming compact cover that makes the development of herb and tree seedlings impossible, as in case of lichen and moss "carpets" in poor dry habitats. And

only when they die or are damaged, especially when little vertical "craters" are formed, the development of juniper seedlings becomes possible, the species being a promotor of further, more crucial changes in vegetation in old-fields (Faliński 1986a).

The course of forest succession in abandoned moist, rich meadows is highly complex. Thus, forest phytocoenoses can be preceded by: gradual transformation of meadow phytocoenoses towards tall-herb communities and willow brushwood, development of tree biogroups, or mosaic of monospecific aggregations of some, among 124, meadow components (Fig. 4). The diversified colonization strategy of species present in mown meadows and environment heterogeneity of unmown meadows result in eminent patchiness of vegetation already in a few years (Fig. 8). This explains high differentiation of succession rate and various ways of forest comeback into the Reski Uroczysko.

In the analysis of vegetation dynamics environment heterogeneity and vegetation patchiness have been often discussed both at micro- and macroscale (Whittaker 1975, Whittaker and Levin 1977, Janson and Vegelius 1981, Istock and Scheiner 1987). The diversity of life conditions results in the formation in each environment of a number of niches colonized by various species which can stimulate or inhibit succession (Connell and Slatyer 1977, Drury and Nisbet 1973).

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REFERENCES

- Balsberg A. N., 1982a. Plant biomass, primary production and litter disappearance in a *Filipendula ulmaria* meadow ecosystem, and the effects of cadmium. *Oikos* 38: 72-91.
- Balsberg A. N., 1982b. Seasonal changes in concentration and distribution of supplied cadmium in a *Filipendula ulmaria* meadow ecosystem. *Oikos* 38: 91-99.
- Begon M., Harper J. L., Townsend C. R., 1986. *Ecology: Individuals, populations and communities*. Blackwell Sci. Publ. Ltd Osney Mead, Oxford.
- Connell J. H., Slatyer R. O., 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *Amer. Nat.* 111: 1119-1144.
- Drury W. H., Nisbet T. C. T., 1973. Succession. *J. Arnold Arnor.* 54: 331-368.
- Falińska K., 1979. Modifications of the populations in forest ecosystems and their ecotones. *Pol. Ecol. Stud.* 9: 89-150.
- Falińska K., 1985. Demography of coenopopulations of forest herbs. In: *The population*

- structure of vegetation, J. White (ed.). Dr W. Junk Publishers, Dordrecht-Boston-Lancaster, pp. 241-264.
- Falińska K., 1986. Demography of *Iris pseudoacorus* populations in abandoned meadows. Ekol. Pol. 34: 583-613.
- Falińska K., 1988. Osobnik, populacja, fitocenoza. PWN (in press).
- Faliński J. B., 1966. Antropogeniczna roślinność Puszczy Białowieskiej jako wynik synantropizacji naturalnego kompleksu leśnego. Disertationes Universitatis Varsoviensis 13: 1-256.
- Faliński J. B., 1980a. Vegetation dynamics and sex structure of the populations of pioneer dioecious woody plants. Vegetatio 43: 23-38.
- Faliński J. B., 1980b. Changes in the sex- and age-ratio in populations of pioneer dioecious woody species (*Juniperus*, *Populus*, *Salix*) in connection with the course of vegetation succession in abandoned farmlands. Ekol. Pol. 28: 327-365.
- Faliński J. B., 1986a. Vegetation dynamics in temperate lowland primeval forests. Ecological studies in Białowieża forest. Geobotany 8: 1-537. Dr W. Junk Publishers, Dordrecht-Boston-Lancaster.
- Faliński J. B., 1986b. Sukcesja roślinności na nieużytkach porolnych jako przejaw dynamiki ekosystemu wyzwolonego spod długotrwałej presji antropogenicznej. Cz. 1 i 2. Wiad. Bot. 30: 25-50. 115-126.
- Grime J. P., 1979. Plant strategies and vegetation processes. John Wiley Sons, Chichester-New York-Brisbane-Toronto.
- Harper J. L., 1977. Population biology of plants. Academic Press. London-New York-San Francisco.
- Horn H. S., 1974. The ecology of secondary succession. Amer. Rev. Ecol. Syst. 5: 25-37.
- Istock C. A., Scheiner S. M., 1987. Affinities and high-order diversity within landscape mosaics. Evol. Ecol. 1: 11-29.
- Janson S., Vegelius J., 1981. Measures of ecological association. Oecologia 49: 371-378.
- Kershaw K. A., 1962. Quantitative ecological studies from Landmannahellir, Iceland. II. The rhizome behaviour of *Carex bigelowii* and *Calamagrostis neglecta*. J. Ecol. 50: 171-179.
- Maarel v.d.E., 1980. Succession. Dr W. Junk Publishers, The Hague-Boston-London.
- Noble J. C., Bell A. D., Harper J. L., 1979. The population biology of plants with clonal growth. I. The morphology and structural demography of *Carex arenaria*. J. Ecol. 67: 983-1008.
- Piotrowska H., 1984. Studia nad rozwojem mieszanych lasów liściastych na nadmorskich wydmach (in press).
- Rabotnov T. A., 1985a. Fitocenologia. Ekologia zbiorowisk roślinnych. PWN, Warszawa.
- Rabotnov T. A., 1985b. Dynamics of plant coenotic populations. In: The population structure of vegetation, J. White (ed.). Dr W. Junk Publishers, Dordrecht-Boston-Lancaster, pp. 121-142.
- Symonides E., 1979a. The structure and population dynamics of psammophytes on inland dunes. I. Populations of initial stages. Ekol. Pol. 27: 3-37.
- Symonides E., 1979b. The structure and population dynamics of psammophytes on inland dunes. II. Loose-sod populations. Ekol. Pol. 27: 191-234.
- Symonides E., 1979c. The structure and population dynamics of psammophytes in inland dunes. III. Populations of compact psammophyte communities. Ekol. Pol. 27: 235-257.
- White J. (ed.), 1985. The population structure of vegetation. Dr W. Junk Publishers, Dordrecht-Boston-Lancaster.
- Whittaker R. H., 1975. Communities and ecosystems. McMillan Publ. Co., New York.
- Whittaker R. H., Levin S. A., 1977. The role of mosaic in natural communities. Theor. Pop. Biol. 12: 117-139.
- Wolf G., 1979. Veränderung der Vegetation und Abbau der organischen Substanz in aufgegebenen Wiesen des Westerwaldes. Schr. Reihe Vegetationskde 13: 115.

Procesy populacyjne roślin w toku sukcesji na porzuconych łąkach. 1. Zmienność i różnorodność kombinacji florystycznych oraz biologiczne mechanizmy wymiany gatunków

Streszczenie

Badania nad tempem i istotą przemian roślinności łąkowej po zaprzestaniu koszenia łąk prowadzono przez 15 lat (1974-1988) na obszarze Puszczy Białowieskiej. Procesy sukcesji śledzono na różnych poziomach organizacji roślinności, stosując w tym celu hierarchiczny system powierzchni o różnej wielkości (rys. 1, 2). Obserwowano przemiany krajobrazu roślinnego na 15 ha, fitocenozy — 4×1 ha, populacji — 24×200 m², rozwój osobników — 6×25 m². Las powraca na porzucone łąki w niejednakowym tempie i w różny sposób, a mianowicie: a) przez stopniowe przekształcanie fitocenozy łąkowych w ziołoroślowe, a następnie w zaroślowe — proces ten trwa około 15 lat; b) przez powstawanie mozaiki jednogatunkowych agregacji kilku spośród 124 komponentów zbiorowisk łąkowych — trwałość tych agregacji jest różna (od 5 do 15 lat); c) przez rozwój bezpośrednio w runi łąkowej biogrup drzew, które stanowią fortpocztę lasu. Różnorodność w przebiegu sukcesji na łąkach jest efektem heterogenności ich siedlisk (mikrorelief, poziom wody) i wielości strategii kolonizacji gatunków obecnych w sytuacji poprzedzającej sukcesję. Ich znaczenie w sukcesji jest różne, mogą: 1) stymulować przebudowę fitocenozy łąkowych i inicjować powstawanie nowych (promotorzy), 2) ograniczać wymianę gatunków wskutek tworzenia długotrwałych agregacji (inhibitorzy), 3) nie odgrywać istotnej roli w przemianach roślinności (indefe-rentnych).