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Primary and secondary succession on wooded peat-bogs

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Abstract

Study of primary and secondary succession on wooded peat- bogs are presented. Research has been done on a complex of mountain peat-bogs in the Bohemian Moravian Highland (Czechoslovakia). Natural succession series began with reed sedge and reed stands and terminated with *Viccinio uliginosi-Pinetum*, *Calamagrostio villosae-Piceatum* and *Alnion glutinosae* uder oligotrophic, oligo-mesotrophic and meso-eutrophic conditions, respectively. In marginal parts of peat-bogs (lagg) sedge fens are followed by birch carr. Open pine stands (*Pino rotundatae-Sphagnetum*) is submitted to cyclic succesion. The secondary succession may begin with the *Sphagnum cuspidatum*, *Eriophorum angustifolium* or *Carex rostrata*, and *Carex rostrata* stages, depending on trophic conditions of water. The final stage is usually *Vaccinio uliginosi-Pinetum* or *Pino rotundatae-Spagnetum*. Secondary succession pattern is influenced both by eutrophication and peat-land drainage.

Key words: wooded peat bogs, succession, Pinus rotundata, Czecho-Slovakia

INTRODUCTION

This article is devoted to the memory of an eminent scientist, Prof. Dr. Stanisław Kulczyński, who first elucidated the causal dependence of vegetation dynamics on subcontinental peat-bogs (K u l c z y ń s k i 1940). I would like to present results obtained while doing research on Central European wooded peat-bogs with *Pinus rotundata* including the generalization of long-term observations on some Bohemian wooded mire complexes. The prformance of the overall mire complexes or of their substantial parts has been the object of long-term observations. The main aim of this type of research was not only to contribute to the theory of succession but above all to recognize the possibilities of peat-bog conservation in the exploited agricultural landscape, and of the recovery of those dead or of those almost completely disturbed parts of mires.

MATERIAL AND METHODS

Research of dynamical processes has been done on a complex of mountain peat-bogs in the Žďárské vrchy Hills in the Bohemian Moravian Highlands (Eastern Bohemia, Czecho-Slovakia). Results have been obtained with regard to some wooded peat-bogs in Southern Bohemia. The long-term developmental trends (the seculary succession) were determined according to the peat-deposits layering as well as the mire communities zonation of different gradients (soil moisture, nutrient contents, etc.). Short-term vegetation changes have been carried out in five year intervals, on selected community complexes dating from 1957 to 1988. Data obtained by Klika and Šmarda (1944) have been evaluated as high as possible. Patterns of succession among various mire communities were also estimated according to different types of community zonation in those undisturbed and exploited parts of the peat-bogs in question.

Vegetation sampling and the synthetic evaluation of vegetation units rest upon the Braun-Blanquet method (Braun-Blanquet 1964).

GENERAL CHARACTERISTICS OF WOODED PEAT-BOGS

Wooded peat-bogs under research belong to the Central European type and can be found from the French and Swiss Jura mountains in the West to the Eastern Sudeten-Mountains in the East. They are mainly located in the lower mountains in South Germany (Schwarzwald, Bodenseegebiet, Oberbayern, Böhmerwald), the border mountains of Bohemia (Krušné hory, Šumava, Českomoravská vrchovina, etc.) and in the South Bohemian Basins (the European distribution is depicted in Neuhäusl (1972, p. 89)). Mire complexes of this type occur most frequently in inversion situations in the montane beech forest belt and are rarely found in the upper montane spruce forest belt or submontane (supracolline) mixed oak-fir forests. Their vegetation belongs to the ombrominerotrophic and minerotrophic communities. The upper part of the peat-bogs cannot grow without a stimulation brought about by underground spring (Dohnal et al. 1965). The peat bogs are flat in shape or slightly convex, situated in valleys or on foots of moderate slopes. A well preserved mire complex is covered for the great part by open stands of *Pinus rotundata* with moss layer dominated by bog mosses (*Sphagnum recurvum* agg., *S. nemoreum*, *S. robustum*, etc.). The herb layer is more or less rich in dwarf-shrubs and its composition depends on soil water conditions. On wet sites dominate *Eriophorum vaginatum* and *Oxycoccus quadripetalus*, on less wet sites *Vaccinium myrtillus*, *V. vitis-idaea* and/or *Calluna vulgaris*. This community type has been classified as *Pino rotundatae-Spagnetum* and divided in two phases: wet type with *Eriophorum vaginatum* and dryer type with *Vaccinium* sp. div. — *Calluna vulgaris* (a characteristic in detail has been published by Neuhäusl (1972, 1975)). Treelees peat-bog

communities with *Eriophorum vaginatum* and *Sphagnum recurvum* agg. or with *Sphagnum magellanicum* cover only small parts of undisturbed wooded mire complexes on sites where dystrophic surface water is accumulated or where underground springs of oligotrophic water enhance the soil water saturation. They may be identified with the *Eriophoro vaginati-Sphagnetum recurvi* or with *Andromedo polifoliae-Sphagnetum magellanici*. A mountain pine-birch forest from the alliance *Betulion pubescentis* occur in marginal parts of mire complexes on wet and mesotrophic sites. It occupies relatively shallow organic soils (Carr) and contacts with wet meadows on Anmoor-soils or spurce forest on Gley-Podsols. The terminal stage of development on wooded peatbogs is represented by pine forests with dwarf-shrubs on peaty deposits (*Vaccinio uliginosi-Pinetum*). We find this community mostly in drained parts of peat-bogs. Under natural conditions, this community was probably only fragmentarily distributed in those dry and dead parts of peat-bogs.

Under human influences, most of wooded peat-bogs have been altered in the following different ways: (1) by cultivating meadows and pastures after drainage and recultivation, (2) spruce or pine plantations after drainage and of cutting their natural stands, (3) and in secondary developmental stages after peat digging. Dynamic changes in the natural parts of mire complexes as well as a recovery of peat-bog communities after peat digging will be characterized in the next sections. Nomenclature of taxa follows Neuhäuslová and Kolbek (1982) nomenclature of syntaxa Rybníček et al. (1984).

NATURAL (SECULARY) SUCCESSION

Deposits on the bottom of the sedimentary pan indicate that the seculary succession began in shallow water with communities which may be characterized as reed or reed-sedge swamps or carrs. The geomorphologic situation and the occurrence of different kinds of rocks allow a presumption that the primary natural succession takes place in different types of the original environment.

In the peat-bog under research the following may be distinguished:

1. Succession under oligotrophic conditions in those parts of the basin where oligotrophic rocks form the bottom of the sedimentary pan (Fig. 1). This succession series began with oligotrophic reed, reed-sedge or high sedge stands which had occupied the shallow parts of the basin. After filling in the water basin, *Phragmites* and *Carex* stands may succeed to litoral reed and high sedge stands that are rich in *Sphagnum recurvum*. Both the reed and sedges could not compete with minero-ombrotrophic *Sphagnum* species. Therefore, after a relatively short period of a mixed sedge-*Sphagnum* stand, followed the development of peat-bog communities with prevailing *Sphagnum recurvum* agg. and *Eriophorum vaginatum*. This community was typical of the damp postglacial period (Atlanticum) and which had dominated the greater part of the peat-bogs. In the dryer periods the growth of the peat suface was retarded and the establishment of adapted pine seedlings was possible. At this time (probably Subboreal), the wooded peat-bog

communities (*Pino rotundatae-Sphagnetum*) had invaded the nearly treeless mire complexes. The terminal stage of the primary succession to the oligotrophic sites corresponding to *Vaccinio uliginosi-Pinetum* was, under natural conditions, very rare; it is possible that this vegetation type, primarily occurring on Anmoor soils in the surrounding of peat-bogs, had invaded deeper peat deposits only after human interference. Therefore, *Pino rotundatae-Sphagnetum* which had stabilized the wooded peat-bog habitat may be considered to be a topoedaphic climax (Nesom and Treiber 1977).

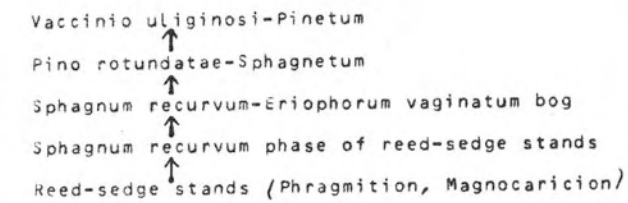

Fig. 1. Patterns of primary succession among peat-bog communities on oligotrophic sites

2. Succession under the oligo-mesotrophic conditions of the Land-forming basin by contact with calcium-rich rocks or under the influence of mineral-rich water from the surroundings. This type of succession takes place in the marginal parts of a Land-forming basin, on the siliceous rocks. All the communities in this series belong to the minerotrophic types (Fig. 2). At the bottom, the *Phragmites communis* peat deposits indicate more eutrophic conditions or a more stable water balance as in the previous series. The course of succession is consonant with the situation in recent landforming basins. In addition to the reed communities, there follow sedge-rich swamps, additional sedge-moss fens that are characteristic of the wet climatic period including birch carrs in dryer climatic periods. Under supplementary water saturation, sedge swamp communities may substitute the phase of sedge-moss fens. The invasion of spruce forest, rich in *Sphagnum girgensohnii*, may be considered to be an impact of artificial drainage.

3. Succession under meso-eutrophic conditions in these parts of the land-forming basin where chalk rocks prevail and which are under the influence of water flowing from chalk sediments. The productive stands of *Phragmites communis* began the succession under litoral conditions; these succeeded, having filled in the basin, to high-sedge communities invaded by *Alnus glutinosa* which tended to stabilize this habitat (Fig. 3). Only in those parts continuously saturated with mineral-rich water fen communities of the *Scheuchzerio-Caricetea fuscae* type developed instead of alder swamps. At present, both alder swamps and sedge fens are extremely rare because most of them have been drained and turned into productive mesophilous meadows.

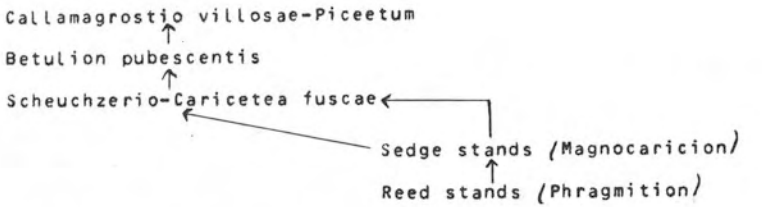

Fig. 2. Patterns of primary succession among peat-bog communities on oligo-mesotrophic sites

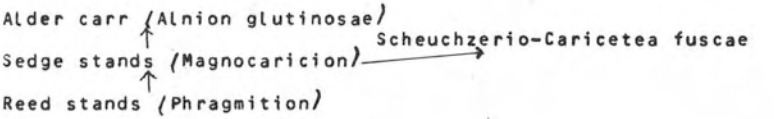

Fig. 3. Patterns of primary succession among peat-bog communities on meso-eutrophic sites

4. In marginal parts of peat-bogs (lagg) where surface water from the central part of the mire intercepts and flows away, very young succession series may be found. There is evidence that the lagg is permanently shifting across the mire border if the peat-bog grows. Two types of communities have been identified in the lagg-zone only (Fig. 4): sedge fens rich in mineral substances (Anmoor) followed by birch carr. The outer margin of the lagg is usually represented by minerotrophic small-sedge communities of *Scheuchzerio-Caricetea fuscae* on Anmoor soils.

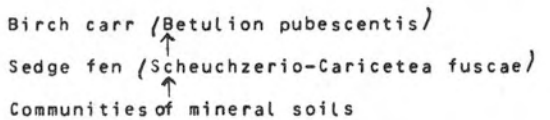

Fig. 4. Patterns of primary succession among peat-bog communities in lagg

It is clear that in different parts of a mire complex a variety of succession processes takes place. In the first stages, the water regime and mineral riches brought about by parent rocks cause the differentiation of initial communites. The heterogeneity of the community pattern grows with the development of the peat-bog. The human impact disturbes the natural structure of the mire complexes and enhances the biological diversity at first. However, the long and intensive human disturbance of peat-bogs has a devastating effect on the community composition.

CYCLIC SUCCESSION IN WOODED PEAT-BOG COMMUNITIES

As mentioned above, open pine stands on growing peat-bog (*Pino rotundatae-Sphagnetum*) represent a steady-state (topoedaphic climax) of the central part of Central European supracolline to montane mire complexes. This equilibrium with present climatic and hydropedological conditions is of a biological nature and is submitted to cyclic and dynamic changes. The establishment of woody plants in mire communities is possible (1) on sites with favorable water conditions, (2) with a sufficient nutritive regime and (3) on those sites where woody plants can germinate and grow successfully together with bog mosses which rapidly elevate the soil surface. There are two site types in those wooded peat-bogs where the establishment of woody plants is possible: (1) In rapidly growing marginal pine birch forests representing the lagg community due to a favorable nutrition regime and by adapting the *Betula pubescens* to a rapid increment, (2) in the central part of peat-bog wooded with *Pinus rotundata* and/or *Pinus sylvestris* ecotypes, where the active surface of peat rises slowly due to the regular dry summer periods. In this ecosystem characterized by the *Pino rotundatae-Sphagnetum* saplings of *Pinus rotundata* and *P. sylvestris*, although they grow slowly, they have good prospects of establishing and competing successfully with slowly growing *Sphagnum* carpets. All the more rapidly growing tree species (*Betula pubescens, Picea excelsa*, etc.) avoid habitats with nutrient-poor soils as well as extreme physical soil conditions. The establishment of pine seedlings occurs in *Sphagnum recurvum* bogs if the actual growth of the peat surface decreases from about 20 or more mm per year to about 10 or less mm per year. This situation is brought about by the decrease of the groundwater level, particulary during the dry summer season. In subcontinental wooded peat-bogs, W e b e r (1902) discovered that pine seedlings may survive only in those parts of the mires where bog mosses grow very slowly. Young trees of the *Pinus sylvestris* f. *furfosa* may remain alive if their root-neck is not deeper than 15 to 20 cm.

The invasion of pine seedlings into the *Sphagnum recurvum* bog and their establishment evokes a further decrease of the groundwater level because of the enhanced transpiration. This process leads to an inhibition of the *Sphagnum recurvum* growth and to the development of dwarf-shrubs and to the penetration of forest mosses. After establishment of pines has occurred, the succession of peat-bog vegetation is directed to a forest type that is similar to *Vaccino uliginosi-Pinetum*. The lack of nutrients prevents the development of a closed forest in which a living *Sphagnum* layer cannot survive. This wooded peat-bog ecosystem exists in a steady-state due to the living conditions equilibrium between the open pine stand and closed *Sphagnum* cover. *Pinus rotundata* and *P. sylvestris* may grow under such conditions from 100 to 130 years at most. At this age, they represent adult trees, sometimes more than 10 m high, which cannot keep in the muddy peat, and so they fall down. In that free space, the peat surface recovers. The groundwater level rises due to the interupted transpiration of the

fallen tree (quantitative data in N e u h ä u s l (1975)). Fragments of *Sphagnum recurvum* communities arise respectively in the wooded peat-bog in such a way.

Patterns of cyclic succession described above are depicted in Fig. 5 and presented in terms of phytosociological units. The large-scale change of the *Sphagnum recurvum* (partly *S. magellanicum*) bog into a wooded one presumes a climatic change in the direction to a more continental type of climate. The *Sphagnum recurvum* bog may be invaded by *Pinus rotundata* and *P. sylvestris* relatively soon. A complex of open and wooden peat-bog may succeed to the homogeneous *Pino rotundatae-Sphagnetum* directly or in several stages. At first, on very wet sites, the *Eriophorum vaginatum-Sphagnum recurvum* phase has been established and which is characteristic by very open and young stands of pines. This phase may lead spontaneously to the *Vaccinium-Calluna* phase of the same association or return partly back to the *Sphagnum recurvum* bog if adult trees fall down due to their age or following a windstorm. The *Vaccinium-Calluna* phase represents the terminal stage of peat-bog development. If the climatic and hydrologic conditions stay constant, the wooded pine bog does not turn into the postclimax pine forest (*Vaccinio uliginosi-Pinetum*) but it becomes a complex again with the *Sphagnum recurvum* bog at those places where adult trees fall down. Without human interference, *Pino rotundatae-Sphagnetum* may sustain as the topoedaphic climax of Central European peat-bogs characterized above, considering that under present climatic condition, the growing of peat is very slow.

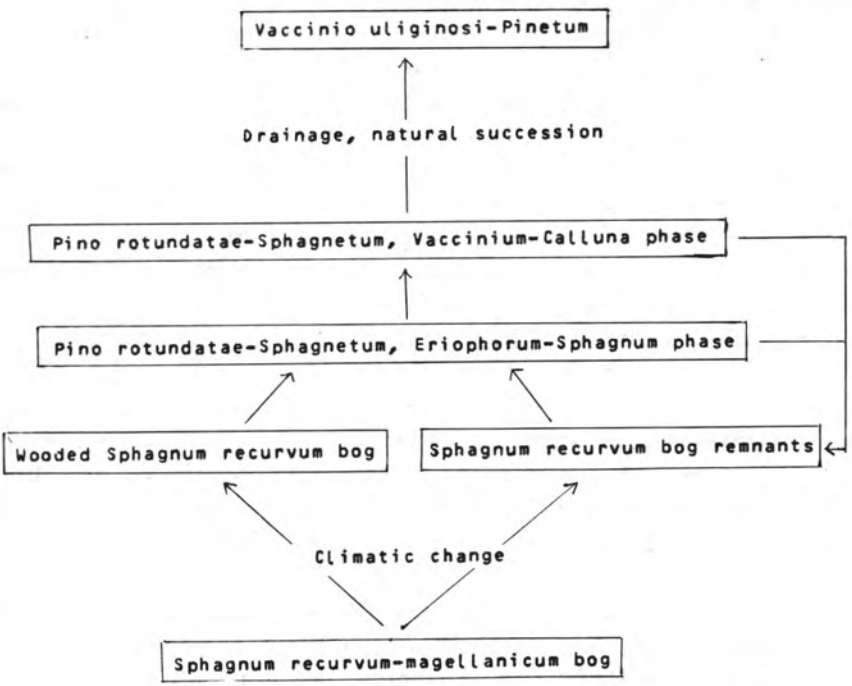

Fig. 5. Patterns of cyclic succession on wooded peat-bog

SECONDARY SUCCESSION

The secondary progressive succession has been studied in pools which arise following the peat digging procedure. As a basis for elaborating the succession, various vegetation zonation patterns have served in pools where the plant cover had recovered as well as the floristic affinity of comparable communities. Changes observed in time reflect a more indirect human impact (eutrophication) or natural events (water disturbance, the flow, etc.).

Patterns of succession among the secondary stages are depicted in Fig. 6. The position of the communities in that picture corresponds to their position on the trophic gredient. The secondary succession may begin with the *Sphagnum cuspidatum* stage in nutrient-poor water, the *Eriophorum angustifolium* or *Carex rostrata* stage under oligo-mesotrophic conditions, *Carex rostrata* stage in mesotrophic water. *Carex* stages prefere slowly moving water. *Carex* and *Eriophorum angustifolium* are relatively selfstanding, rarely make transition types. They represent relatively long-term communities which succeed after filled into the *Eriophorum vaginatum-Sphagnum recurvum* stage. The *Sphagnum cuspidatum* stage occupies with floating bog mosses the deepest part of those pools characterized by dystrophic stagnate water. After filling in the upper part of the water column, this stage succeeds the *Sphagnum recurvum* cover which in some cases (e.g. if *Sphagnum cuspidatum* is absent) may begin the secondary succession as well. The *Sphagnum recurvum* stage usually forms floating islands or blankets. The *Eriophorum vaginatum-Sphagnum recurvum* stage represents an analogue of the natural *Sphagnum recurvum* bog which is dependent on supplementary water saturation from underground springs. Because of an absence of springs in water pools formed after the peat-digging process, the *Eriophorum vaginatum-Sphagnum recurvum* stage represents only a short phase of development. The secondary succession continues with a long-term final stage in which pioneer three *Betula pendula*, together with *Picea abies* and *Pinus sylvestris* are established. At this stage, some elements of peat-bog vegetation (*Eriophorum vaginatum*, *Sphagnum recurvum*, etc.) remain but dwarf-shrubs (*Calluna vulgaris*, *Vaccinium uliginosum*, *V. vitis-idaea*) and grasses (*Molinia caerulea*, *Deschampsia flexuosa*) represent the field cover dominants. Further succession to the *Vaccinio uliginosi-Pinetum* depends on the depth of the peat layer, hydrologic conditions and human interference. In some peat-bogs, under a favourable groundwater regime and hydrochemic conditions, the direct succession of the *Eriophorum vaginatum-Sphagnum recurvum* stage to the *Pino rotundatae-Sphagnetum* may be hypothesized (e.g. the Červené blato peat-bog in Southern Bohemia).

With the exception of the *Sphagnum cuspidatum* stage, we found under the natural peat-bogs plant communities the analogic types to the stages of secondary succession. Sedge fenns in lagg represent natural (partly semi-natural) communities which may be compared with those stages dominated by *Erio-*

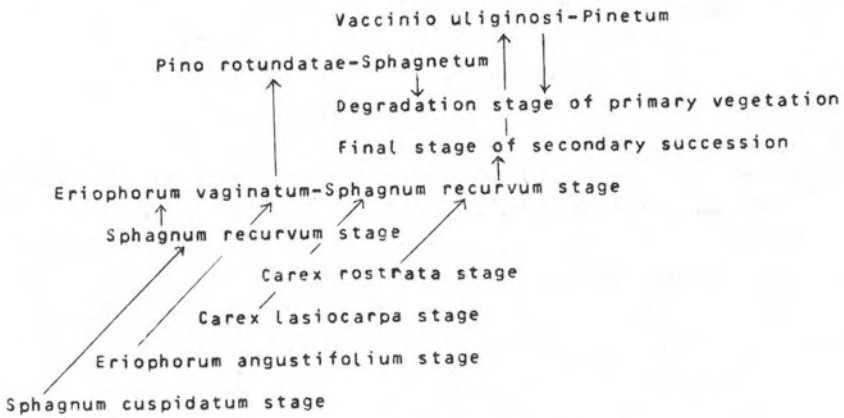

Fig. 6. Patterns of secondary succession of peat-bog communities

phorum angustifolium, *Carex lasiocarpa* and *C. rostrata*. While natural communities are rich in species and resistent to disturbances, secondary stages represent monocoenoses which are more vulnerable. The *Sphagnum recurvum* stage is analogous to wet variants of the *Eriophoro-Sphagnetum recurvi*. Though the structure of both types is more similar as in the case of the sedge communities, the secondary stage is evidently less diverse. The following *Eriophorum vaginatum-Sphagnum recurvum* stage corresponds to those typical stands of *Eriophoro vaginati-Sphagnetum recurvi*. The differences between secondary stages and natural communities are similar as in the *Sphagnum recurvum* bogs. Some characteristic species of *Oxycocco-Sphagnetea* as well as those lower units such as *Andromeda polifolia*, *Carex pauciflora*, *Sphagnum magellanicum*, etc. are missing. *Carex nigra* and indicators of partial desiccation, such as *Molinia caerulea* and *Potentilla erecta* are of an invading nature. The final stage of secondary succession may be considered to be a long-term transitional phase to *Vaccinio uliginosi-Pinetum*. Also *Pino rotundatae-Sphagnetum*, if developed on recovered sites following the peat-digging process, is relatively poor in species and lacking some characteristic species and disturbed by an invasion of minerotrophic species as well as indicators of an unfavourable water balance.

From this point of view, the recovery of natural mire vegetation in disturbed parts of peat-bogs may be considered to be a very long-term process which need not lead to a full restitution of natural ecosystems. Therefore, the rigorous protection of well-preserved mire complexes belong to the main tasks of nature conservancy.

MAN CONDITIONED CHANGES

This type of dynamics may be divided into the changes performed directly in the peat-bogs or in their immediate surroundings (mostly regressive succession)

and those concerning great territorial till global extend. The direct human impact on peat-bogs began a long time ago but it had achieved an important significance in the second half of the last and in the first half of this century. Marginal, dryer and rich nutrient parts have been involved in the first place.

The regressive succession is evident in two community types. Dryer marginal pine forests (*Vaccinio uliginosi-Pinetum*) and wet birch carrs (*Betulion pubescentis*) have been altered following deforestation into semi-natural wet meadows (*Scheuchzerio-Caricetea fuscae*). Following a deeper drainage, sedge meadows have been turned into pastures (*Nardo-Festucetum capillatae*) or into regulary moved, partly after the first harvest grazed mesotrophic meadows (*Molinion caeruleae*). The succession patterns are depicted in Fig. 7.

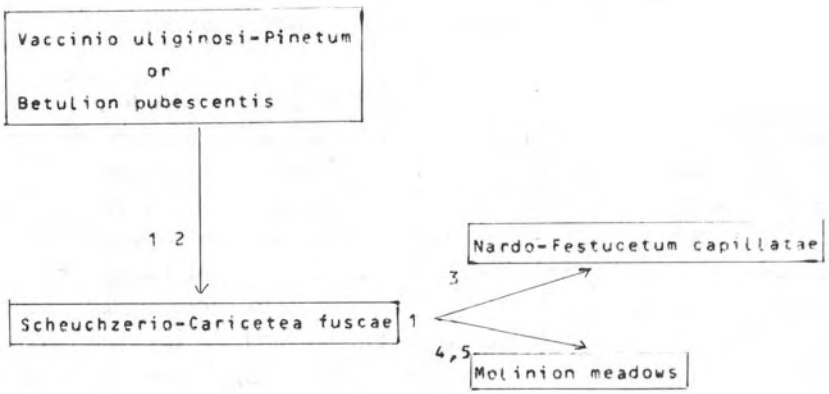

Fig. 7. Regressive succession patterns of pine forests and birch carrs. 1 — drainage, 2 — deforestation, 3 — grazing, 4 — mowing, 5 — manuring

More eutrophic alder carrs have also been deforested and drained. In the first step mesotrophic and partly calcifilous wet meadows (*Caricion lasiocarpae*) occupy the deforested and drained area. Following further drainage, these stands may turn into pastures (*Nardo-Festucetum capillatae*) or into richer productive meadows of the *Molinion* alliance (Fig. 8).

The regressive anthropogenic succession within the tree formation has been observed only through changes of the pine forest (*Vaccinio uliginosi-Pinetum*) or of the wooded peat-bog (*Pino rotundatae-Sphagnetum*) into a degradation stage with an open tree layer, shrubs and a closed dwarf-shrub layer (Fig. 6).

The effect of human activity is highly variable and in some cases leads to higher stages of succession which has been almost always disturbed in different ways. A progressive anthropogenic succession is evident from the following most frequent changes.:

1. Succession of *Pino rotundatea-Sphagnetum* to *Vaccinio uliginosi-Pinetum* caused by artificial, mostly indirect lowering of the groundwater level.

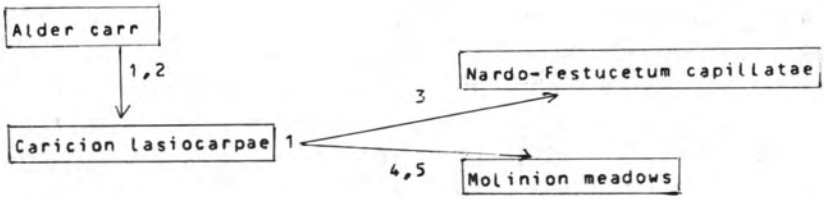

Fig. 8. Regressive succession patterns of alder carrs. 1 — drainage, 2 — deforestation, 3 — grazing, 4 — mowing, 5 — manuring

2. Succession of birch carrs (*Betulion pubescentis*) to pine forests (*Vaccinio uliginosi-Pinetum*) brought about by an intense drainage of stands including the substantial lowering of the groundwater table.
3. Succession of birch carrs to spruce forests (*Calamagrostio villosae-Piceetum sphagnetosum*), spruce being favoured in contact stands and birch and pine being artificially depressed in carrs. In this case, a bilogical drainage effect of spruce is evident.

Large scale environmental changes in the last decades also evoke some modifications of expected succession patterns in wooded peat-bogs. Primary succession appears to be accelerated by means of general landscape desiccation. Topoedaphic climax (*Pino rotundatae-Sphagnetum*) tends to turn into pine forests which cannot recover the peat-bog ecosystem through cyclic succession. Open *Sphagnum recurvum* bogs reduce their extent and create complexes with initial stands of *Pino rotundatae-Sphagnetum*. Eutrophication is evident on open peat-bogs: minerotrophic plants as *Eriophorum angustifolium* and sedges arise their dominance, ombrotrophic species (*Carex pauciflora*, *Sphagnum magellanicum*, etc.) retreat. The evelation of the nitrogen supply has not been observed in vegetation changes of wooded mire communities.

Secondary succession patterns are influenced both by eutrophication and landscape desiccation. The *Sphagnum cuspidatum* stage reduces its area of distribution and is substituted by the more eutrophic and less hydrophilous *Sphagnum recurvum* stage. The last one terminates its active phase developing the moss stage with *Polytrichum strictum* which proceeds directly to the final stage. Under the present environmental conditions, the *Eriophorum vaginatum-Sphagnum recurvum* stage tends to develop on to the final stage in shorter intervals. The tree establishment may be observed not only in the final stages but also earlier on moss islands arising on younger succession stages. The effect of acid rain has not been found in any community type in spite of having observed some slight damage done to the spruce in the distribution area of wooded peat-bogs.

DISCUSSION

Wooded peat-bogs under research belong to the Central European type and occupy inversion situations in the belt of montane beech forests, rare in upper montane spruce forests or submontane oak-fir forests. They are flat in shape or slightly convex, situated in valleys or on foot of moderate slopes. The prevailing vegetation belongs to ombro-minerotrophic mire types. The natural mire complexes are covered for the great part by open pine stands (*Pine rotundatae-Sphagnetum*). Treeless peat-bog communities (*Eriophoro vaginati-Sphagnetum, Andromedo polifoliae-Sphagnetum magellanici*, etc.) cover only lesser parts on very wet sites. The birch-pine carr is situated in marginal parts, in s.c. lagg. The pine forest (*Vaccinio uliginosi-Pinetum*) represents the driest community and grows only in dead parts of wooded peat-bogs.

Four types of natural (seculary) succession have been distinguished in the model peat-bog. Different types of succession take place in different parts of the land forming basin; they depend also on the trophic status of rocks forming the basin and on the situation in the topographic and hydrologic gradient (marginal parts, central parts). (1) Succession under oligotrophic conditions is characteristic for the central parts of peat-bogs if oligotrophic rocks constitute the bottom of the basin. (2) Succession under oligo-mesotrophic conditions in contact with calcium-rich rocks or under the influence of mineral-rich water from the surroundings. (3) Succession under meso-eutrophic conditions in those parts of the land-forming basin where chalk rocks prevail and which are under the influence of water flowing from chalk sediments. (4) Succession in marginal parts of peat-bogs (lagg) where surface water from the central part of the mire intercepts and flows away. The relevant succession patterns are depicted in Figs. 1-4.

Open pine stands on growing peat-bog (*Pino rotundatae-Sphagnetum*) represent a steady-state (topoedaphic climax) of the great part of wooded peat-bogs. Their equilibrium with present climatic and hydropedological conditions is of biological nature and is submitted to cyclic dynamic changes (Fig. 5.).

The secondary progressive succession (Fig. 6) may be partly compared with the primary natural succession. All the analogic communities of the natural succession are more diverse, rich in species, more supplied with characteristic species and poor in indicators of the human impact. From this point of view, the recovery of natural vegetation in disturbed parts of peat bogs may be considered to be a very long-term process which need not lead to a full restitution of natural ecosystems.

The man conditioned dynamic changes may be divided into changes performed directly in peat-bogs or in their immediate surroundings and those concerning great territoria. The first group belongs to regressive succession which occurs in marginal or dryer parts of peat-bogs in the first place. The most

typical changes are depicted in Figs. 7 and 8. The progressive secondary succession is stumulated by the artificial drainage and leads to degradation of natural mire communites which are changed into pine or spruce forests.

Large scale environmental changes evoke some modifications of expected succession patterns. Primary succession appears to be accelerated by means of general landscape desiccation. Eutrophication is evident on open mire communities: minerotrophic plants arise their dominance, ombrotrophic species retreat. The evelation of the nitrogen supply has not been observed in vegetation changes of wooded peat-bog communities.

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Pierwotna i wtórna sukcesja na leśnych torfowiskach wysokich

Streszczenie

Badano procesy pierwotnej i wtórnej sukcesji w zalesionym kompleksie torfowisk górskich na Wyżynie Czesko-Morawskiej (Czecho-Słowacja). Sukcesję pierwotną inicjują zbiorowiska szuwarowe lub turzycowiska (*Phragmition* albo *Magnocaricion*), a kończą zbiorowiska *Vaccinio uliginosi-Pinetum* (w siedliskach oligotroficznych), *Calamagrostio villosae-Piceetum* (w siedliskach oligo-mezotroficznych) lub *Alnion glutinosae* (w siedliskach mezo-eutroficznych). W okrajkowych partiach torfowisk niskoturzycowe zbiorowiska z klasy *Scheuchzerio-Caricetea fuscae* zastępowane są przez brzeziny ze związku *Betulion pubescentis*. Zbiorowiska otwartych i aktywnie rosnących partii

torfowisk, reprezentowane np. przez *Pino rotundatae-Sphagnetum*, stanowią stadia klimaksowe, ustabilizowane z obecnymi warunkami klimatycznymi i hydrologicznymi. W zbiorowiskach tych zachodzą cykliczne zmiany sukcesyjne. Sukcesja wtórna, w zależności od warunków troficznych wod, może rozpoczynać się od zbiorowisk ze *Sphagnum cuspidatum*, *Eriophorum angustifolium* i *Carex rostrata* lub z *Carex rostrata*. Zbiorowiskami końcowymi są wówczas *Vaccino uliginosi-Pinetum* lub *Pino rotundatae-Sphagnetum*. Stadia i tempo sukcesji wtórnej mogą być modyfikowane przez eutrofizację siedlisk i osuszanie terenów.