

Report

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Autogenic Succession in Boreal Mires — A Review

Keywords

Autogenic succession, Bog, Community structure, Soil conditions, Surface topography.

Abstract

ZOBEL M. (1988): Autogenic succession in boreal mires — a review. — *Folia Geobot. Phytotax., Praha*, 23: 417–445. — The main features of autogenic bog development are discussed. Using extensive literature the changes in vegetation, surface topography, soil environment and hydrology are characterized. Oligotrophy and low pH seem to be the most important factors directing bog succession. The decrease in decomposition rates correlates with increase of the content of dissolved oxygen in the soil water. Due to substantial changes in local environment bog succession should be considered first of all as an ecosystem process. In comparison with mineral land communities bog succession is characterized by more deterministic development. Both successional convergence and divergence are observed. In every case the concrete character of bog dynamics depends on the spatial and temporal scales of investigation.

1.1. Succession theory — a brief introduction

Succession theory has played a central role in plant ecology (for reviews see ALEKSANDROVA 1964; KNAPP 1974; GOLLEY 1977 and MILES 1979). The classical interpretation of succession as the development of vegetation through discrete stages culminating in a climax was introduced mainly by COWLES (1899, 1909) and CLEMENTS (1905, 1916), but the notable role of the works of TANSLEY (1920, 1929, 1935) and SUKAČEV (1928) should also be stressed. Simultaneously, an alternative view on succession was developed by GLEASON (1917, 1927). In clementsian theory, and also in its numerous interpretations, succession was considered to be an orderly process of community development that is reasonably directional, and which results from modification of the local environment by the community itself. GLEASON, on the contrary, emphasized the stochastic nature of succession. As per GLEASON, succession is the function of arrival of additional species in the area by migration, invasion (migration, ecesis) and succession (reaction, competition). It seems, however that the initial divergence of the clementsian and gleasonian approaches is amplified through numerous (mis)interpretations, and also by CLEMENTS himself modifying his own earlier ideas. In his earlier work (CLEMENTS 1905), three functions of formations were distinguished: association, invasion (migration, ecesis) and succession (reaction, competition). Thus according to CLEMENTS' initial definition, succession does not involve migration. A similar concept was developed by SUKAČEV (1928, and in a number of later works) who distinguished between syngensis (initial formation of a community) and endoecogenesis (the change of community due to competition and alternation of habitat conditions). According to SUKAČEV, these two processes do not exclude one another.

Beginning with the fifties, the concepts of the spatial pattern of vegetation evolved considerably, but succession theory remained more conservative. The main principles of succession theory, presented by MARGALEF (1963, 1970), E. ODUM (1969, 1971) and WHITTAKER (1975a), do not contain speculative ideas (absolute successional convergence, organismal analogy, etc.) but, in general, do not differ very much from the Clementsian approach. Succession is considered to be an orderly directional process leading to mature climax. Until the seventies, only EGLER (1954) presented some proposals on the classical succession theory, supporting the "initial floristic concept" in addition to the classical "relay floristics". The re-estimation of successional concepts began mainly in the seventies when GLEASON's ideas were supported by a number of authors. Sharp criticism of CLEMENTS can be found in COLINVAUX (1973). DRURY et NISBET (1973) provide a thorough analysis of the existing views and sketch an alternative explanation, based on population processes. Their main conclusion coincides with that of PICKETT (1976): the mechanisms which drive succession are the same as those responsible for the sorting of species on spatial gradients. Species are adapted to positions of the successional gradient in an individualistic manner and thus the so called population parameters are responsible for community succession. The stochastic nature of community succession was discussed by HORN (1975, 1976). CONNELL et SLATYER (1977) present three conceptual models concerning the design of the principal mechanism of succession. PEET et CHRISTENSEN (1980) view succession as a result of underlying plant population dynamics, and the individualistic view of plant community development is also supported by GLENN-LEVIN (1980), PICKETT (1982). Qualitative succession models, operating with life-history parameters, have been developed by KESSEL (1979), CATTELLINO et al. (1979), NOBLEET SLATYER (1980) and VAN DER VALK (1981, 1982, 1985). The role of disturbance regime in managing spatio-temporal patterns of plant communities is emphasized by LOUCKS et al. (1981), HEINSELMAN (1981), HAMILTON (1982), VAN DER VALK (1982), etc. But in system ecology, the holistic view on ecosystems persists, (cf. PATTEN et E. ODUM 1981). H. ODUM (1983) writes that succession is something like self-organization, thus referring to the synergetic nature of ecosystem development. VAN HULST (1980) assumes that vegetation data alone are not always sufficient to predict the community's future stages as sometimes environmental data are needed i.e., one has to study the succession of the ecosystem, not only that of vegetation. Evidently, any one level should not be assumed to be better than any other, and the study of succession must be realized at several organizational levels.

Further, general features of bog development are designed. As per GORE (1983), mire is accepted to be general term and it includes swamps, carrs and fens, which frequently represent earlier successional stages, and also bogs which are final stages. Here the terms bog succession and mire succession are used synonymously assuming that in the boreal zone mire succession ends mostly in the bog stage. Though here only autogenic succession is considered i.e. the self-development of mires, this does not mean that the role of external factors is disclaimed. Moreover, as can be seen in Chapter 9, it is sometimes difficult to differentiate between external and internal factors — it depends on the spatial scale used. Especially in cases when the bog develops in originally less wet site usually carrying forest, the process exhibits the features of allogenic succession and only gradually turns to autogenic development (LISS et BEREZINA 1980, GLEBOV et KORZUHIN 1985).

As to processes succeeding substantial changes in environment (post-fire, post-drainage succession etc.) it is recommended to refer to the special accounts.

2. General course of autogenic bog succession

Information concerning bog succession is mainly gathered in three ways. Two of them — direct observations and side-by-side comparisons — are traditional in successional studies; the former can rarely be used because of the long duration of bog development, but the latter is used more frequently. Due to peat accumulation, initial differences in site conditions disappear and existing differences in peat chemical composition, hydrology, etc. are more or less of successional origin. In his thorough account LOPATIN (1954a) reached the conclusion that the results of stratigraphic investigations and side-by-side comparisons coincide when bog development is studied. Many of the boreal bogs are also in almost virgin state so that differences in management history do not influence the results. The third and most common technique is the study of peat stratigraphy because the composition of peat reflects the floristic composition of earlier communities. But here also serious problems arise — frequently it is difficult to distinguish

which changes represent autogenic succession and which climatic processes. Thus, the stratigraphic information always includes some "climatic noise", the level of which depends upon the time interval studied. Considering that the entire process of bog succession has lasted several thousands of years, it is possible to observe climatic changes even over this duration. There are some references, however, to the effect that the role of climatic processes during several thousand years is not so prominent as is usually assumed (FRENZEL 1983). ILOMETS, ILVES et RAJAMÄE (1984) also demonstrate that many evident changes in peat profiles are not synchronous in the different parts of the same bog (massif) and thus could not be climatically motivated. MÖRNSJÖ (1969) concluded that climate does not influence the principal character of bog succession. Nevertheless it frequently remains extremely difficult to evaluate the proportion of climatic and successional processes. Hence conclusion concerning autogenic bog development should be drawn with some caution when stratigraphic data are used.

Very early ideas concerning bog succession were developed independently in many European countries and usually concerned a few specific regional examples (e.g. in Estonia HUPEL 1774). At the beginning of the 19th century, some generalizations were made about bog development (see GORHAM (1953) for review). In 1810, R. RENNIE considered three ecological factors to be important for bog development: absence of oxygen, low temperature, and lack of fluctuations in moisture and temperature. The description of hydrosere was given by J. A. DE LUC in 1810.

At the beginning of the 20th century, bog succession was studied by a number of authors. Generally, two principal modes of origin of a bog were described: 1) overgrowing and filling-in of bodies of water, i.e. terrestrialization (Verlandung) and 2) bog formation on mineral land, i.e. paludification (Versumpfung) (WEBER 1902, 1908, FRÜH et SCHRÖTER 1904, CAJANDER 1913, SUKAČEV 1926). CAJANDER considered two kinds of paludification — swamping of flood-plains of rivers and swamping of forest soils. In our own day Sjörs (1976, 1980, 1983) also differentiates between two kinds of paludification: a) direct or primary mire formation, i.e. peat being formed upon fresh and moist or wet mineral soil, e.g., after the withdrawal of inland ice from alluvial plains and deltas, onto the land emerging from sea due to crystal uplift and b) paludification of originally less wet land usually carrying forest. KULCZYNSKI (1949) and IVANOV (1953, 1957) consider additionally a special kind of paludification: upslope mire development, which occur sometimes in valleys, but seldom lead to an oligotrophic type of mire. Paludification can also be differentiated according to the origin of the (superfluous) water: either surface or ground water. In the latter case, peculiar spring fens can develop.

Terrestrialization is the classical topic of telmatology and there are a great number of detailed descriptions of this process. Among the authors of the first half of the century SUKAČEV (1906, 1914, 1926), MATTHEWS (1944), ABOLIN (1914, 1928), PEARSHALL (1917, 1921), DOKTUROWSKY (1922, 1927) GODWIN (1936) and RIGG (1940) should be mentioned.

This process was also considered in a general theoretical context by CLEMENTS (1916) and TANSLEY (1939a) and it served as an example of convergent succession towards mesophyte forest. TANSLEY, however, referred to the possibility that blanket bog or raised bog could also be the end point of succession. Paludification, despite its predominance in many areas (cf. Sjörs 1980), has been less investigated. Among earlier attempts, HESSELMAN (1910), CAJANDER (1913), DOKTUROWSKY (1922), SUKAČEV (1926), DURIETZ et NANNFELDT (1925) and AARIO (1932) should be referred to.

SUKAČEV (1906) has also described a peculiar case of paludification — lateral expansion of a mire which initially developed in lake basin. The acceleration of paludification in the surroundings of the mire is also considered by CAJANDER (1913), AARIO (1932), KULCZYNSKI (1949), LOPATIN (1954a), PĚAVČENKO (1953, 1963), NEIŠTADT (1972), FRENZEL (1977), etc.

Recent accounts, dealing with changes in floristic composition of mire communities, using both side by side comparisons and stratigraphic information, can be found in TOLONEN (1967, 1971, 1980), BOGDANOVSKAJA-GUIHENEUF (1969), MÖRNSJÖ (1969), WALKER (1970), OVERBECK (1975), IVANOV (1975), GÖTTLICH (1976), BARBER (1981), LISS et BEREZINA (1981), TALLIS (1983), JURKOVSKAJA (1983), AAVIKSOO, MASING et ZOBEL (1984), RYBNÍČEK (1984), TOLONEN et TOLONEN (1984), PROZOROV (1985) and PĚAVČENKO (1985a), etc. The ecological groups of mire species (BRADIS 1972, LOPATIN 1972) or communities (LOPATIN 1983) also indicate their successional status.

There are several divisions of mire succession into stages, based on vegetation structure, hydrology, nutrient conditions, etc. WEBER (1908) differentiated between three types of mires — Niedermoore, Übergangsmoore, Hochmoore — and between four developmental stages: limnetic, telmatic (plants rooted in shallow water), semiterrestrial (plants rooted above the water level but seasonally flooded) and terrestrial. ABOLIN (1914) observed two stages: limnogenous (the main

nutrient supply originates from the waterbody), soligenous (nutrients originate from rain). SUKACĚV (1926) based his division on differences in the composition of plant communities. KULCZYŃSKI (1949) differentiated between three mire types: rheophilous, transitional and ombrophilous. DURIEZ (1949) introduced the terms minerotrophic and ombrotrophic mire; between them some transitional units could also be distinguished. LOPATIN (1954a) established six mire types (corresponding to successional stages) according to the trophic conditions: eutrophic homogenous, eutrophic with mesotrophic patches, eu-mesotrophic, mesotrophic, meso-oligotrophic, oligotrophic, and, adding later (e.g. LOPATIN 1983), dystrophic type.

The fact that the morphology of bog surface changes during succession was already considered by CAJANDER (1913) and OSVALD (1923). Further, these facts were studied by GALKINA (1946) and IVANOV (1953, 1957). They differentiate between five stages of bog development from the point of view of the topography of a bog and ignoring eutrophic stages: flat mesotrophic mire weakly convex mire with oligotrophic centre, forested bog, convex bog with forest on slopes and bogs with developed ridge-hollow structure. They remark that the regression could further take place in the bog centre. LOPATIN (1954a) gives similar but a somewhat more elaborated division. MASING (1958, 1984), distinguished five structural types of oligotrophic mires, which replace one another in the following order: bogs with a sparsely wooded centre → slightly convex bogs with woody margins and young hollows in its central parts → convex open bogs with parallel hollow rows and sometimes pools on slopes → flattened open bogs with irregular hollow and pool areas or secondary lakes in the centre → open bogs with a slightly concave centre where a water track has broken out. The last stage indicates the formation of a compound bog system or bog massif, consisting of several relatively independent components.

Using aerial photographs, MASING gives minimal diameters of each stage.

MOORE et BELLAMY (1974) also separate five stages of mire development, covering the entire successional process and not only the final stages. The first — initial peat accumulation can take place in two ways, depending upon the water flow directed either below the floating mat or above the peat. During the second stage, which consists of two phases, the accrual of peat tends to canalise the main flow. At the third stage the peat growth diverts the inflow from the basin and during the fourth stage the water input is restricted to rainfall. At the final stage, the mire surface rises above the height of the vertical oscillations of the ground water.

Some attempts have also been made to distinguish the main bog processes (like the six vegetation processes of CLEMENTS), each of which predominates at certain stages of mire succession. As per IVANOV (1957), there are also six main processes: initial peat accumulation, lateral expansion of peat accumulation, replacement of plant communities, change in hydrobiological conditions, changes in bog microrelief and erosion processes. The division of HEINSELMAN (1963) is somewhat different: lake filling, lateral expansion, upslope peat advance, isolation of sites from mineral waters, rise of the peat surface and local water table and development of patterned communities. General features of the changes in functional structure of the bog ecosystem during bog succession are suggested in PĚAVČENKO (1984) where replacement of plant communities is accompanied by changes in the composition and quantity of consumers and decomposers.

Unlike the study of succession of mineral land communities successional changes in species diversity or, simply, richness of mire communities have never been the object of serious discussion. Generally, the change in a number of mire plant species is well documented in many descriptions of community succession, and this clearly depends on the initial conditions. In case of primary mire formation, the diversity increases due to the colonization of the bare substratum by invading species. In other cases the change in diversity during terrestrialization or paludification depends upon the diversity of the primary community. Where the environment is poor in lime (e.g. poor fen, pine forest on podzolic soil etc.), there are no remarkable successional trends in diversity values; sometimes, only a slight decrease in diversity can be observed. But when the starting point of mire succession represents some kind of "rich" community on a calcareous substratum, the decrease in species diversity during the succession is remarkable. The results of observations are dependent upon the spatial scale used (whether the microvariation of bog surface pattern is included or not) and the list of organisms studied.

Standing crop and primary productivity estimations concerning different mire types, including different successional stages, are summarized in accounts by MOORE et BELLAMY (1974), BOTCH (1978), BOTCH et MASING (1979), BRADBURY et GRACE (1983), cf. also MALMER (1975), ILOMETS (1980, 1981) and PĚAVČENKO (1984, 1985a), and thus not repeated here. In general, primary production seems to be higher at earlier successional stages, including both fens and forested mires. The actual productivity estimations may be quite different but taking a very rough annual mean for

boreal mire it could be 700 gr m⁻² in dry weight for fens, 600 gr m⁻² for transitional mires and 500 gr m⁻² for bogs. The realistic upper limit for swamps and marshes is estimated to be 3,500 gr m⁻², and for bogs 1,000 gr m⁻². There are even greater variations in estimated values when the linear increment of *Sphagnum* is taken into consideration, its value depending greatly upon local site conditions. The mean vertical increment of peat in bogs is close to 1.5 mm yr⁻¹.

Taking into account the living biomass, the standing crop is usually higher at early or intermediate stages, but the extremely high variability of this parameter does not permit its presentation in mean values here. The same is true of another parameter — the ratio of below-ground to above-ground biomass. PĚAVČENKO (1967), however, reports its decrease during succession.

In the case of terrestrialization, these trends (decrease of primary production and standing crop) are less expressed than in paludification. When the starting point of succession is a lake with low productivity, both productivity and standing crop increase during the mire development and drop only before the final oligotrophic stages.

In spite of low primary production in bog ecosystems, the deposition of organic matter seems to be among the most rapid types, the average yearly decomposition being only about one third or less of that in other terrestrial ecosystems. The decomposition rate of organic matter clearly decreases during mire succession (MALMER 1975). As concerns the accumulation rate the results are different: 20% (MALMER 1975), 8–33% (PAKARINEN 1975), 4–14% (ILOMETS 1980, 1982), 10% (JELINA et al. 1984) and 16% (KOZLOVSKAJA, MEDVEDJEVA et PĚAVČENKO 1978, PĚAVČENKO 1985a) of primary production is estimated to be deposited as peat.

The decomposition rate, as demonstrated by increasing accumulation, decreases during succession. Such decrease is in accordance with changes in bog habitat conditions (see further), changes in anatomic peculiarities of plant tissues, emergence of certain allelopathic influences, which make the bog environment unfavourable for most soil microbes (cf. CLYMO 1963, 1983, ZAGURALSKAJA 1967, SONESSON 1972, ZAGURALSKAJA et SMANTZEN 1972, KOZLOVSKAJA 1976, KOZLOVSKAJA et al. 1978, DICKINSON 1983 and PĚAVČENKO 1984, 1985a). In bogs, usually, fungi start to predominate over bacteria. The conditions for biogenous fixation of nitrogen also seem to be very unfavourable in bogs, especially due to the acid reaction which does not permit the growth of N-fixing bacteria (*Azotobacter*, *Clostridium*, etc.) and blue-green algae. The purely chemical fixation of ammonium however may be possible (MALMER 1975). PĚAVČENKO (1984) refers to the possibility that ammonium is fixed from the air by *Sphagnum* itself.

The very general trend of bog succession — meiotrophication (sensu Sjörs), i.e. becoming more oligotrophic, does not mean that the ecosystem development is a rigorously determined unidirectional process. The transition probability matrices compiled on the basis of stratigraphic data (WALKER 1970 and AAVIKSOO, MASING et ZOBEL 1984) show that the real picture of successional replacements is predominantly multidirectional, despite the existence of some of the most common successional trends. The great diversity of bog successions is also documented by JELINA et LAR (1980), JELINA et al. (1984), a concrete successional direction being dependent upon initial physiographic-edaphic conditions. Certain successional stages can even be deleted; for example, in some cases, oligotrophic communities typical of final stages already develop during the initial stages. GLEBOV (1970) also points out that when mire succession proceeds in oligotrophic substrate conditions, the mire forest stage is often weakly expressed while in eu- and mesotrophic sites several kinds of paludified forests develop and alternate before the bog phase is reached. PĚAVČENKO (1963, 1967) has even differentiated oligotrophic and eutrophic types of bog development. Thus, mire succession in oligotrophic sites resembles direct or telescoped succession (sensu WHITTAKER et LEVIN 1977, TANSLEY 1929). The multidirectional nature of bog succession is repeatedly stressed by Sjörs (1963, 1980, 1983).

In relation to the continuity or non-continuity of bog succession, only some speculative remarks can be made. One can estimate the continuity of succession using different attributes, e.g., the velocity of change of certain ecosystem parameters or even functional characteristics. KORDE (1960) refers to the noncontinuous character of lake fulfilment. GORHAM (1967) describes the transition from fen to bog: pH slowly decreases from 6 to 5 as organic matter accumulates to about 85% of dry weight. Then as the cationic balance shifts sharply towards hydrogen ion, pH drops to almost 3. Thus, here relatively rapid changes in site conditions and, accordingly, in community composition, as compared to mire succession in general, take place. Such a period of relatively rapid changes may be called temporal ecotone. BARRY et SYNNOTT (1984) also conclude that fen-bog transition is clearly seen to be sharp, this result being fully confirmed by the examination of bryophytes in the profile. TOOM et ZOBEL (unpublished) characterized the trophic conditions in mires by determining the algae growth potential (AGP) in soil water (*Scenedesmus*

brasiliensis was used as indicator algae). A rapid decrease of AGP was observed in intermediate stages (biomasses 12.6 and 1.6 mg/l), when alder-pine carrs with few and abundant *Sphagnum* were compared. Another type of temporal ecotone is described by ILOMETS (1984). The stratigraphic material demonstrates that in a bog complex under investigation a large number of transitions between communities have taken place, but that — certain transitions (usually in one part of the bog) have taken place synchronously during a relatively short time interval. ILOMETS assumes that this should be the result of re-formation of hydrologic network of the bog. The presence of recurrence surface in peat profiles evidently refers to some temporal non-continuity (cf. FRENZEL 1983 and TALLIS 1983 for review).

At the margin of a bog, several types of mire forests are usually found. Such a sequence of communities in space sometimes reflects the sequence in time, but when the dimensions of the bog are quite stable, the marginal forest communities are also more or less stabilized. Thus, the communities which, in principle, represent some intermediate successional stage, are actually in climax stage (i.e. they are relatively stable in the sense that the autogenic succession has almost stopped). Thus, here one meets with "serial climaxes", which could also be called arrested or subclimax, using clementsian terminology, or edaphic climax, as per TANSLEY. Such kinds of ecosystems are supposed to be in unstable equilibrium, because a small change in environmental conditions causes their development towards forest or bog. Transitions between bogs and forests are described e.g. by several Soviet authors (SUKAČEV 1926, KOŠEJEV 1955, PJAČENKO 1963, 1967, 1985a, VOMPERSKIJ 1968, ANTONOVSKI, KORZUHIN et LITVIN 1981, PROZOROV 1981, 1985, GLEBOV et KORZUHIN 1985, ZOBEL 1988a, etc.) and also by American authors investigating forest paludification in Alaska (RIGG 1917, NEILAND 1971, REINERS, WORLEY et LAWRENCE 1971, NOBLE, LAWRENCE et STREVELER 1984). It was demonstrated by ALEKSANDROV et LOGOFET (1984) that trophic and hydrological conditions are both responsible for the further dynamics of the transitional mire ecosystem; changes in trophic conditions themselves do not result in development towards bog. The transition from forest to bog sometimes takes place after forest overcutting or fire, when the total transpiration rate rapidly decreases, part of the nutrients is leached and thus, in moist sites, further paludification takes place.

Finally, it should be mentioned that bog development is considered here without any reference to geographic location. The most important trends and principles of mire succession are evidently common for all bogs in the Boreal zone. For the geographical peculiarities of bog development, KAC (1948) and DAMMAN (1979) are recommended.

So one can see the dualism of autogenic bog succession. On the one hand, the realized successional seres are very diverse. But as the developing mire usually arrives at the oligotrophic stage, the most general trends seem to be more predictable and convergent than, for example, in case of mineral land communities.

3. Changes in bog environment

The most general successional trend in case of bog substrate conditions is meiotrophication or oligotrophication — the creation of more and more oligotrophic conditions (is not true in the case of lake eutrophication stage of course). The more complete descriptions of the successional changes in chemical and physical properties of mire water and peat during succession can be found evidently in Sjörs (1952), GORHAM (1953, 1967), REICHLÉ et DOYLE (1965), BELLAMY (1968), MÖRNSJÖ (1969), HEINSELMAN (1970), MALMER (1975), KARAVAJEVA (1982) and BARRY et SYNNOTT (1984). There are also a number of works where the full successional sere is not considered but a comparison of certain successional stages (e.g. fen, transitional mire, bog) or simply different kinds of mires and peats is given, which provides information about the main alternation of bog environment during succession (SUKAČEV 1926, BULOW 1929, RIGG 1940, TJUREMNOV 1949, NEWBOULD et BORHAM 1956, GORHAM 1956, GORHAM et PEARSHALL 1956, CHAPMAN 1963, TJUREMNOV et LARGIN 1966, PJAČENKO 1967, 1972, 1978, SONESSON 1970, BRADIS 1972, SILLANPÄÄ 1972, TALLIS 1973, GLEBOV et TOLEIKO 1975, TOLONEN et SEPPÄNEN 1976, TOLONEN et HOSTI-SLUOMA 1978, STANEK et al. 1977, DAMMAN 1978, PAKARINEN 1979, GLASER et al 1981, GLASER 1983, KARLIN et BLISS 1984, REINIKAINEN, LINDHOLM et VASANDER 1984, VITT et BAYLEY 1984, PROZOROV 1985 and ZOBEL 1987a, etc.), (see also MOORE et BELLAMY 1974 and CLYMO 1983 for review). General accounts concerning soil chemistry in submerged conditions are given by PONNAMPERUMA (1972) and ŠKORA et KEENEY (1983). One of the best documented trends during autogenic mire succession is the decrease of pH values of both mire water and peat. The results of HEIN-

SELMAN (1970) about mire water are given as an example: in rich swamp the pH values were 6.0–6.5, in poor swamp 4.5–6.0 and in transitional forested bog and semi-raised bog 3.2–3.7. The pH of bog water may be even lower (2.8–3.0). When the starting point of succession is a strongly calcareous fen, pH can be higher (8 and more) in the initial stages. The decrease in conductivity of mire water may also be considerable: in initial minerotrophic stages it is usually over 100–200, sometimes even more than 400–500 $\mu\text{S cm}^{-1}$, but in the final stages it usually does not exceed 40–50 $\mu\text{S cm}^{-1}$. The concentration of most of the ions in mire water also decreases remarkably during the succession, for example, the mean contents of Ca^{2+} and Mg^{2+} are (as per Sjörs 1952; mg/l per litre) 1.8 and 0.9 in rich fens, 0.9 and 0.02 in transitional fens, 0.6 and 0.3 in intermediate fens, 0.1 and 0.03 in transitional poor fens, 0.06 and 0.03 in intermediate poor fens, 0.07 and 0.02 in extremely poor fens and 0.04 and 0.05 in bog of Sweden. Similar, but usually not so eloquent trends are observed in case of K^+ , Na^+ , Mn^{2+} , Cl^- , SO_4^{2-} , CO_3^{2-} ; etc. The contents of NO_3^- and NH_4^+ are usually near or below 0.1 mg/l (KARLIN et BLISS 1984) though it is sometimes difficult to express any clear trends. The successional behaviour of the content of PO_4^{3-} sometimes remains unclear (MÖRNSJÖ 1969, MOORE et BELLAMY 1974, KARLIN et BLISS 1984). Similar trends, i.e. decreases in element concentrations, are also observed in the case of peat. For example, BARRY et SYNNOTT (1984) have determined the total content of eleven and available content of nine elements, plus ash content, pH and C.E.C. (cation exchange capacity) through a number of peat profiles. In one profile, for example, the following results were received: the total content of Ca in percentage of dry weight was more than 1 in the peat of reed swamp and woody fen, less than 0.5 in the peat of the first stages of bog development and less than 0.25 at later bog stages. The available content of Ca decreased from 4,000 ppm to approximately 200. The decrease in the content of Mn was even more remarkable. The total nitrogen decreased from 1–1.5 % in fen stages to less than 0.5 % in early bog stages, but then slightly increased. The changes in P, K and Na content were not very clear, and in case of Mg even an increase during the succession was observed. PĚAVČENKO (1972) gives the following limits for the peat of fen, transitional mire and bog: the content of CaO 1.5–5.0, 0.5–1.5, 0.1–0.7 %; P_2O_5 0.05–0.4, 0.04–0.3, 0.02 to 0.03 %. The total content of nitrogen also decreases during the succession, in fen stages it could be 1.6–3.8 %, in case of bog peat 0.8–2.0 %. So the C/N ratio increases during mire development.

The additional input of chemical elements due to air pollution should also be considered when the chemical composition of peat is studied. As could be seen from the data referred to, considerable increase in many trace elements is observed in the upper peat layer. Discussing the role of aerial input, TALLIS (1985) reached the conclusion that renewed peat erosion in the blanket bog under investigation was caused by the death of *Sphagnum* due to air pollution during the last 200–300 years.

The ash content of fen peat is usually 5–18 %, its decrease during meiotrophication leads to values of 1–2 % in raised bogs peats (cf. GLEBOV et TOLEIKO 1975). The base saturation level could be 50–90 % in fen peat, 25–50 % in peat of transitional mire and 20–25 % in bog peat (PĚAVČENKO 1972).

The process of meiotrophication is connected with the leaching of nutrients, but immobilization of mineral nutrients through peat accumulation is also of great importance. The bogs create a passive supply of matter and energy (MALMER 1975), especially of nitrogen and phosphorus, which are fixed in peat in a form unavailable to plants.

Bog development is also characterized by deterioration of soil aeration conditions. It is known that the soil redox potential is lower in submerged soils as compared with sites in better aeration conditions, and at least in deeper layers reducing conditions prevail, where dissolved oxygen becomes undetectable: corresponding results are found in PONNAMPERUMA (1972), URQUHART et GORE (1973), GIVEN et DICKINSON (1975), CLYMO (1983), SIKORA et KEENEY (1983) and LÖHMUS (1984). The successional dynamics of redox potential have not received any special attention. There is, however, some information available about the content of dissolved oxygen in mire waters. Classical discussions, in accordance with HESSELMAN (1910), assure that the shortage of oxygen in one of the main causes of bog development, leading to progressive peat accumulation. There were some references, however, that the content of dissolved oxygen in mire water was higher in more oligotrophic sites (ORLOV 1958). Later results clearly demonstrate that the oxygen content in soil waters increases during meiotrophication (VOMPERSKIJ 1968, LOOPMANN 1988, ZOBEL 1987a). In eutrophic sites (e.g. alder carr) the content of oxygen in soil waters is usually between 0.5–1.0 mg/l, in woody fens with rare *Sphagnum* 1.0–1.2 mg/l, in transitional pine bog 1.0–2.0 mg/l and in the soil water of bog ridges more than 3.0 mg/l. Here one must keep in mind that the oxygen content itself does not characterize the dynamics of soil aeration conditions,

however, high values of oxygen content in bog soil water are evidently the result of low microbial activity in the soil, which depends on low pH, nutrient shortage, lower soil temperature and other factors.

In swamp forests, where low oxygen contents in soil water are measured, a higher input, e.g. through the well aerated water of little hollows and wind-throw pits, may be accompanied by higher consumption rates (ZOBEL 1987a). The lack of oxygen in the soil environment seems to be a crucial factor of bog development only in the fen or swamp stage, while in bog ridge the aeration conditions are relatively favourable (ZOBEL 1986, TOOM et ZOBEL, unpublished) and the retardation of decomposition is mainly caused by nutrient deficiency and low pH values.

Frequently it is declared that during bog development soil conditions change from wet to dry. This primarily depends upon the surface pattern: for example, in the case of hollows such a trend is not valid. The successional changes in hydrological conditions are analyzed by IVANOV (1953, 1957, 1975). He shows that the depth of the water table and the rate of its fluctuations are correlated — when the water table is near the bog surface, fluctuations are less remarkable. According to IVANOV the mean depth of water table in fen was 24 cm and the mean amplitude of fluctuations 38 cm. In different types of pine bogs the mean depth of water table varied from 29 to 62 cm, and the mean amplitude from 28 to 57 cm. In bog ridges the mean depth was between 20 and 30 cm and the mean amplitude between 26–35 cm. Thus the fluctuations in water table seem to be higher at the intermediate succession stages. When in earlier stages the general water flow direction is from surrounding mineral land to mire, and from mire margins to the centre, then due to the development of convex bog surface the direction of the flow reverses. Instead of primary waterbodies usually the so-called secondary waterbodies arise (e.g. bog pools, secondary lakes in central or marginal parts), etc. When surface pattern develops (cf. Chap. 6) the drier and wetter parts become more differentiated than in the earlier stages. The five hydrological mire types of IVANOV (cf. also GALKINA 1946) and seven hydrological mire types of BELLAMY (1968) (cf. Chap. 2) represent broad generalizations about the development of hydrological conditions. IVANOV's schemes, where the recharge, throughflow and discharge pattern in initial and final stages of mire development is designed, are also presented by INGRAM (1983: 119). During bog development, the water level becomes more dependent upon the direct supply of precipitation water and hardly shows any of the distinct seasonal variations met with in dry terrestrial environment or lakes (MALMER 1975). Evapotranspiration in bogs may be 300–360 mm yr⁻¹ while annual rainfall in 540–600 mm and in fens the evapotranspiration is approximately 10 % higher. In paludifying forest the evapotranspiration is estimated to be 290–400 mm yr⁻¹ (KOŠEJEV 1955, ROMANOV 1953, 1962, PJAČENKO 1984). Thus, the evapotranspiration rate tends to decrease during bog succession. The well-decomposed fen peat contains eight times more water than the mass of moss tissues, and weakly decomposed bog peat contains 15–20 times more water. The throughflow rates are smaller in weakly decomposed bog peat. The formation of an entirely new local hydrological system during bog succession depends mainly upon the surface topography and different throughflow rates in different structural forms of bogs (IVANOV, op. cit.).

Consequently, it can be seen that change in local environmental conditions during bog succession is more directional and also more predictable than in case of many other types of ecosystem. The ecosystem itself is responsible for the creation of quite uniform oligotrophic conditions in initially diverse environment.

4. Mechanism of autogenic bog succession

The actual ecological mechanism of bog succession is quite frequently dealt with by telmatologists but seldom incorporated into the general theoretical framework of dynamic ecology. The concepts of terrestrialization and paludification, and also of climatic rhythms, presented consecutively e.g. by GORE (1983), also represent the widest generalizations about the mechanism of bog succession. To be more precise, the concrete mechanism of initial successional stages may be quite diverse, depending upon the starting point of succession (cf. Chap. 2). But beginning with the stages in which peat accumulation takes place in large quantities, the main mechanism is common for most bog successions. Using the words of SJÖRS (1983: 72), mire successions may cause, and at the same time be the result of, decreasing supplies of mineral nutrients. The soil supplying mineral soil water to minerotrophic sites become acidified and leached, leading to meiotrophication.

The nature of the process, leading from eutrophic mire types to oligotrophic ombrogenous

bog, has been described by several classical authors (e.g. WEBER 1911, OSVALD 1923, SUKAČEV 1926, KAC 1926, VON POST et GRANLUND 1926, etc.) and re-considered by a number of contemporary authors. This process is accompanied by considerable changes in mire environment (Chap. 3). PROZOROV (1981, 1985) gives the principal causal scheme for both paludification and terrestrialization successions. The former includes four steps: decrease of total evaporation or drainage rates → → increase of soil moisture → decrease of soil aeration → deficiency of oxygen leads to peat accumulation. In the later case three steps are distinguished: accumulation of humus of local origin or one alluvially transported → consumption of oxygen in the course of mineralization → → oxygen deficiency and peat accumulation. It is further mentioned by PROZOROV that oxygen conditions are not the only cause responsible for peat accumulation, but temperature conditions also inhibit decomposition. The crucial point in autogenic bog succession seems to be the invasion of *Sphagnum* as they appear to be capable of profoundly modifying the chemical properties of the habitat. The ability of *Sphagnum* to bring about acidification of habitat by uptake cations and the release of equivalent number of hydrogen ions (cf. CONWAR 1949, BELL 1959, CLYMO 1963, etc.) is responsible for the process. Similar properties have also been suggested for some other mosses (TALLIS 1983) such as *Drepanocladus*, *Aulacomnium* etc. The microporous structure of *Sphagnum* sp. gives them great capillary water-holding power. Consequently, the mire becomes able to maintain its own perched water table even when it overlies a permeable substratum (ETHERINGTON 1983).

NOBLE, LAWRENCE et STREVELER (1984) have demonstrated that in Alaska *Sphagnum* invasion takes place preferentially in windthrow pits subsequent to the forest reaching the stage in which blow-downs become more prevalent. The primary colonization of pits relates to the competition-free nature of the site and the competitive advantage of *Sphagnum* in the wetter environment of depressions. Consequently, the ability of *Sphagnum* to make their habitat more acid and poorer in nutrients could by itself have reduced the competitive ability of the fen or swamp species and promoted its supremacy. The death of forest trees and *Sphagnum* development may be in direct accordance with N and P deficiency (HEILMAN 1966, 1968). But the role of other species than *Sphagnum* and especially of those forming mounds of hummocks, should not, however, be neglected. Even if the changes in the chemical properties of the habitat are initially not great, one must agree with BERNARD, SEISCHEB et GAUCH (1983) that microtopographic alternation facilitates further succession.

In summary it may be stated that habitat conditions are considerably altered in the course of the intermediate and final stages of bog development (Chap. 3). There is no doubt that bog development is an autogenic succession in its classical sense because (plant) communities, especially *Sphagnum* sp. are responsible for the alternation of the environment. Bog succession cannot be explained by the alternation of any single environmental factor; the role of, at least, three main factors should be stressed: nutrient shortage, oxygen deficiency and low pH. All these strongly influence microbial activity, thus influencing the decomposition process (cf. KOZLOVSKAJA 1976, DICKINSON 1983, LAINE et al. 1984). But several other factors, including allelopathy, soil temperature, etc. may also be of importance. As was shown in Chapt. 3, aeration conditions can not be easily characterized and usually the real oxygen content in soil waters may be higher in oligotrophic sites than in meso- or eutrophic ones. Still the oxygen input can not be precisely estimated, and hence operation with the factor "oxygen deficiency" remains quite speculative. The most simple principal scheme of bog succession is drawn in Fig. 1.

Excluding the first stages, the mechanism of bog succession, in general, can be explained with the help of the classical facilitation scheme i.e. the plant community itself altering the local environment. Such a conclusion was accepted also by AAVIKSOO, MASING et ZOBEL (1984). Using the ideas of SLATYER (1977) and USHER (1979) to interpret the transition probability matrix they concluded that in the early and intermediate stages, the multidirectional nature of replacements refers to the fitness of the tolerance-model, while in the final stages, where the plant roots are fully isolated from mineral substrate, the process gradually becomes more determined and the facilitation-model better explains succession. This does not mean that one type of mechanism fully excludes another. Bog succession can be considered as an ecosystem process, where certain assemblages of species are replaced by one another due to the changed habitat. BARRY et SYNNOFF (1984) have convincingly demonstrated that bryophyte communities of the fen, transitional mire and bog are almost always specific — species with broad environmental variability are found only very exceptionally. But it does not mean that processes on the population level act only at fen stages. Perhaps only a shortage of the number of species in bogs makes the role of migration, longevity, ecesis, etc. less pronounced than in other ecosystems. Maybe further studies on the

subject of the population ecology of bog species (especially that of *Sphagnum*) will make the role of population processes more explicit. For example, vegetative reproduction tends to be replaced by generative reproduction when conditions become unfavourable for *Sphagnum* sp. (GRABOVIX 1982, 1986), thus the population dynamics may be of importance in some cases.

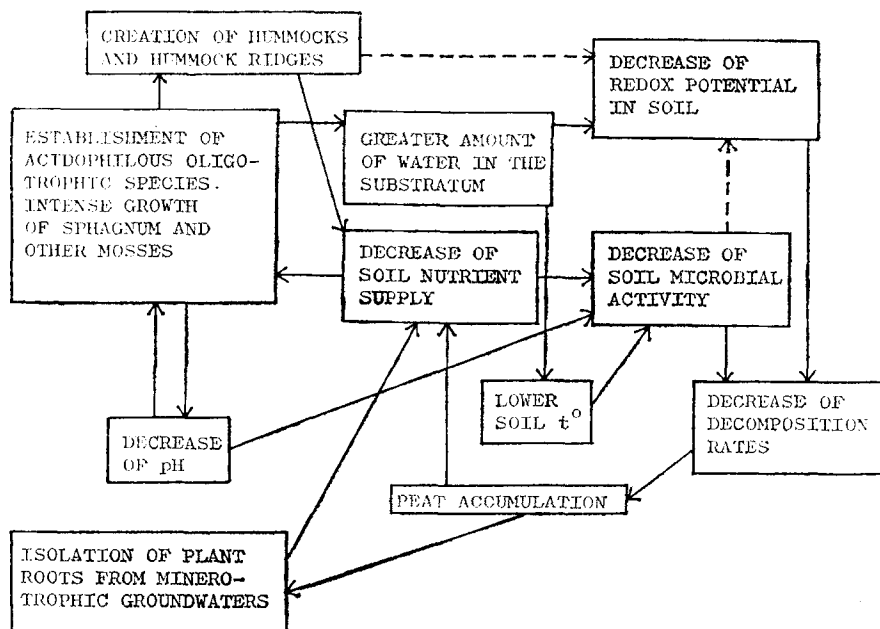


Figure 1. Principal scheme of the main mechanism of bog succession.

— positive impact which enhances the process mentioned. - - - - negative impact.

5. Development of bog surface pattern

One of the most fascinating problems concerning bog succession is the development of surface pattern, which consists of regularly arranged hollows, pools and hummock ridges. The possible mechanism of such pattern development is examined in a number of works, but as Sjörs (1976) writes, these problems are more frequently discussed than actually investigated. More profound accounts on this topic are given by AARIO (1932), IVANOV (1956, 1957, 1975), NICHENKO (1964), AARTOLAHTI (1965), TALLIS (1983) FOSTER et al. (1983), MASING (1984) and PĚAVČENKO (1985a, b), and concerning pool formation also by BARBER (1981).

IVANOV (op. cit.), generalizing earlier ideas about mire surface pattern development, divides the possible causal mechanism into five groups: biological (different growth rates, etc.), climatic (frost), mechanical (thawing), hydrological and synergetic mechanisms.

Considering the fact that the water content in bog peat usually exceeds 90%, the hydrological factors should be of importance in pattern development. The general features, of mire hydrology are described by IVANOV (1956, 1957, 1975), ROMANOV (1961), ROMANOVA (1961) and INGRAM (1983). Then hydrological explanations of development of mire surface pattern could be divided into two groups. First of all, some authors operate with hydrostatic evidence. PĚAVČENKO (1963) discusses the influence of hydrostatic pressure on unevenly frozen bog surface. But the influence of hydrostatic pressure should not be restricted to the winter period as it can be of importance in warmer period also, at least in marginal bog slopes (cf. GETMANOV 1925, AARIO 1932, GALKINA

et al. 1949, ROMANOVA 1953). Other authors refer to hydrodynamic mechanisms (IVANOV 1956, 1957, ROMANOV 1961). Ridges and hollows are usually oriented at right angles to the direction of the slope (exceptions are met in valley mires of the Far East and aapa-mires — ČAKOV 1983, JURKOVSKAJA 1983) thus also to the direction of the waterflow. The size of bog structural forms depends upon the convexity of the bog surface. But a more precise explanation is still lacking. IVANOV's hypothesis (1956) should be considered to be synergetic rather than purely hydrological, despite this it operates with low water perlocation rates through hummocks. The waterflow which tends to pass the hummock is divided into two marginal directions. As a consequence, the two marginal sides of the hummock receive considerably higher amounts of nutrients which enhances the growth of *Sphagnum*. Hummock plants begin to grow, the hummock enlarges laterally and finally a hummock ridge develops. This explanation is criticized by NICENKO (1964), BOGDANOVSKAJA-GUIHE-NEUF (1969) and PJAČENKO (1985a, b).

Some classical authors have supported the idea that peat surface perpetuates the irregular character of the underlying surface (WEBER 1902, OSVALD 1923). This idea has been rejected by several authors (cf. TALLIS 1973, 1983). There are a lot of examples where the underlying surface pattern does not correspond to bog surface pattern, thus such a explanation may be true in exceptional cases, only.

The "solifluction-hypothesis" or "tearing-hypothesis" — that bog surface tears as semiliquid peat mass moves downslope — was initially presented by WEBER (1910) and then supported by TANTTU (1915) and AUER (1920). The formation of hollows and ridges in this way is facilitated, by uneven melting of the bog surface in spring. Further this hypothesis was developed by KRASNEV (1941), PEARSHALL (1956) and PERRON (1979) also support this idea, while IVANOV (1956) BOATMAN et TOMLINSON (1973), FOSTER et al. (1983) reject such an explanation. Downslope movement of peat is well documented only in singular cases; for example, SCHOUTEN (1984) demonstrates that the surface tearing and sliding of the upper peat mass may be responsible for the creation of pools in specific situations, e.g., at the margins of a large bog complex.

The role of uneven freezing of peat in winter as an independent mechanism of pattern differentiation is referred to by some authors (cf. SJÖRS 1961, MASING 1984). In the opinion of FOSTER et al. (1983) this explanation is inadequate because winter frost is absent from large areas where bogs with stiring pattern occur and differential heaving during annual frost has not been documented. The new outlook on this question is supported by PJAČENKO (see further).

FOSTER et al. (1983) offer, as an explanation, a causal mechanism which declares that the surface water tends to pound in low spots and the initial hummocks between those low spots are subsequently occupied by good peat producers, and hollows by weak peat producers. Such an idea is not new, the differences in productivity rates of *Sphagnum* in hollows and hummocks were referred to by CAJANDER (1913), ABOLIN (1914, 1928), AUER (1920), OSVALD (1923), KUDRJAŠOV (1929), etc., but the role of these differences is still unexplained.

Some authors refer to the possibility that *Sphagnum* growth in depressed microforms could be suppressed by several ecological factors. EUROLA (1962) proposes that immersed conditions are sub-optimal for *Sphagnum* growth, but no data support this opinion. Moreover, LOPATIN (1954b) and RYDIN (1985) have demonstrated, that hummock species usually tolerate wetter conditions in hollows, but hollow species do not resist dry conditions on hummocks. SJÖRS (1961) refers to competition from algae which adversely effects *Sphagnum* growth. BOATMAN (1984) draws the conclusion that the development of hollows and pools is a consequence of the poor growth and low production of hydrophilic species of *Sphagnum*. As per BOATMAN this evidence is also connected with the underlying surface pattern of mineral ground, as the water content of the peat overlying the basin would have been greater than that overlying the ridges.

In many sources, however, it is demonstrated that the productivity of *Sphagnum* in hollows seems to be even higher than on hummocks or ridges.

As per PAKARINEN (1977) *Sphagnum* carpet is more productive in hollows than in hummocks. The results of BOATMAN (1984) himself demonstrate that productivity tends to decline from the ends to the centres of the hollow, but the productivity limits of *Sphagnum papillosum* on ridges (0.30–1.91 g/dm²) seem not to differ significantly from that of *S. cuspidatum* in hollows (0.39 to 2.02 g/dm²). ILOMETS (1980, 1981, 1982) has determined the productivity (g/dm²/yr) and linear growth (mm gr⁻¹) of *Sphagnum* communities in different bog microsites, and found that productivity tends to be higher in hollows. For example, productivity of a *S. balticum* community in hollows is 1.9–7.6 g/dm²yr⁻¹ and of a *S. magellanicum* community in hollows is between 1.5 to 4.1 g/dm²yr⁻¹. The productivity of a *S. rubellum* community on hummocks was measured to be 0.7–2.4 g/dm²yr⁻¹, and of a *S. fuscum* community on hummocks 0.8–2.4 g/dm²yr⁻¹. Similar

differences were observed in relation to linear growth. In subarctic mire bryophyte productivity was also be higher in depressions (SONESSON et JOHANSSON 1974). Consequently, different productivities can not be responsible for the creation of surface pattern. It has been shown that the key factor in determining the net vertical peat growth is decay, not production (TOLONEN et al. 1985: 5) so that "good peat producer" should mean "low decomposition rate". But there are still few data about the actual decomposition rates in different microforms. BOTCH (1978) did not find differences in decomposition rates in ridges and hollows, while KOZLOVSKAJA, MEDVEDJEVA et PJAČENKO (1978) report a somewhat higher decomposition rate in hollows. ILOMETS (1982) recognized the prevalence of fine particles in hollow peat — this indicates more intense decomposition there.

A somewhat different idea of the development of surface pattern, is given by LOPATIN (1958). According to him the invasion of several bog species during succession does not take place simultaneously over the entire bog area, but, initially, distinct patches arise. The rise of such patches further enhances the development of bog microrelief. GLASER et al. (1981) discuss the possibility that strings may be formed due to the clonal growth of certain species, thus offering quite a similar mechanism.

Hummock initiation, i.e. the first phases of hummock development, has been described by a number of earlier authors (cf. BOGDANOVSKAJA-GUIHENEUF 1936 for a review). As per WEBER (1902), JOSEPHY (1920) etc. shrubs and trees establish something like a skeleton for hummocks and thus enhance the further differentiation of bog surface pattern. Among more recent studies on this theme BOATMAN et ARMSTRONG (1968), BERNARD et al. (1983), SEISCHAB (1984), GLASER et al. (1981), LUKEN, BILLINGS et PETERSON (1985) should be referred to. BOATMAN, GOOD et HULME (1981) stress that some kind of biological processes combined with hydrological effects should be taken into consideration and they reject explanations based only upon climatic and erosional processes. TYLER (1981) demonstrates that in rich fens calcareous groundwater simply does not reach the higher parts of tussocks formed and thus *Sphagnum* may invade the tops of tussocks.

MASING (1984) gives some examples of the influence of fire — sometimes the burnt depressions initiate the development of a new hollow or even a pool. METS (1963) has shown the role of bog gases (mainly methane) in the deepening of pools.

The "relict-hypothesis" should be also mentioned when discussing the development of bog surface pattern. The earlier concept concerning the origin of bog pools claimed that they are simply those parts of an initial lake which are not overgrown by mosses and other plants. It was also assumed that, at the bottom of pools, an inflow of mineral ground water takes place. It is interesting to mention that the "relict-hypothesis" was also used to explain the genesis of elevated structural forms: BOGDANOVSKAJA-GUIHENEUF (1936) talks about relict hummocks, referring to the relative stability of hummock communities. Concerning pool formation, several other explanations (development from streams, sinking of bog surface, etc.) have also been presented by a number of earlier authors (CAJANDER 1913, GERASSIMOV 1922, OSVALD 1923, POLYNOV et JURJEV 1924, TITOV 1952, etc.), for review cf. BARBER (1981).

Recently PJAČENKO (1985a, b) has developed his own earlier ideas about the role of winter frost in the formation of bog surface pattern. According to him, the initial cause of the development of hollows and/or pools are the fissures in frozen surface peat, which arise due to the hydrostatic pressure of inner semiliquid peat masses and the rate of which depends on the convexity of bogs. In southern regions, where winter frost is absent, the pools, hollows and ridges do not form any regular pattern — a more thorough account concerning geographical variation of bog surface pattern is found in KAC (1984).

Some Estonian authors have referred to the different contents of oxygen in the surface or peat water of hollows and ridges. In the water of hollows higher contents have been measured (METS 1978, LOOPMAN et PAIDLA 1981). LOOPMANN (1988) presents the explanation which suggests that initially wetter places accumulate more solar radiation and the water is enriched with oxygen due to the better aeration and moss photosynthesis. Both higher temperature and oxygen content enhance decomposition and may thus amplify the initial differences in surface pattern.

There are some more data about the actual differences in ecological conditions of hummocks and depressions, or ridges and hollows. Most of such data concern nutrient conditions. GORHAM (1961) reports that ash content and nitrogen content were both higher in hummock peat, but pH was higher in the case of hollow peat. BELLAMY et RIELEY (1967) characterize the differences in pH between the top and base of 56 cm high *S. fuscum* hummock. Lower pH values were measured at the top. The content of heavy metals, as being in negative correlation with the *Sphagnum* growth rate, was measured to be lower in *Sphagnum* sp. of hollows (PAKARINEN 1977).

SOKOL (1978) has determined the available supply of six (in peat) and eight (in water) ions at two depths while comparing ridges and hollows. In peat all the elements studied (K, P, Ca, Mg, Fe, N), except Fe, were present in greater amounts. In mire water the contents of available Si, K, Na, Fe, P were higher in ridges, and only Mg and S in hollows, pH_{KCl} of peat was lower in ridges, (2.6 in comparison to 2.8–2.9) and the pH of mire water was also lower there. In hollows of the mesotrophic mire, the contents of most of the elements were higher than those of the elements in oligotrophic mire. DAMMAN (1978) reports that the contents of N, P, and Mg were higher in hollow peat (*S. magellanicum*), but Mn in hummock peat (*S. fuscum*). BOTCH (1972) has found that the contents of Ca^{2+} , Mg^{2+} , P_2O_5 , K_2O were higher in the hollow peat of subarctic mire, the same was true in relation to ash content. The contents of several elements, pH, conductivity and ash content of the peat of hummock and mire plane lawn were compared by WESTMAN (1981), but no statistically significant differences were found. REINIKAINEN et al. (1984) did not find significant chemical differences between the peat and water of hummocks and depressions. JELINA et al. (1984) report that the chemical composition of the peat layer at the depth of 10–20 cm was somewhat different below hummocks and depressions, but at the depth of 5–10 cm the differences were negligible.

Thus there are not always clear differences in element storages when the peat or mire water of different bog microforms is compared. It should be pointed out, however, that storage itself does not characterize real nutrition conditions and that for more precise analysis the differences, at least, in nutrient input and consumption rates should be measured.

There are also certain differences in physical conditions between elevated or depressed microforms. In ridges the mean water level is 15–30 cm and in hollows 5–15 cm (ROMANOVA 1960). The porosity of peat within the upper layer is higher at the depressed structural elements, a melted profile is generally smaller at elevated elements in subarctic mire (RYDEN, FOES et KOSTOV 1980). The oxygen content of mire water including surface water in lower sites is higher in hollows (depressions) than in ridges (hummocks) (ZOBEL 1986, LOOPMANN 1987). But generally the soil aeration conditions are more favourable in hummock peat, where the thickness of the better aerated layer exceeds that of depressions through all the vegetation period (ZOBEL, op. cit.). In subarctic mire, the frost-free period in soil environment was longer in depressed forms (RYDEN et KOSTOV 1980). Specificities of hydrological conditions are considered by LOPATIN (1972, 1980) in different structural forms. The changes in water table are more rapid in hummocks. The response of hummocks and hollows to drainage impact may also be quite different (cf. LINDHOLM et MARKEKULA 1984).

One particular question is the temporal variability of surface pattern. A classical concept — the regeneration cycle theory — was suggested by VON POEL et SERNANDER (1910), but similar ideas were presented by AITON already in 1811 (cf. GORHAM 1953). Further, the regeneration concept was supported by OSVALD (1923, etc.). According to that theory it is assumed that hummocks accumulate peat slowly, and thus upward growth of hollow community eventually raises these areas to form new hummocks. This, at the same time, floods the low-lying area occupied by the old hummocks. The history of this problem and current opinions are well documented by BARBER (1981) and TALLIS (1983) and thus not repeated here. It should be pointed out, however, that even some earlier authors had difficulty in demonstrating the regeneration cycle. For example, GODWIN et CONWAY (1939) follow OSVALD and present the scheme of the ideal cycle, but remark that the degradation stages are particularly hard to find.

Serious criticism of the regeneration theory was put forward by several authors (WALKER 1961, OVERBECK 1963, TOLONEN 1970, BAKEUS 1972, etc.). In a number of investigations, the relative stability of structural units of bog (including pools) is documented (BOGDANOVSKAJA-GUIHENEUF 1936, GODWIN 1952, WALKER et WALKER 1961, CASPARIE 1972, BOATMAN 1977, MOORE 1977, SCHMEIDL 1977, KAROFELD 1985). However, the actual boundaries of microforms change: in time and space, depending upon retarded and rejuvenated peat growth. Consequently, in case of marginal communities of hollows, hummocks and ridges one can speak about small-cyclic or short-cycle regenerations or rejuvenation cycles (WALKER et WALKER 1961, TOLONEN 1971, 1980, BARBER 1981, TALLIS 1983, TOLONEN et al. 1985). It does not mean that cyclic succession between hummock and hollow communities does not take place at all, but this should probably be considered an exception, rather than the rule.

The wide diversity of concepts and even controversy in results indicates the great complexity of the problems considered.

Generally, two questions should be kept in view in discussing the origin of bog surface pattern. Pattern initiation should be the first. The creation of loci with different microconditions (tempera-

ture, aeration, nutrient supply, shade etc.) evidently takes place in a random manner and may be connected, e.g., with the growth forms of predominating plant species. The more regular disposition of structural forms in boreal bogs refers to certain deterministic mechanisms and PJAČENKO's hypothesis could be considered as one fully possible explanation.

Another question is the manner in which the initial differences in micro-conditions and community composition are amplified so that entirely different communities develop. The re-distribution of mineral nutrients due to changes in the direction of underground and surface flow, higher temperature and higher oxygen content in the surface water of wet spots, and several biological effects together are evidently responsible for this, and it is hardly possible to separate some crucial factor here. Using the words of NIČENKO (1964), one mechanism does not include another. Thus the pattern development could be considered as a typical synergetic process where the heterogeneous structure is created from initially more homogenous plant cover and environment.

To receive further more precise information about the ecological factors, influencing the decomposition rates in different structural forms, it would be necessary: 1. to study developing, not stabilized pattern, and 2. to study input rates (oxygen, nutrients) not only contents.

6. Climax in bogs

The climax theory is one of the widest and also the oldest generalizations in contemporary ecology. Different climax concepts have frequently been presented but also as frequently criticized. The main climax concepts are the monocl意思 theory (CLEMENTS 1916), polyclimax theory (TANSLEY 1920, 1935) and climax-pattern theory (WHITTAKER 1953). In addition, two other concepts should be mentioned. First, the concept of climax-swarm or climax-group (TÜXEN et PIEMONT 1938) should be considered as generalization of the original polyclimax concept of TANSLEY. Secondly, the concept of multiple steady states (WHITTAKER et LEVIN 1977, LEVIN 1978) synthesize the polyclimax theory and climax-pattern theory, operating with some ideas based on the theory of non-linear differential equations. The discussion about the role of the climax concept itself in dynamic ecology is beyond the tasks of this paper. ZOBEL (1988b) has presented the viewpoints of different authors. It should only be mentioned that most of the criticism regarding the climax concept concerns dogmatic interpretation of climax. It is recommended to read TANSLEY (1939b: 515) who writes: "...the apparent equilibrium of every climax is a false equilibrium, that slow changes are always taking place... the ecologist is justified in giving weight to the time factor, in adopting the concept of relative equilibrium to apply to systems in which the changes are so slow that the system does not lose its essential character...". When the term climax is further used by us, it refers namely to some kind of relative equilibrium, where autogenic succession has more or less stopped, but other kinds of ecosystem dynamics take place with differing intensity.

First it should be considered whether the climax concept is applicable for mires. Lake filling-in and bog development were brought as examples of convergent succession by some classical authors (CLEMENTS, TANSLEY, etc.), by them the mesophytic forest was usually supposed to be the climax. TANSLEY (1939a), however, refers to the possibility that in some cases it may be blanket bog or raised bog. The fact that mesophyte forest is not the endpoint of bog succession is stressed by HEINSELMAN (1963, 1970), WALKER (1970) and MILES (1979). For telmatologists this is not surprising because careful examination of a number of peat profiles does not indicate any trend towards mesophytic forest. However, it rather seems that existing telmatologic information is not generalized within the framework of succession theory.

Among the telmatologists various opinions regarding the term climax and the concept itself have been met. SJÖRS (1961, 1980) rejects the term climax because he feels that it contributes little to the understanding of the changes in northern peatlands. The existence of a number of successional directions and the successional divergence of bog development is Sjörs' main argument. HEINSELMAN (1970) is in full agreement with Sjörs and also regards the climax concept as unnecessary when studying bog succession. VAN DER VALK (1982), studying succession in temperate North-American wetlands, draws the conclusion that all distinctions between climax and successional vegetation are meaningless.

Some authors, however, use the term climax in case of bogs. WALKER (1970) writes that throughout the British isles the true climax of an initially topogenous hydrosere is not a terrestrial woodland but an ombrogenous bog. PJAČENKO (1985a) writes that ridge-hollow complex should be considered as a climax stage of bog development. AAVIKSOO, MASING et ZOBEL (1984) studied the transition probability matrix, compiled on the basis of stratigraphic material. The calculation

of dominant eigenvector showed the probability distribution between types. It becomes evident that in the final stages only five community types from a total of seventeen will occur with higher probability.

Consequently, two different aspects should be mentioned while examining bog succession. First, one must agree with Sjörs (1980) that the general trends of mire succession may be described as convergent in a very broad, over-all sense. This means that the present vegetation and structure of peatlands are not clearly related to their origin. Despite the variety of initial edaphic conditions, generally similar bog environment is created during succession. But secondly, mire succession could be declared divergent, the creation of hummocks and hummock ridges, hollow and pools on a bog surface being an example of a divergent set of successions. Alternative steady states may arise in initially similar habitat conditions. Thus, on a regional scale, when only broad formations are considered, it could be stated that bog succession is generally convergent, and the situation more or less corresponds to the poly-climax concept. But at community level the situation is more complicated. There is evidence that supports the multiple steady state concept, because alternative stable communities are to be found in bogs. But, at the same time, similar community types (e.g. *Sphagnum fuscum*-*Calluna vulgaris* community on hummock ridges) could originate from entirely different set of earlier communities. Thus, none of the existing climax concepts entirely describes the general nature of bog succession. An adequate explanation should evidently include some generalizations of the multiple steady state concept, stating that "one could be created from many, and many from one".

But the fact that the ecological situation in bogs is not sufficiently described by existing climax concepts does not mean that the term climax should be entirely rejected. Vice versa, the bog ecosystems seems to be a suitable object for further correction of climax concepts. The bog climax should be treated as in dynamic equilibrium, where evidence of autogenic succession is negligible. Such a viewpoint does not include any dogmatic considerations and simply represents some kind of ecological steady state concept.

It should be mentioned (cf. also Chap. 2), that when the area of a bog is approximately constant, the communities of mire margins also become stabilized in the successional sense and hence should also be treated as representatives of a relatively steady state, i.e. climaxes, despite the fact that in an other situation they might represent some kind of transitional stage in mire succession.

7. Spatio-temporal pattern of bog and bog communities

The relatively simple but expressive surface pattern of bogs makes it possible to study bog succession also in a "spatial context". The morphology of bog surface pattern could be studied in various spatial scales. Depending on the scale, one could distinguish different structural level of bog (mire) landscapes. Partly these levels could be in accordance with biological organization levels. Two main levels — bog community and bog complex — were already distinguished by CAJANDER (1913) and ABOLIN (1914). Further, the level of community complex (Assoziationskomplex) was introduced by OSVALD (1923). GALKINA (1946) made a difference between principal structural levels in mires: community, microlandscape, mesolandscape and macrolandscape. The last includes different types of mire systems, i.e., systems consisting of several mires. Such systems are met mainly in virgin, natural landscapes (as some regions of the Soviet Union, etc.). In western Europe mire systems are almost absent. The concepts of GALKINA were further elaborated and motivated by IVANOV (1957 etc.). A more general approach was suggested by MASING (1960, 1974, 1984): the number of structural levels of landscape (and respectively, of vegetation) is not objectively limited, and thus depends upon the subject (i.e. investigator). Thus, at first, one should define the scale and determine the number of levels that would be studied on that scale. In the case of bogs MASING has used mainly five basic levels: community, microform, microlandscape (or mire site, or mire facies), mire complex and mire system, and if necessary some other levels could also be included: clone, microcoenosis, compound microform, etc. In later works (BOTCH et MASING 1979, MASING 1982, 1984), the concept of self-regulative structural units has been introduced — in bogs those are simple structural forms like clone, simple microform and bog complex as opposed to compound structural forms (nanoform, sometimes synusia, compound microform and mire system). In the present topic, six principal levels are considered.

The finest structural unit is nanoform, corresponding to small loci on the bog surface (e.g. the top of the hummock). The assemblage of plant specimens growing on nanoform could be

synusia (consisting of species which belong to similar life form) or clone. The term patch could also be used. Microform is the elementary unit of bog surface pattern, bearing one or several synusiae which form a microcoenosis. Hummocks and depressions of various sizes (usually from 1 to 10 sq. m) are the most typical microforms in bogs.

Compound microform represents the result of co-operative development of microforms — such a result may be hummock ridges or strings (due to “amplified development of hummocks”) or hollows or flarks (due to “amplified development of depressions”). In some bogs pools and pool bank ridges, which are usually higher and covered by trees, can be seen. Both these may also be called compound microforms. Compound microforms are characterized by specific plant communities, which could usually be classified as association or some related unit. It should be stressed that simple and compound microforms were (and are) not distinguished in many works: e.g., the terms bog feature of Sjörs (1948) or microform of MASING (1974) include both simple and compound microforms.

Frequently, the bog areas where one, two or more structural units predominate, have received special names: hollow-ridge complex, hollow-pool-ridge complex, lawns (where developed compound microforms are absent), etc. These areas are named mire facies (GALKINA 1946) or mire sites (Sjörs 1948).

Mire complex represents the whole bog which has developed more or less as one dynamic entity. Mire system consists of distinct single bogs with their own history which presently form a joint entity.

Such a division is somewhat simplistic but all the same useful for generalizing bog development. In principle, succession as a developmental process could be studied at different structural levels (MASING et LÄÄNELAID 1976, cf. also GLEBOV 1979). ZOBEL et MASING (1987) suggest distinct successions (directed qualitative changes) and oscillations (cyclic, and thus quantitative changes) — the distinction between these two kinds of community dynamics should simplify the compromise between various existing divisions — and regard community dynamics at different structural levels (i.e. in different spatial scales) and in different temporal scales. In the table (Tab. 1) three structural levels and four temporal scales (from some years to decades, from decades to centuries, from centuries to thousand of years, several of thousands of years) are considered. Autogenic succession should be observed at all three levels (microcommunity succession in microform scale, community succession in compound microform scale, and vegetation development in the entire bog scale), but the velocity of development is different in all cases. The development of the micro-community takes place in the course of several decades or a century; the succession of bog community, resulting, e.g. in *Pinus-Ericaceae-S. fuscum* community on ridges, *S. rubellum-Calluna vulgaris-Eriophorum vaginatum* community in lawns etc., takes place in the course of several centuries or even a thousand years. The development of the whole bog resulting in centric, epicentric or random patterns of hollows, ridges and pools in final stages, takes place in the course of several thousands of years (these processes are spaced in Table 1). When the development of any kind of natural system in the course of a short time interval is studied (compared to the time needed for stabilization), the direction of the development does not become visible. One can recognize only short drifts, i.e. oscillations or fluctuations of the system under investigation. When the time interval is too long, compared to the “life-time” of the system under investigation, developmental trends cannot again be recognized, as the developmental cycle repeats several times during this period. Thus again, only the oscillations can be observed. In Table 1 it can be seen that when the temporal scale of observation is shifted by one step, the directional change at this structural level cannot be recognized but the cyclic dynamics become apparent.

Similarly, the dynamics of any biotic system should be studied in a certain spatial scale. But when the spatial scale is diminished, i.e. only a small part of the system is taken under investigation during the same time interval, the development trends of the whole system are not observable and only some cyclic or irregular oscillations during the time interval used are recognized. And alternatively, when the spatial scale is enlarged and all neighbouring systems are also taken into consideration, a number of different developmental processes which are not synchronous or identical are recognized. Thus only oscillations are seen and for the study of developmental directions of the spatially larger system a longer time interval is needed.

Consequently, when one of the two — spatial or temporal scale — is shifted by one step, the nature of the process under investigation changes qualitatively. If it was previously observed to be directional leading to some kind of steady state, it now becomes (irregularly) cyclical and vice versa. For example, the development of a certain compound microform and its community is observed to be in directional succession towards some stabilized state. But when the spatial scale

Table 1. Several kinds of bog community (ecosystem) dynamics in different spatial and temporal scales

TEMPORAL SCALE	SPATIAL SCALE		
	MICROFORM	COMPOUND MICROFORM	BOG COMPLEX
from some years to decades	fluctuations (oscillations in the composition of microcommunity)	—	—
from decades to centuries	microsuccession	oscillations due to the drift in local environmental conditions	—
from centuries to thousand(s) of years	microform oscillations (developmental cycle can be repeated many times)	community succession	adjustmental oscillations (nonsynchronous dynamics of different bog communities)
several thousands of years	—	compound microform oscillations (rearrangement of the set of compound compound microforms in the course of bog development)	macrosuccession (development of the whole bog)

is enlarged and the process is studied at the level of bog complex, it can no longer be considered as a directional succession, because the development of communities does not take place synchronously in all parts of a bog and a mosaic of different successional stages is observed. When this process is studied at the simple microform level, e.g., a single hummock or depression is considered no directional succession of a microcommunity can be observed because it takes place considerably faster. Thus, only some oscillations, which are caused by repeated successions, i.e. some kind of cyclical regeneration or irregular drifts in environmental conditions, are observed.

Analogically, the succession of a compound microform community is not observable when the time scale is changed and the interval used becomes too short or too long. Consequently, the nature of community (ecosystem) dynamics is greatly dependent on the spatial and temporal scales used. The different results of several authors sometimes refer not to the different nature of the process itself but rather to different scales of investigation.

Such a scheme also makes it possible to take into account allogenic changes, which are usually treated separately from autogenic processes. It can be seen that the bog ecosystem changes as a whole, but when the attention of an investigator is focussed on certain spatial and temporal scales, the bog dynamics exhibit new features. The changes, which should be treated as autogenic (e.g. the development of the hydrological network inside the bog complex) in one scale, could be external when another scale is used (change of hummock microcommunity due to the emergence of a new streamflow etc.). In some cases, the distinction between external and internal factors is difficult, hence, in principle, all factors not belonging to the specific level studied may be considered as external. For example, from the "point of view" of a single hollow or ridge, it is not important whether the fluctuation in the water table is caused by rainfall or by the emergence of a new streamflow in some part of the bog.

Analogous schemes are also used in other fields of science: the Stommel diagram in oceanography could serve as an example (STOMMEL 1963, HAURY, MCGOVAN et WIEBE 1978).

Successional dynamics of the spatial structure of vegetation has received little attention in plant synecology. In addition to some results concerning nucleation, i.e. spatial heterogeneity of community formation at early successional stages (TANSLEY 1929, YARRANTON et MORRISON 1974), only the works of WHITTAKER (1975b) and WHITTAKER et LEVIN (1977) could be mentioned. Bogs are evidently a good subject for a further study of these problems. The role of population processes, especially of the vegetative propagation of *Sphagnum*, in the development of the patchiness of moss communities (cf. ILOMETS 1988) should be also taken into consideration.

8. Models of bog development

The number of models which are dedicated to successional development of *Sphagnum* bog ecosystems is not large. There are no well-defined conceptual models (i.e. brief and telescoped explanations as F-, I- and T-model of CONNELL et SLATYER 1977) concerning bog development. Perhaps the classical regeneration cycle theory would represent such a kind of model. A qualitative population dynamics model to describe the succession of certain temperate North American wetland communities is presented by VAN DER VALK (1981, 1982, 1985).

Most of the existing quantitative models simulate the accumulation (and sometimes also decomposition) of the organic matter. Thus, as peat accumulation is a crucial process, differentiating mires from other types of ecosystem, these models may be called functional. Among earlier attempts, the model of JENNY et al. (1949) should be mentioned, the next step evidently belonging to GORE et GLASEN (1967). During the next eleven years three models were completed: those of JONES et GORE (1978), CLYMO (1978) and WILDI (1978). The last is the largest with all the advantages and disadvantages of such large models. It also tries to describe the development of the spatial structure of bogs. SILVOLA et HANSKI (1979) have made an attempt to simulate carbon accumulation in a raised bog on the basis of laboratory measurements of CO₂ exchange. ALEKSAKANDROV et LOGOFET (1985) have presented the model, describing the cycles of C and N during the first stages of forest paludification. It became evident from the model that the direction and rate of succession is determined by the cooperative effects of nutrition conditions and hydrology.

The theoretical model, describing the transitions between forest and bog ecosystems is presented by GLEBOV et KORZUHIN (1985), the thickness of peat layer is considered to be the function of nutrient status, plant phytomass and aeration conditions.

More thorough discussion of the topic of bog succession models can be found in CLYMO (1983) and GORE (1983). It should be pointed out that, unlike many other models of community and ecosystem dynamics, the above-mentioned models of peat accumulation cannot be included in the two extreme types of models: theoretical or simulative. They represent rather some kind of compromise between the two.

There are also some examples of Markov chain models, if the presentation of the transition probability matrix can be called a model at all. For such matrices (cf. WALKER 1970, AAVIKSOO, MASING et ZOBEL 1984), the probabilities of transformation between different types of communities (or between species) should be estimated. This can be possible when the stratigraphy of peat profiles is studied. The use of Markovian models in the case of stratigraphic data is discussed by HARBAUGH et BONHAM-CARTER (1970). The possibility of realizing the Markovian presumptions while modelling plant community succession (stationarity, the first order of the process and the possibility to operate with discrete states), is discussed by AAVIKSOO, MASING et ZOBEL (1984). Considering that due to peat accumulation each community creates a new substratum for the subsequent community, and that most mineral uptake, even in the case of shrubs, occur in the upper 15 cm of the substratum (BOGGIE, HUNTER et KNIGHT 1958), the use of a Markovian model to describe bog succession seems to be more justified than in the case of other types of biotic communities.

The relatively little number of the models of autogenic bog succession may be connected with the smaller area of bogs in comparison with many other types of ecosystems, and evidently also with the low economic value of such models. The main effort has been directed to the problems of bog drainage. On the other hand, the relative autonomy, clear boundaries, few species and interesting spatial pattern make bog development a suitable topic, at least, for theoretical models.

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SUMMARY

Analysis of the extensive literature concerning autogenic bog succession allows us to make some general conclusions.

During bog succession several communities replace each other until a more or less stabilized state is achieved. Succession is simultaneously convergent (the same type of community can arise from entirely different initial communities) and divergent (different stable communities can arise from the same type of community).

The general successional trends in ecosystem parameters are predictable: the decrease of the contents of most nutrients in soil (peat) and soil water, decrease of pH and increase of the content of dissolved oxygen in soil water, decreasing soil microbial activity, decrease in species diversity, establishment of certain assemblages of oligotrophic species etc.

The mechanisms responsible for bog succession are quite diverse and can be explained with the help of both tolerance and facilitation models. But with regard to peat accumulation facilitation (i.e. the changes in local environmental conditions facilitate the replacement of different sets of species) gradually becomes more important.

The formation of bog surface pattern is a synergetic process the causal background of which is not sufficiently known. Evidently some hydrostatic factors can play a certain role in pattern initiation, and the differences in nutrient and oxygen inputs and temperature further cause divergences in decomposition rates in different sites.

In principle bog succession could be studied in different spatial and temporal scales. The character of the process under investigation is greatly dependent on the scale used. When another scale is used, new features of the process become evident.

Knowledge of bog succession could be useful for general succession theory. It becomes evident that a different concept could be applied in the case of bogs and the use of a certain concept in one case does not mean that all other concepts should be rejected. In the case of bog succession the stochastic and deterministic nature of succession, convergency and divergency, population processes and the changes in populations due to the transformation of local environment, directional and reversible changes etc. become evident, when different sides of the process are studied.

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