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THE HOLISTIC VIEW OF SUCCESSION RECONSIDERED

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Abstract. The popularity of the reductionist approach led to a considerable advancement of succession theory. Its methods are particularly adequate for the analysis of short-term secondary processes. It is emphasized that in the interpretation of long-term primary successional seres the holistic approach has also been useful and relevant. Of the various primary seres, any sequence of stages that lead to a climatically zonal community may be selected as a reference basis. As an example, two seres of the Hungarian Great Plain are analyzed and compared.

Introduction

The antiholistic-reductionist views, rooted in the individualistic community concept of Gleason, have dominated interpretations of succession for 40 years. The essence of this, as Harper's (1982) classical definition emphasizes, is that all community-level events may and must be understood on the basis of populations. The literature published since Drury and Nisbet (1973) abounds in studies describing and modelling successional processes through population dynamics, physiology and, more recently, resource utilization potentials. Most of the significant results in the field of vegetation dynamics stem from the reductionist approach.

It is often forgotten, however, that short-term successional events can only be interpreted by methods relying on the reductionist approach. The majority of results concern secondary succession usually with rapid initial steps, so that hypotheses may be tested experimentally within a few years.

The situation is different for primary succession. As indicated by the relatively fewer publications and less powerful results presented therein, our knowledge is more limited than in the case of secondary succession. Nevertheless, quite a few attempts have been made to evaluate the revegetation processes on secondarily developed sterile surfaces, such as spoil banks of open coal mines. Studies of reductionist attitude are often restricted to the description of initial stages. If we consider that some primary seres develop in thousands of years (see *e.g.*, Walker's (1970) postglacial hydroseries), then weakness of the reductionist approach becomes even more obvious. The differences between temporal scales (cf. Major 1974) causes problems for the comparison of primary seres, but comparisons are even more difficult for secondary seres. Explanation of the primary seres with usually long time-span is difficult with reductionist methods on their own. In my opinion, this is when holistic methods are acceptable so that we can concentrate upon some more general characteristics of succession. In the meantime, we can identify similar seres for identification purposes, so typical of the holistic approach. Note that typification, a fairly ambiguous term for many, is not understood here as mere pigeonholing.

Materials

Introductory notes.

We are sure that climax is still extremely important among the concepts of primary succession, but it should not be associated with any "superorganistic" views. A distinguished type of the climax, or terminal, stages is the climatic climax. This is a community type best reflecting the macroclimate of the given region. The central role of climatic climax is the ease of its definition and its uniqueness, contrary to the edaphic climax stages. The climatic climax is therefore a reference basis, whose importance is underlined by the fact that it is the most frequent among the community types in the more or less intact vegetation. Furthermore, it is also true that climatic climax and climatic zonal community are identical. The latter term originated from the Russian pedological literature, and has also been adopted by the central and eastern European schools of vegetation science. (On the identity of climax and climatic zonal communitities, see Walter 1954.) We have detailed information on the climatic zonal communities of Hungary, mostly resulting from the mapping projects in the 1950-60's (see also Borhidi 1961).

Given a reference basis, which includes not only the climax itself but also the full successional sere leading to it (called the *zonal* sere), tests of departure from this basis will become possible. This study attempts to formulate and perform such tests.

Two seres will be examined, both distributed in the forest steppe zone of the Danube basin. The term forest steppe reflects that the communities are located on the border of two formations; local conditions dictate which of them will actually manifest itself. The macroclimate is modified by microclimate (exposition) and, especially on the Alföld, by soil moisture. The study area (Fig. 1) lies on the climatic border. For example, at the meteorological station of Kecskemét climatic data for 110 years (Zólyomi and Kéri, in press) suggest that 41% of the years belong to the steppe climatic type (Köppen's (1929) xx' and BSK (x' x") types). It is therefore clear that physical properties of the soil are substantial.

The stages of the two seres are:

Loess sere. Loess is an excellent substrate for vegetation. It is rich in mineral nutrients; the clay minerals ensure a well-structured soil with high cation- absorption capacity and favorable water balance.

As to the stages of the sere, many surveys contributed to a consensus in the Hungarian phytosociological literature. Zólyomi's (1957, 1958, 1967, and unpublished manuscripts) works are fundamental in this regard. The stages are as follows:

Agropyro-Kochietum. An open, species-poor, primary semi-desert community on the edge of loess cliffs. Very limited in distribution.

Salvio-Festucetum rupicolae. Vertically well-structured, almost completely closed (up to 90-95% cover) steppe community rich in broadleaf dicots. Eight to ten potentially dominant grass species occur, their competitive hierarchy is decisive for the vegetational changes of the steppe and subsequent stages (including degradation!). Some forest species are also present in this rich community type.

Amygdaletum nanae. Commuity composed of dwarf shrubs. The transitional position between the previous and the subsequent stages is reflected by 40% steppe species and 40% forest species (Zólyomi 1967), so that this community represents a real connection at the border of two formations.

Aceri (tatarici) - Quercetum. Climatically zonal forest; the terminal stage of the sere. It is a physiognomically homogeneous community with a dense shrub layer. Extensive loess areas of the Alföld and its neighborhood were formerly covered by this vegetation type. These forests have been replaced by agricultural fields with original soils transformed to highly fertile lands. In the few fragmented remnants of the community the primary stages and their dynamics are still observed.

Sand sere. The sand of the Danube plain is coarse grained; the clay and silt content remains below 4-5% so that water holding capacity is very low. In the semi-arid climate soil formation, the humification processes and the migration of mineral nutrients are very slow.

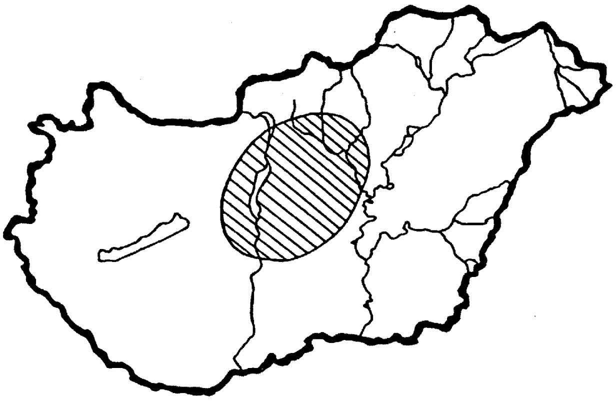

Figure 1. The study area is in the north-central part of Hungary. Its approximate extent is indicated by shading in the map.

Of the many successional seres described from sand we refer to only one relevant series, a xeroseries that is independent of soil water. This typical vegetation and flora of the Hungarian plains have attracted the attention of the pioneers of vegetation science. Kerner (1863), who contributed much to the early development of succession theory, must be mentioned first. Based on the ideas of Rapaics and Soó, this vegetation type and its primary succession was described in detail by Magyar (1933), Hargitai (1940) and Zsolt (1943) (see also Simon 1979, Précsényi 1981, Fekete *et al.* 1989).

The stages of the sere are as follows:

Festucetum vaginatae. Perennial grassland of the partly fixed sand. The most extensively distributed community with a cover of 50%. Many species that tolerate sand cover, and occasionally some annuals constitute the first stages of the primary series.

The dominance of annuals (*Stipa capillata, S. sabulosa, Festuca wagneri*) indicates minor but sharp phytosociological differences.

Poplar and juniper stands. Pure or mixed stands of *Populus alba* and *Juniperus communis,* occasionally intermingled with forest shrubs and sand steppe species. The physiognomic structure is varied, tree height is 2-10 m.

Astragalo-Festucetum rupicolae. Sand steppe-meadow. The stands are composed of some xerophilous and xeromesophilous grasses, dwarf sedges in the lowest layers, many microphyllous and only a few broadleaved dicots. Some stands contain sand steppe species; elsewhere the number of mesophilous meadow species is high.

Quercus robur and Qu. pubescens-dominated oakwoods (Festuco-Quercetum). These have scattered distribution with loose cover, stunted trees, dense shrub layer and a few forest species.

Methods

Introductory notes

The forest steppe vegetation appeared first in the Danube basin through invasion and directed migration in the boreal and atlantic phases of the postglacial era. It was followed by predominantly mesophilous forests. There has been a continuity in the plant cover originating from the boreal and atlantic phases in the Hungarian Plain; the vegetation survived because, unlike in the maountains, the subsequent forest phases did not establish permanently. Therefore, the forest steppe zone of the plain reflects more clearly the former boreal and atlantic phases than the vegetation of hills and mountains of the Carpathian Basin. A summary of palynological records is found in Járai-Komlódi (1987).

On the reconstruction of succession

The past successional stages appear recently in form of a spatial coenocline, for example, the loess vegetation along an ecological gradient associated with a steep hillside. The dynamics of neighboring stages and migration of populations are still obvious.

The successional trends on sand were revealed by repeated mapping projects. On the two major study sites a vegetation map at a scale of 1:1000 was prepared. Basic information was provided by recording the invasion of some key populations, *i.e.*, those showing the direction of changes *in statu nascendi.* Experience of foresters on habitat types and on the ability of tree species to establish in different communities also represented an important source of information.

Statistical analyses

Published tables and unpublished phytosociological records served as a basis for analyzing the two seres (Zólyomi's cited works and unpublished data for the loess sere, and Hargitai (1940), Zsolt (1943), Szodfridt (1969) and my unpublished relevés for the sand sere).

The extent to which the community is coordinated was estimated by calculating the average similarity of all relevés of a stage to all the others. The r contingency coefficient related to the χ^2 values computed for presence/absence data was used. Habitat packing was estimated using the W categories expressing soil moisture preference for each species (see the T-W-R indicator system of Zólyomi and Précsényi 1964). The frequency values of these categories were used to compute the *habitat-width* of communities by Levins' B_i index (to the analogy of niche breadth). The overlap of community habitats (habitat packing) was measured through Levins' α (see Levins, 1968, for both coefficients).

Results

In this section, attention is focused on the interpretation of differences between the primary successional seres, with emphasis on characteristics due to zonality. The interpretation is holistic in the sense that we start from the "holon", from the high levels of organization to the low (see Table 1).

Ecosystem evolution

The analysis of vegetation-soil interrelationships is a classical topic of plant ecology. High correspondence is expected for zonal situations, since both vegetation and soil (*i.e.*, genetic soil types) have a definite zonality. Correspondence within a successional sere has seldom been investigated.

The distinction of zonal seres and the fact that early stages have less developed soil are striking. In the sand sere, however, the same successional stage may appear on different soil types and several community types may just as well occur on the same substrate (Table 2).

We conclude that interaction between vegetation and soil is clear for the whole zonal sere. This interaction is less pronounced for the sand sere. A difficulty with this comparison is that the zonal sere has a wider range of soils than the sand sere.

The high correspondence and strict parallelism focuses our attention on the coevolution of vegetation and soil. This is well-organized in the zonal sere, whereas soil development is slow, or - if you prefer the other way - vegetation changes are too fast, in the sand sere.

Sere properties

The primary dynamics of the two seres are shown in Figs 2-3. The graph is simple, showing linear relationships, for the zonal sere (Fig. 2). The course of succession is not even. The pioneer *Agropyro - Kochietum* community represents a place of abrupt change judging by the composition. Due to spatial isolation of the stands this community has very little influence on the initialization of successional processes. The relationship of the steppe meadow to forests is manifested at two temporal scales: at the historical scale because steppe meadows were replaced by the forest steppe at the end of the boreal phase; and at the scale of tree generations. The regeneration of fragmented steppe meadows from propagules is possible at sites with dying trees of mature stands (Zólyomi 1957).

The primary dynamics of the sand vegetation is more complex and requires a more detailed discussion. The concept of primary succession as understood here is different from the traditional interpretation of the Hungarian phytosociologists.

The xeroseries is displayed as a large circle (Fig. 3). The succession terminates at the *Junipero- Populetum* along many lines; this community corresponds to the real forests in this sere. The starting point is usually the

Table 1. Hierarchically dependent organizational attributes: zonal versus extrazonal series

	Climatic zonal forest steppe series (on loess)	Edaphic extrazonal semi-desert series (on sand)
Ecosystem evolution		
Vegetation-soil interaction	Expressed	Non-expressed
Vegetation-soil evolution	Parallel	Non-parallel
Series properties		
Graph structure	Linear	Reticular
Determination of the sucession	Strongly determined transitions between stages	Stochastic transitions
Origin of climax stage	Homogeneous	Heterogeneous
Succession as direct life form progression	Expressed	Non-expressed
Series compositional differentation	Well-differentiated	Slightly differentiated
Series habitat packing	Loosely packed	Tightly packed
Sociological properties		
Species diversity in the stages	High (with decline at the transition of formations)	Low. Especially low flora density in the climax stage
Level of coordination of stages (between-site sociological similarity)	High	Lower, especially low in climax stage
Stratification (differentiation of coenostates having dynamic importance)	Well-stratified stages	Mostly poorly stratified stages
Stability: resistance against invaders	Mainly by the sociological structure	By the extreme nutrient-poor habitat
Population features		
Life form diversity in stages	Average	High
Diversity of other type (physiological, biochemical)	Average	High
Dominant strategy	Competitive	Stress tolerator
Competitive hierarchy among populations	Expressed	Low
Biogeography		
Area-forms of constituting species	Mainly continuous	Many disjunct areas
Formation of endemisms	In all phases poor	Rich in endemisms

Table 2. Vegetation-soil correspondence in zonal and extrazonal series

Zonal series	*Agropyro-Kochietum*	*Salvio-Festucetum rupicolae*	*Amygdaletum nanae*	*Aceri tatarici - Quercetum*
	Skeleton soil on loess	Black earth	Degraded black earth	Black earth and brown forest soil
Extrazonal series	*Festucetum vaginatae*	*Astragalo-Festucetum rupicolae*	*Junipereto-Populetum*	*Festuco-Quercetum*
	Skeleton soil on moving sand	Somewhat humic sand, black earth, dry meadow soil	Skeleton soil on moving sand, buried meadow soil	Black earth, shallow brown forest soil, buried meadow soil.

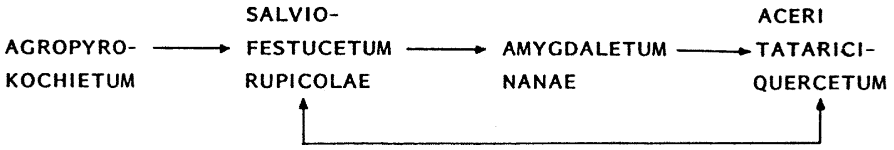

Figure 2. Graph of primary succession: zonal series

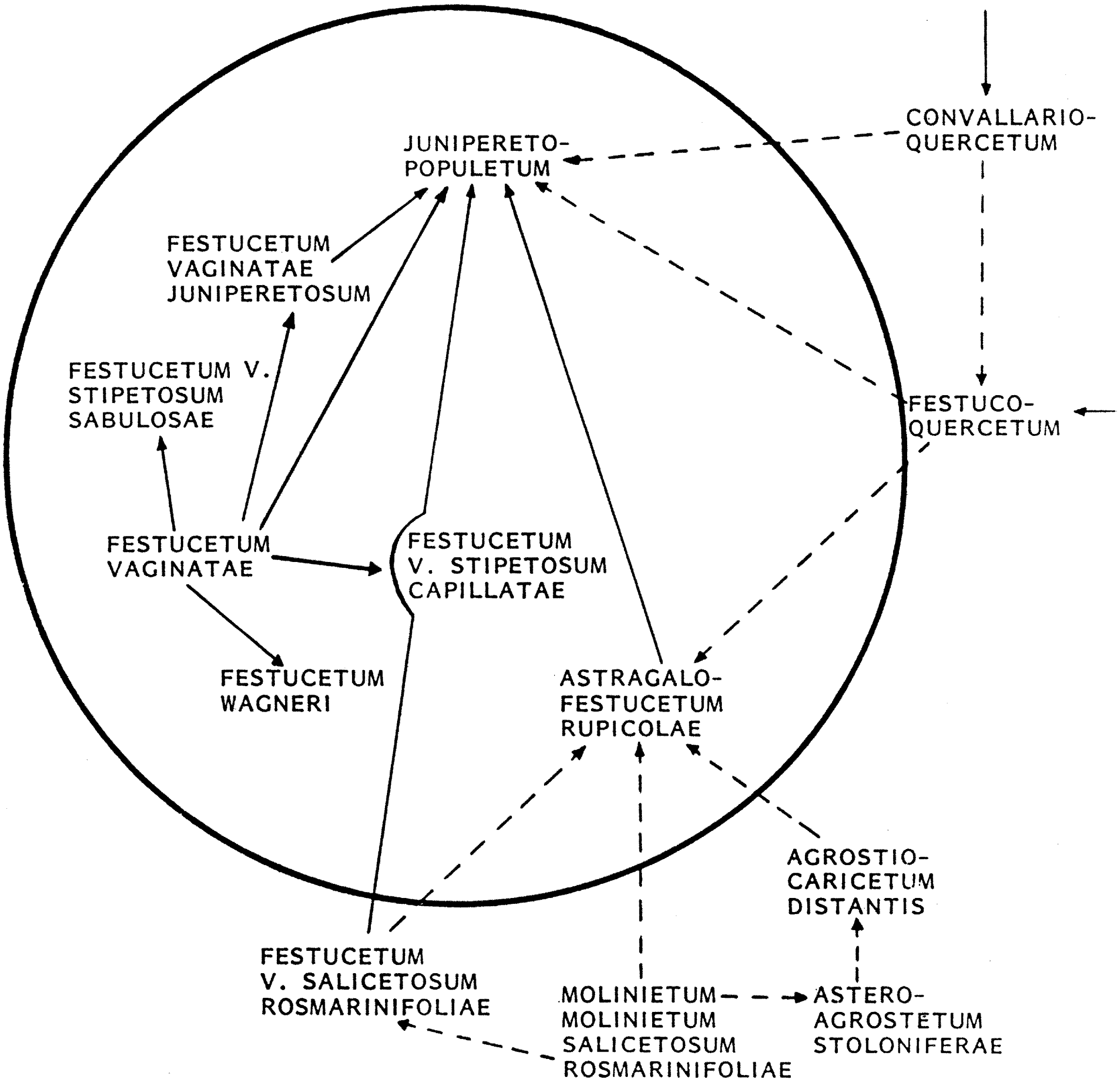

Figure 3. The pathways in xeroseries

Festucetum vaginatae community. The proliferation of xerophilous grasses (*Stipa* spp., *Festuca wagneri*) often stops the process. A substantial difference from the zonal sere is that the steppe meadow does not fit the pioneer grassland-shrub line. The pioneer grassland does not accumulate sufficient humus for the establishment of steppe-meadow species. Steppe meadows do develop as derivatives of other vegetational changes, *e.g.*, as a result of the dehydration and transformation of mesophilous meadows (semi-saline meadows, wet meadows). In the plain this is due to the permanent decrease of water table in the past decades. Soils of logged oakwoods are also suitable substrates for steppe meadows, however. The disappearance of steppe meadows from the main successional line makes the graph reticulated in this sere.

The stands of sand oak wood found on some places in the study area are habitat-dependent; they require fossil soils or the presence of a water-holding clayey fraction of the soil to decrease the amount of run-off water. The progression from sand vegetation towards oakwoods cannot be indicated now. The degradation of oakwoods causes the development of poplar - juniper stands (Kárpátiová *et al.* 1961).

As far as dynamics is concerned, the *Junipereto-Populetum* is a terminal stage. Yet, it is not a climatically zonal forest. Climatically zonal communities will not occur on sand substrates nor will slope vegetation occur in excess sunshine. On southern slopes as well as on sand we find extrazonal vegetation. One difference being that on sand, shortage of available water represents significant differences from the macroclimatic conditions, rather than high temperature. For these reasons, when discussing sand substrates we shall refer to extrazonal vegetation seres.

The graph structure indicates a highly deterministic character of the zonal sere and stochasticity between stages of the extrazonal sere. This is true of transitions from *Festucetum vaginatae,* particularly at transitions to the terminal stage. Thus, the climax has a heterogeneous origin, just as the steppe meadow itself.

We have mentioned the wide range of soils as expression of progression. Such features may be examined on the side of vegetation as well. Life-form progression, for example, may be used to measure advancement of succession (see Numata 1969). This progression is more pronounced in the zonal sere. In the *Agropyro-Kochietum* we find many therophytes, the steppe meadow is dominated by hemicryptophytes. Mesophanerophytes dominate the *Amygdaletum,* whereas megaphanerophytes are most abundant in the oakwood, regarding both species number and biomass. In the azonal sere no such clear correspondence occurs.

An important case of differentiation is compositional. Comparison of phytosociological tables suggests that species change between the pioneer and terminal stages is incomplete in the extrazonal sere: species turnover is only 68%. In the zonal sere almost all species have been replaced (97%).

At this point it is useful to analyze both seres based on different criteria for analogous phases. We cannot be rigorous, however, because the physiognomically distinct phases do not follow the same sequence in the two seres. The steppe meadow, as mentioned earlier, joins the series on the "sideline". Nevertheless, the reference basis must be an identical physiognomical entity (you cannot compare grasslands and forests, or grasslands and shrublands).

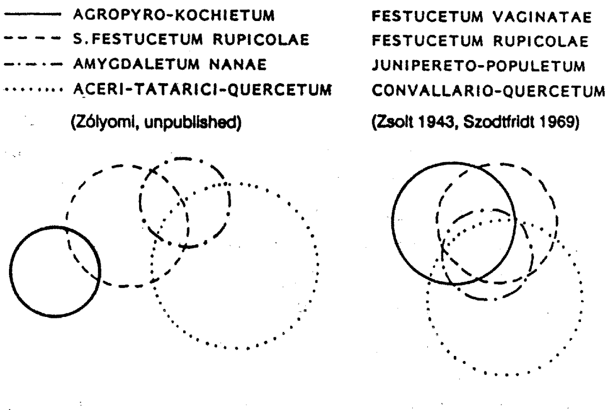

Figure 4. Diagrammatic representation of packing of the stages of both series in the habitat space. The diagrams illustrate the calculations on one dimensional habitat width and overlap (Levins' B_i and α) based on water-indicator values (see Zólyomi and Précsényi 1964) of all species comprising the stages. On the left: zonal series. On the right: extrazonal series.

Habitat packing of stages differs with the seres (Fig. 4). Again,the zonal sere exhibits particular differentiation (looser packing) and in the one-dimensional habitat space the separation of the pioneer stage is obvious, too. The appearance of a 4-stage overlap in the extrazonal sere indicates considerable habitat packing.

Phytosociological attributes

Species diversity was simply expressed as the number of species (total number of species of each table). Relative evenness in the stages of the extrazonal sere is due to the uniformizing influence of *Festucetum vaginatae* on the species composition of *Junipereto-Populetum*, and even on the steppe meadow. The high species richness of the zonal sere decreases upon the change of formation (Fig. 5).

Coordination is stronger in every stage of the zonal sere than in the extrazonal (Fig. 6). We may assume that biotic regulation through high species richness is responsible for the high similarity of "replicate" stands in the zonal sere. On the contrary, relatively strong coordination of the *Festucetum vaginatae* semidesert community can be explained on the basis of strong abiotic stress and its selective power. Resistence to weeds has probably a similar explanation.

Discussion

1. Following the steps of Table 1, the term population attributes shows that we entered the realm of reductionist methods. However, there are many things in common with the above holistic interpretation. The advantage of the holistic approach is its ability to find some useful reference points. Such a reference is the observation that coenological stratification is high in

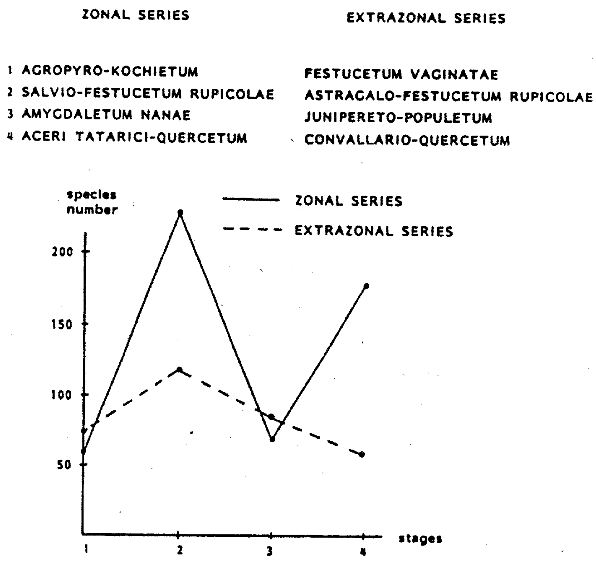

Figure 5. The number of species in the consecutive stages.

many stages of the zonal sere, particularly in the steppe meadows. This is shown by many syntaxonomical subunits described in the phytosociological literature if we consider either degraded stages or the vegetation differentiation along extended ecoclines. These subunits or coenostates often have dynamic importance. Phytosociological stratification in the zonal sere harmonizes with the competitive strategies that dominate there. Functioning is ensured by the competitive hierarchy of species, mainly grasses. This hierarchy is apparent in undisturbed cases only; degradation rearranges this hiearchy (*e.g.*, *Botriochloa ischaemum* → *Festuca pseudovina* → *F. pseudovina*). The aim of current research is to recover the population dynamic and physiological background of such hierarchies.

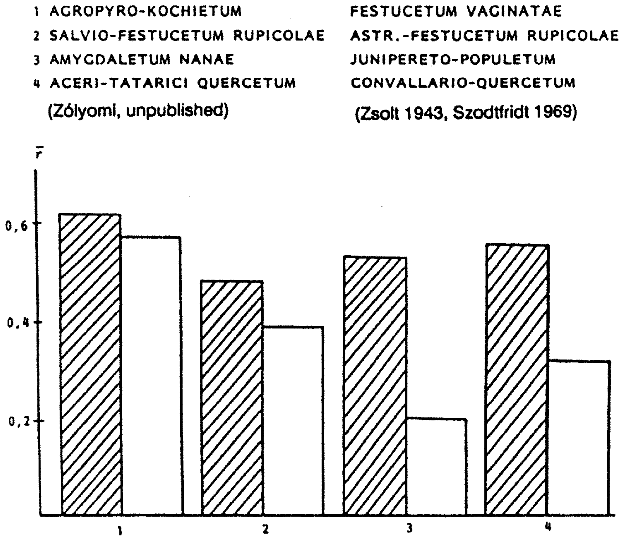

Figure 6. The degree of the sociological coordination in the two series expressed in average similarity values (r̄) of the relevés representing the same stage (pairing of comparable stages). The r̄ values are based on presence/absence scores. Shaded columns: zonal. Other columns: extrazonal series.

Evidence suggests that in the *Festucetum vaginatae,* the most extensive stage of the extrazonal sere, the stress-tolerant rather than the competitive strategy is successful. We refer to the high proportion of species with C_4 (C_3-C_4) and CAM-type photosynthesis (Fig. 7), reflecting adaptation to dry conditions, which is beyond example in the central European vegetation (Horánszky and Nagy 1977, Nagy and Horánszky 1980). Many alternative solutions to resist drought stress have evolved and these adaptive physiological strategies simultaneously appear in the same community (Tuba 1984). The diversity of Raunkiaer life forms is also high in the stages of the extrazonal sere. These findings indicate that high life-form or other functional diversity is a static character reflecting the survival of the stage. This view is supported by the above discussion of life-form progression.

2. The attributes of the two seres examined here are compared with the assumption that differences are attributable to the zonal or extrazonal character of the sere.

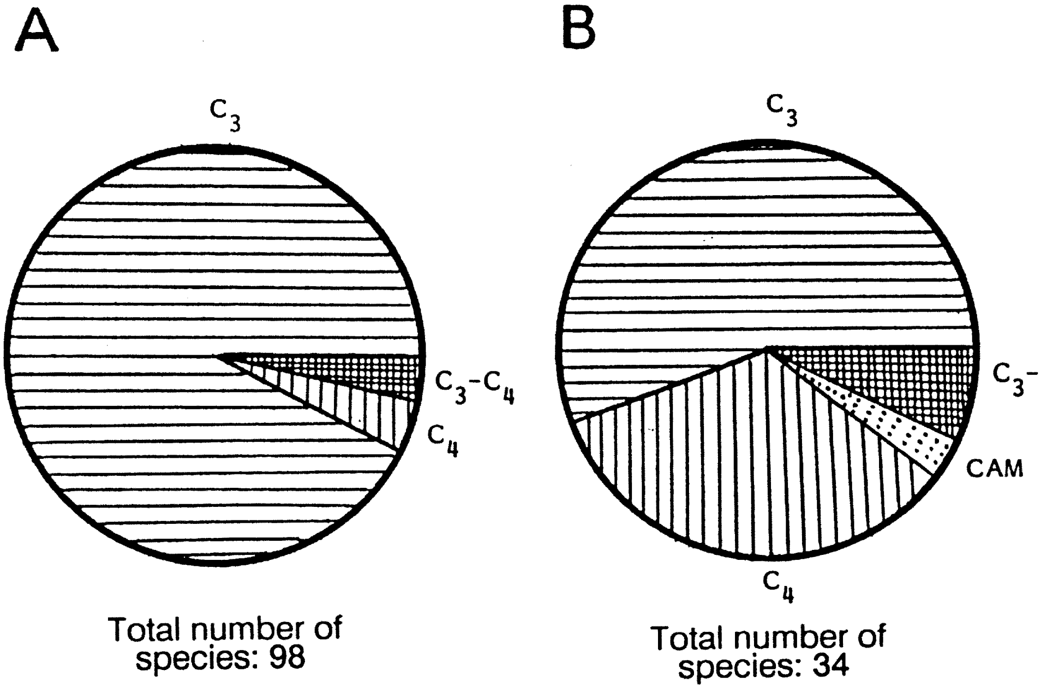

Figure 7. The distribution of the photosynthetic types in the grasslands of the two series. A: *Salvia - Festuca rupicola* community (loess steppe meadow); B: *Festuca vaginata* community (perennial sand grassland)

Features characteristic of the zonal sere: co-differentiation and coevolution between primary succession of vegetation and genetic soil development; and distinctiveness of successional steps. This process can be described well in terms of compositional similarities. The direct progression of life-forms is also detectable ("one phase- one life-form"). The background process is a clear habitat differentiation with minimum collective overlap.

The weak differentiation of stages in the extrazonal sere may be attributed to the weak differentiation of soil types. The low correspondence between vegetation and soil causes uncertain stage transitions, expressed by the reticulate graph structure.

An important criterion of improved supraindividual organization of the zonal sere is the better coodination of stages. This coordination can be interpreted well from "above"; the sere is strongly deterministic and the phases have a homogeneous origin.

3. Spatial constraints must be used in the elaboration of the above topic. The zonal vegetation usually covers extensive areas; the stands are less fragmented than the azonal communities. Thus, isolation causes very little reduction of species number. In the zonal vegetation average species number is usually higher than in the corresponding extrazonal type, and migration of species is possible in larger areas. Taxonomic richness (many species, ecological vicariants) facilitates refined niche partitioning in the stages.

The extrazonal vegetation is almost always fragmented and isolated, as reported primarily from mountainous areas. In the sand sere species absences and eliminations are often observed: there is sometimes no species suitable to occupy certain niches. Instead, substituting species that do not completely perform in the same way will appear. A good example is the shrub phase of the succession. Many species are specialized to this phase of the zonal sere (*Amygdalus nana, Cerasus fruticosa, Rosa pimpinellifolia*), all associated exclusively to the forest steppe zone. In the extrazonal sere, however, this stage is composed of non-specific constituents. Thus, the appearance of *Populus alba* is just a substituting phenomenon, because the habitat of this species is the gallery forest. Similarly, *Juniperus communis* is also a "Jolly Joker" in the phytosociological sense, as shown by its wide geographical range.

4. It is worth pointing out two further phenomena that are relevant to the present discussion. If the communities of the two seres are analyzed according to the distributional types of constituting species, consistent differences may be identified. In the zonal sere the majority of species have a more or less continuous geographical range, with disjunctions, whereas in the sand sere there are many species with disperse distribution. These differences support the above conclusions. Furthermore, if we consider the distribution of species restricted to the Danube Basin (Pannonian endemics, cf. Soó 1964) we find many in the extrazonal sere (*e.g.*, *Festuca vaginata, F. wagneri, Dianthus regis stephani, D. diutinus, Sedum hillebrandii, Linum glabrescens*). In the communities of the zonal sere no such species occur.

Two notes are in order regarding geographical area types and endemics: 1. We are again faced with an areal-geographical phenomenon, 2. The development of these phenomena required many years; and the historical facts are relevant. The endemics listed above are all heliophytes, restrcited exclusively to the sand steppe (*Festucetum vaginatae*). Speciation was possible in a situation similar to the present, when succession was arrested to some extent or, at least, the shrubby and forest phases had a very slight chance to develop.

The other phenomenon is phytosociological. In the different sections of the Danube-Tisza interregion the terminal shrublands have different composition. In some cases *Populus alba* is dominant on the dunes, elsewhere *Populus canescens (P. alba x P. tremula). P. alba* and *Juniperus communis* may also be dominant together, and in the south *Crataegus monogyna* dominates. West of the Danube *Juniperus communis* is absent. This compositional uncertainty may be explained by the process of phytosociological drift which is in good agreement with the graph structure of the sand vegetation and the stochasticity of succession.

5. I must emphasize again that I do not have doubts about the importance of the reductionist approach in the interpretation of succession, but I reject its absolute, exclusive validity. Holism and reductionism both have their own field of relevance and they are equally useful concepts of succession theory.

In principle, reductionism has a methodological-analytical nature; it encourages the elaboration of analytical tools to reveal fundamental mechanisms of succession. On the other hand, it is also true that these mechanisms are controlled by external constraints. It has been shown, for example, that some secondary successional mechanisms can be interpreted in terms of allocational trade-off (*e.g.*, between nitrophily and halophily, Tilman 1990). Even Tilman himself points out that these vegetational trade-offs have been subject to environmental contraints.

The holistic view is important for hypothesis-generation (*e.g.*, in recognizing different types of primary succession). In addition, the holistic approach has shown that for each type sets of constraints along a habitat series may be identified. These constraints act at higher levels of organization (vegetation, community) and control the lower level mechanisms.

REFERENCES

Borhidi, A. 1961. Klimadiagramme und Klimazonale Karte Ungarns. Ann. Univ. Budapest Sect. Biol. 4: 21--50.

Drury, W. H. and I. C. T. Nisbet 1973. Succession. J. Arn. Arb. 54: 331-368.

Fekete, G., Z. Tuba, and E. Melkó 1988. Background processes at the population level during succession in grassland on sand. Vegetatio 77: 33-41.

Hargitai, Z. 1940. Nagykőrös növényvilága II. A homoki növényszövetkezetek (Plant life of Nagykőrös. II. Plant communities on sand). Botanikai Közlemények 37: 205-240.

Harper, J. L. 1982. After description. In: Newman, E. I. (ed): *The Plant Community as a Working Mechanism*, pp. 11- 26.

Horánszky, A. and A. H. Nagy 1977: Study of assimilation types in species of a sand steppe community. Acta Bot. Hung. 23: 91-95.

Járai-Komlódi, M. 1987. Postglacial climate and vegetation history in Hungary. In: Pécsi M. and Kordos L. (eds). *Holocene environment in Hungary.* Budapest.

Kárpátiová, V., Kárpáti, I., Krippelová, T. and E. Krippel 1961. Spolocenstvo topolá bieleho a borievky obycajnej pri Sturove. Biologia 16: 481-492.

Kerner, A. M. 1863. *Pflanzenleben der Donaulander* Innsbruck.

Köppen, W. 1929. Typische und übergangs-Klimate. Meteorologische Zeitschrift 46.

Levins, R. 1968. *Evolution in changing environment.* Princeton, New Jersey.

Magyar, P. 1933. A homokfásítás és növényszociológiai alapjai (Afforestation on sand and its phytosociological basis). Erdészeti Kísérletek 35: 1-89.

Major, J. 1974. Differences in duration of successionnal seres. In: Knapp, R. (ed). *Vegetation dynamics,* pp. 155- 159. Junk, The Hague

Nagy, A. H. and A. Horánszky 1980. Productivity and photosynthetic flexibility in some species of a grassland community. Acta Bot. Hung. 26: 389-395.

Numata, M. 1969. Progressive and retrogressive gradient of grassland vegetation measured by degree of succession. Ecological judgement of grassland condition and trend IV. Vegetatio 19: 96-127.

Précsényi, I. 1981. Changes in the diversity of the vegetation during succession, Acta Bot. Hung. 27: 189- 198.

Simon, T. 1979. A Kiskunság Nemzeti Park növényvilága (Plant life in Kiskunság National Park). In: Tóth, K. (ed). *Nemzeti Park a Kiskunságban* (Kiskunság National Park), pp. 165-175. Natura, Budapest.

Soó, R. 1964. *A magyar flóra és vegetáció rendszertani- növényföldrajzi kézikönyve* (Taxonomical-phytogeographical Manual of the Hungarian Flora and Vegetation). Akadémiai Kiadó, Budapest.

Szodfridt, I. 1969. Borókás-nyárasok Bugac környékén (Juniper-poplar stands in the environs of Bugac). Botanikai Közlemények 56: 159-166.

Tilman, D. 1991. Constraints and tradeoffs: toward a predictive theory of competition and succession. Oikos 58: 3-15.

Tuba, Z. 1984. Rearrangement of photosynthetic pigment composition in C_4, C_3, and CAM species during drought and after recovery. J. Plant Physiology 115: 331-338.

Walker, D. 1970. Dirrection and rate in some British post-glacial hydroseres. In: Walker, D. and West, R. G. (eds.). *Studies in the Vegetational History of the British Isles,* pp. 117-139. Cambridge University Press, Cambridge.

Walter, H. 1954. Klimax und zonale Vegetation. Angewandte Pflanzensoziologie, Festschrift 1: 144-150.

Zólyomi, B. 1957. Der Tatarenachorn-Eichen-Lösswald der zonalen Waldsteppe. Acta Bot. Hung. 3: 401-424.

Zólyomi, B. 1958. Budapest és környékének természetes növénytakarója (Natural vegetation of Budapest and its environs). In: Pécsi, M. (ed.). *Budapest természeti képe* (Natural portray of Budapest), pp. 511-642. Akadémiai Kiadó, Budapest.

Zólyomi, B. 1967. Amygdaletum nane pannonicum. In: Zólyomi, B. (ed.). *Guide der Exkursionen des Internationalen Geobotanischen Symposiums,* Ungarn, pp. 61-62.

Zólyomi, B. and Précsényi, I. 1964. Methode zur ökologischen Charakterisierung der Vegetationseinheiten und zum Vergleich der Standorte. Acta. Bot. Hung. 10: 337-416.

Zsolt, J. 1943. A szent-endrei sziget növénytakarója (The vegetation of Szentendre Island). Index Horti Botanici Univ. Budapest. 6: 1-19.

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