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# МАТЕМАТИЧНА ЕКОЛОГІЯ

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## NONLINEAR THEORY OF SUCCESSIONS IN FORESTRY BIOGEOCOENOSES: MATHEMATICAL ASPECTS

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Systems analysis of biological phenomenon of succession has been carried out. The history of the subject and the current state of art are considered. Classification of both succession process as a whole and separate succession stages are proposed. Interaction between two main gears of succession – competition between plant species and their interaction with abiotic part of the biogeocoenose – are considered. Extreme nature of succession process and polygenetic structure of biogeocoenose, as a result of succession, are demonstrated.

*Key words: biogeocoenose, succession, systems analysis, woodland, mathematical model.*

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### НЕЛІНІЙНА ТЕОРІЯ СУКЦЕСІЙ ЛІСНИХ БІОГЕОЦЕНОЗІВ: МАТЕМАТИЧНІ АСПЕКТИ

Проведено системний аналіз біологічного феномену сукцесій. Розглянуто історію проблеми та її сучасний стан. Наведені окремі класифікаційні схеми і для сукцесій, як процесів у цілому, і для окремих сукцесійних стадій. Розглянута взаємодія двох основних механізмів сукцесії – конкуренції між продуцентами та їхня взаємодія з абіотичними компонентами біогеоценозу. Показано екстремальний характер процесу сукцесії та полігенетичний характер біогеоценозу як результат сукцесії.

*Ключові слова: біогеоценоз, сукцесія, системний аналіз, ліси, математична модель.*

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### НЕЛИНЕЙНАЯ ТЕОРИЯ СУКЦЕССИЙ ЛЕСНЫХ БИОГЕОЦЕНОЗОВ: МАТЕМАТИЧЕСКИЕ АСПЕКТЫ

Выполнен системный анализ биологического феномена сукцессий. Рассмотрена история проблемы и современное состояние. Представлены отдельные классификационные схемы и для сукцессий, как процессов в целом, так и для отдельных сукцессионных стадий. Рассмотрено взаимодействие двух основных механизмов сукцессии – конкуренции между продуцентами и их взаимодействие с абитотическими компонентами биогеоценоза. Показан экстремальный характер процесса сукцессии и полигенетический характер биогеоценоза как результат сукцессии.

*Ключевые слова: биогеоценоз, сукцессия, системный анализ, леса, математическая модель.*

Consider issues related to biological gears of successions understanding of which is necessary for adequate mathematical models of ecosystem dynamics construction. We shall examine successions in land (uppermost forest) biogeocoenoses. Succession biological specificity issue is closely connected with emergency of succession ecological system

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problem (Vasilevich, 1983; Peregudov, Tarasenko, 1989; Gorelov, 1998), whereas they could be examined as specific peculiarities display of synecological systems or as simple step-by-step substitution of one plants by the others not obeying certain special laws. We shall hold to the first approach and show that succession may be examined like nontrivial process of homeostasis and ecosystem self-organization (Kolesov, Majorov, 1986; Armand, 1988; Chernyshenko S.V., 1995). Meanwhile, emergent properties of successions are, from our point of view, based on two quite clear ecological processes:

- dialectical interaction of biota and stagnant environment (against the background of evolutionary fitness of species to certain ecological characteristics);
- interspecific competition for ecological resources (phased-array, biogenic elements, water, etc.).

### **Ecological phenomenon of successions**

Succession changes have been being at the centre of attention of biogeocenologists for more than century and have been staying one of the most urgent problems of ecology. There is a huge number of publications, dealing with this subject. Short review Russian-language publications is given in the volumes (Krivolutsky, Pokarzhevsky, 1990; Berezovskaya and others, 1991; Gorelov, 1998), and foreign publications (Pianka, 1994; Krebs, 1994). But until now these processes have not been interpreted and generally accepted for their complexity, diversity and long-term character. There are no integrated approaches to their practical research (Austin, 1977).

Probably the term “succession” was first used in the paper “Disappearance of pine wood of south breeds as an argument of production change tendency on the same soil existence in nature” published by American forester J. Edlam in 1806. In 1863 the other American scientist G.D. Toro used the notion “forest succession” for characterization of substitution of pine by deciduous breeds in New England. In XIX century the conception of forest succession was developed in works of T. Douglas and G. Sernander (the latter suggested the theory about dynamics of plant “formations”). Finally in 1899 American botanist G.K. Karaulz published the results of classical research of successions on sand dunes of Lake Michigan, which has not lose its urgency yet and has been examined in majority of ecology textbooks (Spurr, Barnes, 1984).

F. Klements philosophically (now we could say “systemically”) generalized the results of predecessors. His theory became a remarkable phenomenon in theoretical ecology development. It had global character, the author tried to construct on the base of quite simple and clear assumptions logically proportioned model, globally explaining the diversity of observed phenomena. From this point of view the idea of self-organization of biogeocenose is quite organic in his theory. Really at succession lightening each stage of succession prepares own changing itself; as a result of such step-by-step self-development process, more determined, biogeocenose returns to its optimal for the climatic zone form – “climax”.

Construction of similar global theories has become the principle direction of physical science development in the last three hundred years, has changed the period of empirical data accumulation and first shy generalizations in the time of Newton. But even at comparative simplicity of physical phenomena (as compared to biological) the theories value not always seemed evident for practice. High abstractness giving the theory depth and generality creates inevitably certain problems with its application to real, far from being abstract objects.

Studying extremely complicated, multiple-factor biological processes such problems appear particularly sharp. Refined theoretical constructions of F. Klements and his followers are checking up with difficulty in practice. For instance reveal of factors furthering the development of the following stage, or, on the opposite side, their absence conclusion is a very complicated task methodologically. Besides, any biological theory, in contrast to physical, wittingly does not describe the whole diversity of possible phenomena. Intention to describe maximum large quantity of real situations made Klements considerably complicate his theory, add there large quantity of complementary terms, why the theory had lost its orderliness and seemingly increase its practical value insignificantly.

Works of V.N. Sukachev and L.G. Remensky played a remarkable role in succession studying in domestic biogeocenology. A separate chapter (written by V.N. Sukachev)

formed a part of the major work on forest biogeocenology, monograph (The basis of forest..., 1964). The chapter deals with dynamical processes in BGC and contains a number of important theoretical generalizations. V.N. Sukachev regarded successions as many-sided notion, covering a wide range of dynamical processes, progressing in biogeocenoses. Following this approach, it could be considered, that fundamental forms of global dynamics of BGC, starting with seasonal fluctuations and finishing with phylocoenogenesis, have in their character many common features and could be united under the general term of successions. Nowadays such approach is supported by the majority of world ecologists (different points of view on this question could be found for instance in (Ehrlich, Roughgarden, 1987)).

Succession is a display of two the most important properties of biogeocenoses – to homeostasis and to self-development (though sometimes it is said about “conditionality” of ecosystems’ self-regulation (Danilov, 1978), but it is difficult to agree with such opinion). Self-development processes (evolutional successions, phitocenogenesis) are caused by inner reasons – micro- and macroevolutional processes, progressing in the components of biogeocenose populations – and become the display of general tendency of matter to self-development.

Homeostatic and adaptation processes are activated by violation in the structure of BGC occurrence or by environmental condition change. Violation degree of equilibrium in BGC is defined by succession complexity and duration. Succession ability is a display of homeostatic and adaptation properties of biosphere, which strives for its viability preservation mutating environmental conditions. Homeostasis and successions relationship is evident; and examination of homeostasis on the ecosystem level without mentioning of successions (as it sometimes occurs (Golubets, 1982)) is presented incompletely. As I.G. Emelyanov pointed, environmental mutation “cause adequate reorganization in structure of species populations, communities, biotas” (Emelyanov, 1992). Successions are exactly these reorganizations on the level of biogeocenoses.

Successions are defined by non-linear character and come to step-by-step change of several succession stages – several dominating vegetational associations. In the paper (Chernyshenko, 1997) for such associations the term “cenoma” was suggested, meanwhile the view on the succession stage in the capacity of biogenic elements cycle will be developed. But in many cases more simple approach could be used, considering that for succession stage description it is sufficient to examine the vegetational association dynamics (and even – the dynamics of edificators’ populations of these associations).

We should note the important relations of successions and spatial heterogeneity of biogeocenoses. The both phenomena could be connected with external against the biota factors. Vegetational associations (which could be naturally named “parcels” here) reflect heterogeneity of phytocenosis in the area, and successions reflect the same but through the time. G. Valter, for instance, wrote about similarity of temporal and spatial aspects of biogeocenoses mutability. He suggested to fix for spatial analogs of successional stages a well-known name “ecological range” (Valter, 1982).

Vegetational associations (ecological ranges) change each other in the area by the gradient of natural factors. Successional stages also change each other during the gradual mutability of one or several natural factors, but this mutability occurs not in the area but in the time. Endogenous successions deals with environment-forming properties of successional stages, which create the gradient of factors in the time.

Steppe dendrology gives illustrative examples of spatial changes, reflecting temporal changes. The boundary between steppe and forest areas are often characterized by intermediate conditions zone existence, where the ecological ranges could be observed (for example “squawbush forests – blackthorn – elm-black-maple oak-forests – elm-ash oak forests – lime-ash oak forests – lime oak forests” (Belgard, 1950)). In the conditions of restless age-old successions ecological ranges shift (to steppe or forest areas), so in every spot the successional changes of applicable vegetational associations occur.

#### **Succession classification multistage processes**

In the classification of V.N. Sukachev (The basis of forest..., 1964) the dynamics of biogeocenoses is divided into two large forms: cyclic (periodical) processes and

successions. The dynamics of BGC relating with diurnal and annual rhythms (generally too significant) does not really deal with its development direction, global trend, which is the basic observable phenomenon in succession theory. A.L.Belgard calls the first form of dynamics “dynamics of phytocenosis” and the second – “dynamics of vegetational cover” (Belgard, 1950).

But to connect periodicity and reversibility directly (as well as aperiodicity and irreversibility), as it was done in mentioned definition of B.M.Mirkin and G.C.Rozenberg, to our point of view, is not quite reasonable. As V.N.Sukachev mentioned (The basis of forest..., 1964), successions, induced by external action on BGC, could be reversible, when periodical external actions could not lead to reversibility in BGC dynamics. There are forms of dynamics, when demutation (by G.N.Vygotsky, 1950) do not occur, i.e. when restoration of external ecological parameters does not lead to BGC restoration (Rabotnov, 1983). In system theory such phenomena, on the ground of physical analogies, are called hysteresis.

Phenomenon, which is similar to periodic dynamics by several features, is so-called fluctuations of vegetation (Rabotnov, 1974). Fundamental joint feature of these two types of dynamics is conservation of the main features of vegetational community in their progress. In systems approach it is more preferable to use the interpretation of vegetational grouping, changing each other in the progress of fluctuations, as different display forms of integrated plant association. The majority of phytocenologists hold this definition (Nitsenko, 1971; Rabotnov, 1974; Mirkin, 1974) and do not consider that in the case of fluctuation of environmental parameters the reversible change of plant association occurs (Vasilevich, 1983). Fluctuation and periodical dynamics, as well as succession, is a homeostatic process, but in contrast to successions at relative transience and moderate character of environmental mutability of association adaptation is reached not by radical reconstruction of system (replacement of elements and change of relationship between them), as it occurs at succession, and by condition of elements change of existing system without structure change.

Classification of successional processes (including several stages - from the beginning to the "climax") is usually based on an analysis of two indicators - the causes of succession and its duration. Such approach has certainly justified itself, especially in solving practical problems of ecology. At the same time in the theoretical study of the succession there is a necessity to develop the classification of successions by the nature of internal processes in BGC in the succession progress, which are connected with two mentioned parameters, but not one-to-one correspondence. Consider possible causes and duration of successions from the position of system analysis, using the obtained results in this area (Aleksandrova, 1964; Vasilevich, 1983), and then discuss a possible interpretation of the systemic nature of different successional processes.

We begin by considering the possible causes of succession. Following the common practice of dividing the succession to the endogenous (autogenic) and exogenous (allogenic), it should be noted that at the end, almost all successions are caused by external factors. An exception could be considered phylocenogenetic processes (which are also stimulated by instability of the environment) related to the global process of self-development of matter and micro-evolutionary population processes.

By the interpretation of V.N.Sukachev we should refer phylocenogenesis to endogenous succession processes. In this case, we should refer to successions only "coherent" phases of phylogenesis (Zherikhin, 1987), which occur under conditions of relative stability of native environment. Abrupt and global climate changes (or other catastrophic events) can destroy biogeocenosis, after that a mass extinction of the old and the intensive formation of new species occurs (Zherikhin, 1987) - a process that can also be referred to adaptation, but which by its nature has few common features with classic succession.

Exogenous successions are divided into two categories (according to the character of causing them external influences):

- autonomous succession, if the influence was nonrecurrent and relatively short-term (the appearance of island on the river sediments, BGC destruction by fire, etc.);

- non-autonomous succession, in the case of a constant destabilizing external influences (global climate change, industrial pollution, moderate economic use of man, etc.)

Notion of "autonomous" and "non-autonomous" system are widely used in system theory (Kalman and others, 1971; Mesarovich, Takahara, 1978; Van-Gig, 1981). Autonomous call system, impact of the environment on which does not change through the time (or changes spontaneously, at random), and non-autonomous - a system the dynamics description of which requires taking into account the parameters of the environment depending on the time. Applying these terms to the dynamics of biogeocoenoses, we can unite under the term "autonomous succession" the types of succession, the course of which is determined by internal processes in BGC, with no significant effect of changes in external to BGC environment. These are primary successions, syngeneses, exogenous catastrophical (by V.D.Aleksandrova, 1964 - "postcatastrophical) successions. V.I.Vasilevich (1983) proposes to unite all the successions of this kind under the notion postcatastrophical, however, the term "autonomous successions" seems to us more appropriate, firstly because the beginning of such successions do not always associated with catastrophic events (for example, in the case of syngeneses), and secondly, following the common terminology of systems theory makes this term more transparent for specialists-systemologists.

For successions, caused by permanent and having a tendency to change in the external environment, V.I.Vasilevich uses the term "permanent" or "continuous" succession. Concepts of continuity and permanence in mathematical systems theory have somewhat different shades of meaning. We suggest, in consideration of unsettled character of terminology, to call such succession with term understood in the framework of systems analysis - "non-autonomous" succession.

To the reasons causing the non-autonomous succession we can refer solar variability, which have periodicity, but to which there are no special adaptive devices in biogeocenosis (the mentioned restriction of T.A.Rabotnov is connected with taking into account the possibility of such factors on a long period of "periodic" processes).

Thus, on the basis of their causes, we can divide the successions into three categories:

- phylogenogenesis (the only in the full sense of the endogenous process);
- autonomous successions - caused by a nonrecurrent and short-term external influence (by this feature - exogenous), but then progressing under the influence of internal biogeocenotic processes (in this sense - endogenous);
- non-autonomous successions - caused by constantly progressing changes in the external environment (in the full sense of an exogenous process).

For autonomous successions it is naturally to define three main types of violation, "launching" the succession (they can be often combined):

- the environmental parameters change (for example, change in water regime as a result of a reservoir creation);
- the change of the number biocoenosis species - a violation of equilibrium, a balance of species (for example, the destruction of undergrowth and most of the plants of the lower tiers as a result of ground fire);
- changes in species composition of biogeocenosis as a result of extinction or introduction of species (for example, delivery of rabbits in Australia).

Autonomous succession caused by the first type of violations, we suggest to call autonomous parametric, the second - autonomous balanced, the third - syngeneses (in accordance to the established terminology). To call the dynamic process, caused by any of the mentioned reason, a succession (in accordance with the definition of the latter), changes in BGC must be radical enough. The violation must be in such degree that the return of biogeocenosis in the initial state could not be possible within the existing structure, and requires step-by-step modification. Maintaining and restoring the balance processes without structural rearrangements progress constantly in BGC and can also be referred to the forms of dynamics. They can be referred to the mentioned fluctuation dynamics (if we understand the fluctuations in extended sense).

Now we shall consider the issues related to the duration of succession. The division of the succession into short-term and age-old reflects the nature of the processes within an

ecosystem in a less degree, as related primarily to the characteristics of the external factors causing succession or ecological features of the dominant species in BGC.

Apparently, autonomous successions are always relatively short, but even they, if among the edificators of successional stages long-lived tree species are presented, could last for centuries. At the literal meaning of the term we could refer such succession to "age-old", but now the scale of age-old succession is considered to be of thousands or millions of years.

Duration of non-autonomous succession depends primarily on the duration of the external factors causing them. Non-autonomous successions reflect BGC tendency to adapt to changing environmental conditions, so the usual succession of this kind may be called adaptive. Among the non-autonomous successions are usually distinguished hologenesis – an age-old succession, which is caused by global climate change, “development of river valleys, epirogenetic fluctuations of land and the evolution of soil types” (Belgard, 1950). To our point of view, age-old successions of this kind do not differ fundamentally from other non-autonomous successions, as based on the same mechanisms of homeostasis of biogeocenosis. The exception is the micro-and macroevolutional BGC processes, which in the case of hologenesis may complement a more adaptive processes. In this case, we believe that parallel to hologenesis the other process progresses, which is also commonly referred to age-old successions - phylocoenogenesis.

Microevolution, which is manifested in a change of some population characteristics of the species-edificators, can occur at fairly short intervals of time and play an important role during the succession (Becking, 1968). Microevolutional component in phylocoenogenesis is relatively short, while a more global macroevolutional process on its own time scale even greater than that which is usually attributed to age-old succession.

As stated in the book (Gorelov, 1998), "one of the major achievements of ecology was the discovery that not only the organisms and species develop, but also ecosystems do." Between the evolution of individual species and biogeocenosis generally there are dialectical relationships. On the one hand, natural selection carries out on cenotic level, and in this sense biogeocoenosis "controls" evolution. On the other hand - the emergence of BGC of new life forms (species, subspecies, races - have arisen on-site or migrated from the outside) can cause rearrangements in BGC ("flashes", by V.D.Fedorov (1970)), which are also agreed to classify as successions. If we exclude the introduction or accidental entry of new species by man (unfortunately, getting a colossal scale in the last century) - these phenomena we refer to the reasons of syngensis - processes of self-development of BGC progress very slow, even compared to other types of successions that are traditionally related to the age-old ones. For such successions we suggest the term “evolutionary successions”, which underlines their difference from short-term and age-old ones as in the time and the inner nature (the system not only keeps or restores its structure, but changes, “improves” it).

The proposed classification of dynamic processes in forest biogeocenoses is presented in the table.

The proposed classification is convenient for system analysis and succession modeling. Selection of phylocoenogenesis in a separate category is justified, since the processes of self-organization (Levitin, 1975), consisting of the fact that the system can themselves change their structure, represent a special category of systems theory yet not well studied models. As a simple example of this approach in the article (Chernyshenko, 1996) a model of successional shifts based on the hypercycle model of M. Eigen is considered, in which biogeocoenosis itself "chooses" the level of its complexity.

Non-autonomous successions compose a special group in the analysis of dynamic processes. Non-autonomous (or nonstationary) models with time-dependent coefficients correspond to these successions. If the time variable tends to infinity, these coefficients do not tend to some constant values, the ecosystem is also not likely to move in a certain state, and its dynamics will be determined, ultimately, the dynamics of the coefficients. To study such systems there are not developed universal methods, although some of their properties (for instance, sensitivity, and inertia with respect to a change in the coefficients) can be investigated.

#### **Classification of dynamical processes in forest BGC**

Type of dynamics	External influences	Type of succession		Duration
Endogenous successions	—	phylocoenogenesis	evolutional succession	"age-old"
			microevolution	"age-old", medium
Exogenous successions	constant, with certain tendency	non-autonomous successions	hologenesis	"age-old"
			adaptation	small, medium
	nonrecurrent	autonomous (postcatastrophic) successions	parametric	small, medium
			balanced	
		syngeneses		
Periodic dynamics	constant periodic with small period			small
Fluctuation	constant with accidental dispersion			small

In the case of autonomous successions for the mathematical description of the process the nature of the initial disturbance is significant. In the case of changes in the number of species (balance autonomous succession) the disturbance of the system state (with no change in itself) occurs. In this case, the stability of the system "in the initial conditions" is interesting, the qualitative behavior of the system can be studied on the basis of the theory of Lyapunov (Liapunov, 1950; Bautin, Leontovich, 1990).

At the system parameters change (parametric autonomous succession) the system in terms of systems analysis, changes its properties. The "structural stability" of the system should be researched, and as a well-developed mathematical apparatus the bifurcation theory may be used (Yoss, Joseph, 1983).

The case of changing the structure of the system (syngeneses) is the most difficult methodologically because it is difficult to describe quantitatively the relationship between a system, in which there are new elements or old disappeared, and the initial system. The study of the structural stability of this kind is naturally carried, bringing this case to the previous. For example, when modeling the appearance of a new type of model introduced a new element with some weighting factors that define the extent of its connection with other species, which then can be changed from zero to determine the critical values associated with qualitative changes in the dynamics of the system.

Volterra systems (Volterra, 1976; Maynard Smith, 1974; Svirezhev, 1983) provide a convenient way to reduce the latter case is not to the more complicated the second, and the first case. These models have the property that the population with a zero number can not be developed, so simply "zeroing" population size, we exclude it from BGC. Similarly, when the introduction we "includes" the species at BGC just giving it the number of non-zero value. Below at the modeling of successions, we shall use this technique.

When balanced autonomous successions change population size is not going beyond the boundary of the attraction of the current equilibrium point corresponds to the fluctuation dynamics. We can talk about succession, if the violations are so large that they lead to a change in the equilibrium position (structure of BGC changes and the succession process begins).

When parametric autonomous successions we are dealing with fluctuations, until the change of parameters does not lead to a bifurcation (a catastrophe). Bifurcation, meaning a radical change in the dynamic properties of the system, means the beginning of a new successional stage.

If we consider the model of not only the biotic part of BGC, but also include in it biostagnant parts and the part of stagnant components, changes in the environment, which is an essential part of succession, is expressed by the change of the system, rather than its external parameters. Those effects, that were associated with bifurcations of the system, become the result of "internal bifurcation" (Chernyshenko, 1995a). So restructuring of the system is the result of its internal development, rather than external influences. Not all the

abiotic factors may be included in such a way to the model of BGC (for example, in the constructions of F.Clements BGC detects even a relief, but beyond its borders of BGC climatic conditions still remain), but some of them - such as the parameters of soil, litter, the nature of wetting etc. should preferably not be seen as external, but as internal parameters of BGC.

Finally, we should note the importance of the territorial aspects of succession. Succession in the ecosystem do not and can not progress regardless of ecosystems, surrounding it. Except start-up island in the ocean, the relationship of primary succession in which other ecosystems are mediated (but which exists, and without which these successions are impossible! "); the actual succession passes in the territory, surrounded by other biogeocenoses, and in most cases - in which can be considered as part of some of the existing ecosystem. A classic example of a primary succession - the formation of a new biogeocoenose on the river flats - can be interpreted (perhaps more correctly) and as an extension of the territory of the existing floodplain BGC. Destruction of forest BGC in a fire can be considered not starting the process of syngeneses on the affected area, which disappeared most of the species, but the beginning of the balanced autonomous succession in BGC, in which the density distribution of many species turned into zero. Restoring of an ecosystem will be progress not only by successional processes in the territory, violated by fire, but also by the diffusion occupation of it from the surrounding undisturbed parts of BGC.

#### **Mechanisms of succession. The role of competition of populations of producers-edificators and their interactions with the abiotic environment**

As mentioned at the beginning of this article, the change of the dominant association in succession process occurs under the influence of two driving mechanisms: interspecific competition between plants-edificators and their dialectical interaction with the stagnant environment.

Consider in the beginning the first process - the competition of the associations for the major environmental resources, which has a number of specific features (such as forest successions its course is largely determined by the properties of the soil block – as L.O.Karpachevsky writes (1995) "Soil is the basis of competition").

The role of competition in the successions was highlighted by many researchers. So, in a monograph (Fundamentals of forest ..., 1964), which gives a classic description of the forest biogeocenology, appears the following statement. "In development of the forest biogeocenotic cover the main role played by successions of phytocenoses; mechanism of any phytocenoses change, and the change biogeocenoses in general is the displacement of some other species in the process of inter-species fighting for survival and competition. ... In the process of ecosystem change of one another ... the main leadership role played by inter-species relationships." Around this the same idea is expressed in the monograph devoted to the cybernetic analysis of biological systems. "Succession ... is ... the process of logical sequential change of competing with each other ... communities." (Biological Cybernetics, 1977).

Competition between species-producers (edificators of plant associations, relevant successional stages) is the main (or, if you ignore the minor details - the only) mechanism for actuating the succession of inhibition and tolerance. However, in the case of "relief" when the previous cenoma in a sense, "promotes" the development of the next, there is always competition between edificators for resources, i.e. observed the effect of "inhibition". As noted by the TA Rabotnov, "should not be forgotten ... that the change occurs phytocenoses while continuing influence of plants on each other, primarily because of competitive interactions (Rabotnov, 1983).

The fact that competition plays an important role in the functioning of biological communities, is a universally recognized fact. The interest in the competition, especially increased after the triumph of the ideas of Darwin, in which "the struggle for existence" is considered as the main driving force behind the evolutionary process. Numerous studies have demonstrated the fruitfulness of this approach, particularly when considering the dynamic processes in Biogeocenoses (Budyko, 1977; Basics forest ..., 1964; Gall, 1976;

Gilyarov, 1990; Holubec, 1982; Dylis, 1973; Krivolutsky, Pokarzhevsky, 1990 ; Nomokanov, 1989; Rabotnov, 1983; spurrite, Barnes, 1984).

The most important stage in the development of competition began in the early twentieth century work of Lotka (Lotka, 1925) and Volterra (Volterra, 1931; Volterra, 1976), containing the fundamental mathematical description of the competition. Using these models, G. Gause based on extensive experimental material has formulated a well-known principle of competitive exclusion - "the principle of Gause» (Gause, 1934). The latter is sometimes considered very broadly, assuming that it operates at different levels of ecological systems, up to the scale of the noosphere (Gorelov, 1998) (although sometimes its universality is questioned, even for phytocenoses (Bigon et al, 1989)).

The interest to the problem is not reduced nowadays. On the one hand, reached ever deeper understanding of the internal mechanisms of competition, but on the other hand, all the more deeply we study the role of competition in real ecosystems, Biogeocenoses. In particular, many studies have been devoted to constructing models of competition for forest BGTS (Rosenberg, 1984, Berezovsky and others, 1991). Many works are devoted to studying the role of competition in the formation of plant associations in successional processes (Biological Mechanisms of ..., 1964). A significant development was the doctrine of life forms and environmental policies as a result of competitive interactions of different types (Forest Principles ..., 1964; MacArthur, Wilson, 1967; Pianka, 1994).

Regarding the second mechanism - the interaction of populations of producers with inert environment and their mutual influence - note that it plays an important role when these two components BGTS not balanced (or, in other words, when there existed a dialectical contradiction.) This contradiction is resolved by changes in both components, which changes the biogeocoenosis, leading to the formation of a new successional stage. Previous stage is not "programmed" to self-depression or training environment for the next stage. A process of harmonization of biotic and abiotic components BGTS, resulting in biocoenosis changes its structure - replacing one plant association comes another. It is in this sense (in his non-compliance with the inert medium), one prepares the next stage of succession, "facilitates" its development.

Famous examples of chemical "self-depression" of explerents at early successional stages (Whittaker, 1981) can hardly be regarded as genetically programmed "facilitation" of succession, as a manifestation of overorganism regulating its flow. Correct to speak about genetically fixed "doom" of these species in competition with the energetically more powerful species. Their strategy is to generate 1-2 produce sufficient for the survival of a population of seeds. Energy as the cost of establishing and supporting the physiological mechanisms (or a service population of the consorts, decomposers), aimed at the possibility of long-term coexistence with the products of its own metabolism, are presented in this meaningless. Another possible explanation "samougneteniya" contained in the paper (Rabotnov, 1983).

Successions of facilitation play a major role in the early stages of primary succession, where the discrepancy of biota and environment is particularly high. To some extent the effects of "harmonizing with the environmental conditions" must be manifested at all stages of succession, but in the latter stages of their influence in comparison with the competition is much weaker.

To account for the effect of facilitation it should be entered into the model the dynamics of abiotic factors, which significantly complicates the construction of a methodological part. Sometimes this can be avoided by introducing a special nonlinear relationships between the populations of plant-edificators that allow implicitly consider the impact of the effects of facilitation on interpopulation interactions.

#### **BGC as polygenetic system. Biogeocenosis compatibility of associations**

Conventional progressive succession are a gradual change in the dominant populations edificators - from simpler to more specialized species with more power. In this case, the fate of the previous stage may be different. There are two main possibilities.

The first of them occurs when the previous dominant completely disappears as a structural whole, after the environmental conditions become favorable for the development

of the next stage of succession. Most of its constituent species fall out of the forming of ecosystem (as a result of changing environmental conditions of habitat and / or interspecific competition with species belonging to the new stage) and turn into a "virtual" form. They are stored in a seed bank as a result of the influx of seeds and / or individuals from neighboring biogeocoenoses, in the form of relict groups tied to specific areas of relief, etc. If conditions change, they tend to be fast enough to return to biogeocoenosis, and create a certain "energy pressure" on the dominant association, forcing it to expend energy on a constant struggle with the return. At the same time they play a minor role in the transformation of matter and energy prevailing of BGC. An example of this kind of stage can serve as a grouping ruderals arising on post-fire known as the temporal association, which does not leave a noticeable trace in the emerging after it biogeocoenoses.

In the second case, the earlier association, albeit in a modified standing, becomes a part of a new stage of BGC, and species, its components, occupy a position in consort of the new dominant. In this case we can speak of "*biogeocenosis compatibility*" of the two associations. Such an outcome is very real, especially in the later stages of succession. Types of previous stages may be presented in BGC long enough, and some of them (especially soil decomposers) can even play an important role in the functioning of new communities. Real BGC is always a combination of several associations. This is especially true for amphiceneses (Belgard, 1950) - biogeocoenoses in border environmental conditions.

The number of associations, "overlapping" one by one in the progress of succession (or, equivalently, the amount passed successional stages) we shall call the dimension of BGC. Of course, this conditional value largely depends on the subjective understanding of what should be counted as successional stage, and what - intermediate amphicenose (Belgard, 1950). However, with the same approach to multiple BGC, the dimension may be used to estimate the relative complexity of these ecosystems.

More favorable conditions (in terms of the number of available for the photosynthetic assimilation of energy) create preconditions for more successional stages changing each other, and thus for higher dimension (and complexity) level of climax community. In severe conditions the flow of available energy does not allow BGC pass more than a few initial steps of succession.

Overlapping of successional stages is one of the factors promoting the biodiversity enrichment in biogeocoenoses. The relationship between biodiversity and informational and entropic indices is universally recognized. We emphasize that a certain degree of conditionality of biodiversity level by evolutionary effects (Emelyanov, 1992) is associated with progressive evolution of the energy-producing capabilities of producers-edificators. The latter is a result of competition and pressure of the populations of heterotrophs (Chernyshenko, 1997a). The expanding power base creates the conditions for "proliferation" of ecological niches at all levels of the trophic net.

## REFERENCES

- Александрова В. Д.** Изучение смен растительного покрова / В. Д. Александрова // Полевая геоботаника. – Л. : Наука, 1964. – Т. 3. – С. 300-447.
- Арманд А. Д.** Информационные модели природных комплексов / А. Д. Арманд. – М. : Наука, 1975. – 126 с.
- Арманд А. Д.** Самоорганизация земной поверхности (географическая синергетика) / А. Д. Арманд // Математическое моделирование сложных биологических систем. – М. : Наука, 1988. – С. 33-49.
- Багоцкий С. В.** Различные механизмы упрощения водных экосистем при росте поступления органических загрязнений и биогенных элементов / С. В. Багоцкий, В. А. Вавилин // Математическое моделирование сложных биологических систем. – М. : Наука, 1988. – С. 128-133.
- Баутин Н. Н.** Методы и приемы качественного исследования динамических систем на плоскости / Н. Н. Баутин, Е. А. Леонтович. – М. : Наука, 1990. – 488 с.
- Бельгард А. Л.** Лесная растительность юго-востока УССР / А. Л. Бельгард. – К. : Из-во КГУ, 1950. – 264 с.
- Березовская Ф. С.** Моделирование динамики древостоев: эколого-физиологический подход / Ф. С. Березовская, Г. П. Карев, А. З. Швиденко. – М. : Из-во ВНИИЦлесресурс, 1991. – 84 с.

- Бигон М.** Экология. Особи, популяции и сообщества / М. Бигон, Дж. Харпер, К. Таунсенд. – М. : Мир, 1989. – Т. 1. – 668 с.
- Биологическая кибернетика** / Под. ред. А. Б. Когана. – М. : Высшая школа, 1977. – 408 с.
- Будыко М. И.** Глобальная экология / М. И. Будыко. – М. : Мысль, 1977. – 415 с.
- Вальтер Г.** Общая геоботаника / Г. Вальтер. – М. : Мир, 1982. – 264 с.
- Ван-Гиг Дж.** Прикладная общая теория систем / Дж. Ван-Гиг. – М. : Мир, 1981. – 350 с.
- Василевич В. И.** Очерки теоретической фитоценологии / В. И. Василевич. – Л. : Наука, 1983. – 248 с.
- Вольтерра В.** Математическая теория борьбы за существование / В. Вольтерра. – М. : Наука, 1976. – 264 с.
- Высоцкий Г. Н.** Учение о влиянии леса на изменение среды его произрастания и на окружающее пространство / Г. Н. Высоцкий. – М. : Изд-во АН СССР, 1950.
- Галл Я. М.** Борьба за существование как фактор эволюции / Я. М. Галл. – Л. : Наука, 1976. – 156 с.
- Гиляров А. М.** Популяционная экология / А. М. Гиляров. – М. : МГУ, 1990. – 184 с.
- Голубец М. А.** Актуальные вопросы экологии / М. А. Голубец. – К. : Наукова думка, 1982. – 158 с.
- Голубец М. А.** Загальна схема механізмів саморегуляції в живих системах біосфери / М. А. Голубец // Вісник АН УРСР. – 1978. – № 1. – С. 76-85.
- Горелов А. А.** Экология / А. А. Горелов. – М. : Центр, 1998. – 238 с.
- Горстко А. Б.** Введение в моделирование эколого-экономических систем / А. Б. Горстко, Г. А. Угольницкий. – Ростов : РГУ, 1990. – 110 с.
- Губанов В. А.** Введение в системный анализ / В. А. Губанов, В. В. Захаров, А. Н. Коваленко. – Л. : ЛГУ, 1988. – 268 с.
- Данилов Н. Н.** Равновесное состояние биогеоценозов / Н. Н. Данилов // Биогеоценология, антропогенные изменения растительного покрова и их прогнозирование. – К. : Наукова думка, 1978. – С. 13-14.
- Дылис Н. В.** Основы биогеоценологии / Н. В. Дылис. – М. : МГУ, 1973. – 152 с.
- Емельянов И. Г.** Роль разнообразия в функционировании биологических систем / И. Г. Емельянов. – К. : Ин-т зоологии АН Украины, 1992. – 64 с.
- Жерихин В. В.** Биоценологическая регуляция эволюции / В. В. Жерихин // Палеонтол. журн. – 1987. – № 1. – С. 3-12.
- Зонн С. В.** Географо-генетические аспекты почвообразования, эволюции и охраны почв / С. В. Зонн, А. П. Травлев. – К. : Наукова думка, 1989. – 216 с.
- Йосс Ж.** Элементарная теория устойчивости и бифуркаций / Ж. Йосс, Д. Джозеф. – М. : Мир, 1983. – 302 с.
- Казенс Д.** Введение в лесную экологию / Д. Казенс. – М. : Лесная пром-ть, 1982. – 142 с.
- Калман Р.** Очерки по математической теории систем / Ф. Калман, П. Фалб, М. Арбиб. – М. : Мир, 1971. – 400 с.
- Карпачевский Л. О.** Проблемы экологического почвоведения / Л. О. Карпачевский // Экологія та ноосферологія. – 1995. – Т. 1, № 1-2. – С. 48-55.
- Колесов Ю. С.** Пространственная и временная самоорганизация в одновидовом биоценозе / Ю. С. Колесов, В. В. Майоров // Динамика биологических популяций. – Горький: ГГУ, 1986. – С. 3-13.
- Криволицкий Д. А.** Введение в биогеоценологию / Д. А. Криволицкий, А. Д. Покаржевский. – М. : МГУ, 1990. – 104 с.
- Левитин К.** Все, наверное, проще / К. Левитин. – М. : Знание, 1975. – 176 с.
- Ляпунов А. А.** Кибернетический подход к теоретической биологии / А. А. Ляпунов // Биология и информация. – М. : Наука, 1984. – С. 38-45.
- Ляпунов А. М.** Общая задача об устойчивости движения / А. М. Ляпунов. – М. : Гостехиздат, 1950. – 412 с.
- Месарович М.** Общая теория систем: математические основы / М. Месарович, Я. Такаха. – М. : Мир, 1978. – 312 с.
- Механизмы** биологической конкуренции. – М. : Мир, 1964 – 317 с.
- Миркин Б. М.** Закономерности развития растительности речных пойм / Б. М. Миркин. – М. : Наука, 1974. – 174 с.
- Миркин Б. М.** Толковый словарь современной фитоценологии / Б. М. Миркин, Г. С. Розенберг. – М. : Наука, 1983. – 134 с.
- Моисеев Н. Н.** Экология человечества глазами математика / Н. Н. Моисеев. – М. : Молодая гвардия, 1988. – 256 с.
- Мэйнард Смит Дж.** Модели в экологии / Дж. Мэйнард Смит. – М. : Мир, 1974. – 184 с.
- Ниценко А. А.** Растительная ассоциация и растительное сообщество как первичные

- объекты геоботанического исследования / А. А. Ниценко. – Л. : Наука, 1971. – 184 с.
- Номоконов Л. И.** Общая биогеоценология / Л. И. Номоконов. – Ростов-на-Дону : РГУ, 1989. – 455 с.
- Одум Ю.** Основы экологии / Ю. Одум. – М. : Мир, 1975. – 740 с.
- Основы** лесной биогеоценологии // Под ред. В. Н. Сукачева и Н. В. Дылиса. – М. : Наука, 1964. – 576 с.
- Пасеков В. Н.** Экстремальные свойства и эволюционная оптимальность в модели биологического сообщества, учитывающей энергетику жизнедеятельности / В. Н. Пасеков, Л. Л. Овсянников // Математическое моделирование сложных биологических систем. – М. : Наука, 1988. – С. 133-140.
- Перегудов Ф. И.** Введение в системный анализ / Ф. И. Перегудов, Ф. П. Тарасенко. – М. : Высшая школа, 1989. – 368 с.
- Плотников В. В.** Эволюция структуры растительного сообщества / В. В. Плотников. – М. : Наука, 1979. – 276 с.
- Работнов Т. А.** Луговоеведение / Т. А. Работнов. – М. : МГУ, 1974. – 384 с.
- Работнов Т. А.** Фитоценология / Т. А. Работнов. – М. : МГУ, 1983. – 294 с.
- Раменский Л. Г.** Введение в комплексное почвенно-геоботаническое исследование земель / Л. Г. Раменский. – М., 1938.
- Реймерс Н. Ф.** Азбука природы. Микроэнциклопедия биосферы / Н. Ф. Реймерс. – М. : Знание, 1980. – 208 с.
- Розенберг Г. С.** Модели в фитоценологии / Г. С. Розенберг. – М. : Наука, 1984. – 266 с.
- Свирижев Ю. М.** Математические модели в экологии / Ю. М. Свирижев // Математические методы в биологии. – К. : Наукова думка, 1983. – С. 97-106.
- Свирижев Ю. М.** Нелинейные волны, диссипативные структуры и катастрофы в экологии / Ю. М. Свирижев. – М. : Наука, 1987. – 368 с.
- Свирижев Ю. М.** Устойчивость биологических сообществ / Ю. М. Свирижев, Д. О. Логофет. – М. : Наука, 1978. – 352 с.
- Спурр С. Г.** Лесная экология / С. Г. Спурр, Б. В. Барнес. – М. : Лесная пром-ть, 1984. – 480 с.
- Травлеев А. П.** Лес и почва в условиях степи / А. П. Травлеев, Л. П. Травлеев. – Д. : ДГУ, 1988. – 85 с.
- Тринчер К. С.** Биология и информация / К. С. Тринчер. – М. : Наука, 1964. – 100 с.
- Уиттекер Р.** Сообщества и экосистемы / Р. Уиттекер. – М. : Прогресс, 1981. – 328 с.
- Федоров В. Д.** Особенности организации биологических систем и гипотеза "вспышки" вида в сообществе / В. Д. Федоров // Вестн. МГУ. Сер. биол., почвовед. – 1970. – № 2. – С. 71-81.
- Ханин М. А.** Экстремальные принципы в биологии и физиологии / М. А. Ханин, Н. Л. Дорфман, Н. Б. Бухаров и др. – М. : Наука, 1978. – 256 с.
- Чернышенко С. В.** Качественное исследование двумерной модификации гиперцикла Эйгена и внутренние катастрофы / С. В. Чернышенко // Вопросы прикладной математики и математического моделирования. – Д. : ДГУ, 1995а. – С. 129-134.
- Чернышенко С. В.** Термин "информация" и математическое описание информационных процессов в экологических системах / С. В. Чернышенко // Экология та ноосферология. – 1995b. – Т. 1, № 1-2. – С. 137-150.
- Чернышенко С. В.** Системный подход к задаче моделирования сукцессионных процессов в фитоценозах / С. В. Чернышенко // Вопросы степного лесоразведения и лесной рекультивации земель. – Д. : ДГУ, 1996. – С. 71-77.
- Чернышенко С. В.** О математическом моделировании динамической структуры биогеоценозов / С. В. Чернышенко // Экология та ноосферология. – 1997а. – Т. 3, № 1-2. – С. 65-86.
- Чернышенко С. В.** Системный анализ динамической структуры биогеоценоза / С. В. Чернышенко // Вопросы степного лесоразведения и лесной рекультивации земель. – Д. : ДГУ, 1997b. – С. 18-31.
- Шредингер Э.** Что такое жизнь? / Э. Шредингер. – М. : Атомиздат, 1972. – 88 с.
- Эйген М., Гиперцикл** / М. Эйген, П. Шустер. – М. : Мир, 1982. – 272 с.
- Эрроусмит Д.** Обыкновенные дифференциальные уравнения. Качественная теория с приложениями / Д. Эрроусмит, К. Плейс. – М. : Мир, 1986. – 244 с.
- Austin M.P.** Use of ordination and other multivariate descriptive methods to study succession // Vegetatio. – 1977. – V. 35, N 3. – P. 165-175.
- Becking R.W.** Vegetational response to change in environment and change in species tolerance with time // Vegetatio. – 1968. – V. 16, N 1-4. – P. 135-158.
- Brooks D.R., Wiley E.O.** Evolution as entropy: toward a unified theory of biology. – Chicago & London: The University of Chicago Press, 1988. – 416 p.
- Chernyshenko S.V.** The open Eigen Hypercycle and selforganization of ecological systems //

- Sustainable Development: environmental pollution and ecological safety. – Dnepropetrovsk: Dnepropetrovsk University Press, 1995. – P. 42-43.
- Clements F.E.** Plant succession: Analysis of the development of vegetation. – Washington: Carnegie Institute of Washington Publications, 1916.
- Drury W.H., Nisbet I.C.T.** Succession // J. Arnold Arboretum. – 1973. – V. 54, N 3. – P. 331-368.
- Dunbar M.J.** The ecosystem as unit of natural selection // Growth by intussusception. – N.Y.: Trans. Conn. Acad. Arts Sci., 1972. – T. 44. – P. 113-130.
- Ehrlich P., Roughgarden J.** The science of ecology. – N.Y.: McMillan, 1987.
- Fox J.F.** Alternation and coexistence of tree species // Amer. Natur. – 1977. – V. 111, N 977. – P. 69-89.
- Gause G.F.** The struggle for existence. – Baltimore: Williams and Wilkins, 1934.
- Hart A., Begon M.** The status of general reproductive-strategy theories, illustrated in winkles // Oecologie. – 1982. – V. 52. – P. 37-52.
- Kershaw K.A.** Quantitative and dynamics plant ecology. – L.: Assley, 1973. – 308 p.
- Krebs C.J.** Ecology. – N.Y. & Harlow: Addison Wesley, 1994. – 802 p.
- Lawton J.H.** Are the assembly rules for successional communities? // Colonization, succession and stability. – Oxford: Blackwell, 1987. – P. 225-244.
- Lotka A.G.** Elements of Physical Biology. – Baltimore: Williams and Wilkins, 1925.
- MacArthur R.H., Wilson E.O.** The theory of island biogeography. – Princeton & New Jersey: Princeton University Press, 1967.
- Margalef R.** On certain unifying principles in ecology // Amer. Natur. – 1963. – V. 97, N 897. – P. 357-374.
- Margalef R.** Perspectives of ecological theory. – Chicago: Chicago University Press, 1968. – 102 p.
- Noble I.R., Slatyer R.O.** Concepts and models of succession in vascular plant communities subject to recurrent fire // Fire and the Australian biota. – Canberra: Australian Academy of Science, 1981.
- Odum E.P.** Fundamentals of ecology. – Philadelphia: Saunders, 1971.
- Odum H.T.** Environment, power, and society. – N.Y. Wiley, 1971.
- Pianka E.R.** Evolutionary ecology. – N.Y.: Harper Collins, 1994. – 486 p.
- Volterra V.** Lecons sur la theorie mathematique de la lutte pour la vie. – Paris: Gauthier-Villars, 1931.
- Woods K.D.** Reciprocal replacement and maintenance of codominance in a beech-maple forest // Oikos – 1979 – V. 33, N 1 – P. 31-39.

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