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**CURRENT STATE OF  
BROAD-LEAVED FORESTS  
IN RUSSIA, BELORUSSIA, UKRAINE:  
historical development, biodiversity, structure and  
dynamic**

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The article contains the population-ontogenetic analysis for many species from the tree, shrub and herb synusia in the broad leaved forests. It demonstrates the specificity of a population behavior of species that depends on their life strategy. The authors suggest the original method for an estimation of dominant species' population sustainability. The theoretical model of the species compositions, stand structures, and biodiversity of the native forests is described. We evaluate a successional status of communities as a result of comparing their current state with the corresponding geographical variant of the theoretical model. Furthermore, the long-term forest dynamics are modeled by the means of the original computer program.

## INTRODUCTION

### General characteristics of broad-leaved forests and problems of nature preserving

Zonal broad-leaved forests of the European part of the former USSR cover the territory from the East Carpathian Mountains to the Western Ural Mountains. These forests are as a rule the multispecies' communities with polydominant tree layer, the key species of the latter being a species with wide ecological amplitude, i.e., *Quercus robur* L.. This tree grows on black fertile soil (chernozem) as well as on gray forest soil, acid forest soil (podzol), and brown forest soil with rather diverse moisture level. According to the areas of satellite species, the following geographical variants of broad-leaved forests are distinguished: 1) hornbeam-oak and beech-oak forests with durnast (*Q. petraea* Liebl., *Q. robur* L., *Fagus sylvatica* L., *Carpinus betulus* L., *Acer pseudoplatanus* L., *A. platanoides* L., *A. campestre* L., *Ulmus scabra* Mill., *Tilia cordata* Mill., *Cerasus avium* (L.) Moench); 2) beech-oak forests comprising *Quercus robur* L., *Fagus sylvatica*, *Fraxinus excelsior* L., *Tilia cordata* Mill., *Acer platanoides* L., *A. campestre* L., *Carpinus betulus* L., *Cerasus avium* (L.) Moench, *Tilia argentea* Desf., *T. platyphyllos* Scop., *Ulmus* sp.; 3) hornbeam-oak forests with *Fraxinus excelsior* L., *Acer platanoides* L., *A. campestre* L., *Tilia cordata* Mill., *Ulmus scabra* Mill.; 4) ash-lime-oak forests including the above-mentioned species except *Acer pseudoplatanus* L. and *Carpinus betulus* L.; 5) oak forests with lime, Norway maple, and elm.

The geographical distribution of oak forests of the first type has its eastern borderline in Cis-Dniestria (Pridnestrov'e). The forests of the

second type are distributed till Volhynia-Podolia Hills. The forests of the third type are situated till the western part of the Ukrainian left-bank forest-steppe. Forests of the fourth type are delimited by the Volga. Finally, the forests of the fifth type possess the western side of the Ural as their borderline (Vegetation of the European part of the USSR, 1980). The ecological and floristic study of broad leaved forests of the former USSR was carefully performed by Yu.D.Kleopov in the 40-s of the XX century. The posthumous monograph of the author (Kleopov, 1990) is dedicated to this item. Using the Braun-Blanquet method, he worked out the following classification of broad-leaved forests of the Russian plain.

## 1. Order *Fagetalia*.

### A. Link *Fagion*.

- 1) Beech forests of Podolia (*Fagetum podolicum*) including 111 species.

### B. Link *Nemorion*.

- 2) Forest-steppe hornbeam forests of the Ukraine (*Carpineto-Nemoretum ucrainicum s.l.*) situated in forest-steppe between the Dniester and Vorskla rivers ( 236 species).
- 3) Hornbeam forests of Polesye (*Carpineto-Nemoretum polesicum*) distributed in Ukrainian right-bank Polesye (150 species).
- 4) Broad-leaved forests of the Don river basin (*Mixto-Nemoretum tanaiticum s.l.*) situated in forest-steppe of the Don basin with the Severskii Donets river in the part from the Vorskla to Khoper rivers (160 species).
- 5) Northern lime forests of the Oka river basin (*Tilieto-Nemoretum okense*) situated in the "Tula zaseki" reservation (127 species).
- 6) Lime forests of the Middle Volga basin (*Tilieto-Nemoretum volgense*) situated in forest-steppe right-bank of the Volga from Zhiguli to Saratov ( 103 species).
- 7) Broad-leaved forests in the western side of the Ural (*Mixto-Nemoretum praeuralense*) situated in the southern part of the Western Ural (100 species).
- 8) Lime forests of the Ural (*Tilietum uralense*) distributed in the western foothills of the Southern Ural (82 species);

## II. Order Quercetalia pubescentis-roboris-sessiliflorae

### C. Link *Quercion pubescentis-roboris-sessiliflorae*.

9) Durmast oak forests of Moldova (*Quercetum Petraeae caricosum moldavicum*) distributed in the southern part of the Bug-Dniester watershed (123 species).

10) Oak forests with spiny shrubs (*Spinoso-Fruticeto-Quercetum herbosum thyraico-borysthenticum*) distributed in southern limits of the Ukrainian right-bank forest-steppe (81 species).

11) Steppe gully shrubby oak forests of Moldova (*Fruticeto-Quercetum vallense moldavicum*) distributed on the left bank of the Dniester river in Moldova (88 species).

12) Steppe gully shrubby oak forests of Donets coal basin (*Fruticeto-Quercetum vallense donetzicum*) distributed in Donets basin (172 species).

13) Sedge shrubby oak forests of the Don river basin (*Fruticeto-Quercetum caricosum tanaiticum*) distributed in forest-steppe of the Don basin (99 species).

14) Herb shrubby oak forests of the Middle Volga basin (*Fruticeto-Quercetum herbosum volgense*) distributed in forest-steppe of the Volga right-bank from Zhiguli to Saratov (104 species).

15) Herb oak forests in the Western Ural (*Quercetum herbosum praeuralense*) distributed in the southern part of the Western Ural (106 species).

Literature analysis and long-term investigations of the authors show that both the modern boundaries and species composition and the structure of broad-leaved forests are to a slight degree caused by the natural peculiarities of the zone. The boundaries are to a higher degree the result of long anthropogenic disturbance of the territory under consideration. Throughout several millennia of active human exploitation of the East European territory covered by broad-leaved forests, their area has sharply decreased, while their structure has undergone irreversible changes. As the sequence of that, the continued forests are now replaced by their separate fragments surrounded by open spaces. Most of such "island" forests cannot upkeep the necessary conditions for the surviving of the set of species so the latter need

active outer support (East European broad-leaved forests, 1994). Due to that, the attempt is especially urgent to reconstruct the structure and natural dynamics' traits of prehistoric broad-leaved forests. The latter may be considered as a model to estimate damages of nature. Moreover, it contributes to work out methods of biodiversity preservation and restoration, as well as to use natural resources on the basic ecological principles.

From the viewpoint of restoration and preservation of natural resources, it seems now the question of vital importance to solve the following problems.

1) To reconstruct the limits of zonal broad-leaved forests maximal square of distribution in the Holocene and to analyze its changes caused by human economic activity.

2) To study structure, dynamics, and floristic diversity of recent climax ecosystems.

3) To study the methods of nature exploitation in the prehistoric and historic time and to reveal dependencies of structure and dynamics of successional ecosystems in disturbed areas.

4) To work out methods of estimating successional status and then to build models for a prognosis of the development of recent forests. The prognosis may be concern both natural conditions and different scenarios of biodiversity restoration or demographic stabilization.

## METHODS

In order to solve these problems, field data were collected in 35 areas in Ukraine, Belarus, and Russia during 20 years (Fig. 1) within the associations distinguished by Yu.D.Kleopov namely *Fagetum podolicum*, *Carpineto-Nemoretum ucrainicum s.l.*, *Carpineto-Nemoretum polessicum*, *Mixto-Nemoretum tanaiticum s.l.*, *Tilieto-Nemoretum okense*, *Tilieto-Nemoretum volgense*, *Mixto-Nemoretum praeuralense*, *Tilietum uralense* (Kleopov, 1990). In every area, detailed mapping was made and population descriptions were performed both in nature reservations (undisturbed territory) and in territories subjected to different degrees of past or present anthropogenic disturbance.

In most highly structured and multispecies forest communities located within protected territories, permanent sample areas, from 1 to 4 (12) ha, were established. In these areas, stand mapping of all trees (the smallest being 2 cm in diameter), adult shrubs, and groups of herbaceous species was made with the scale 1:100 and 1:200. While studying mosaic structure in herbaceous layer, mapping was done with the scale 1:10 and 1:20. Special attention was paid to habitat elements connected with tree-falls which accompanied by soil perturbation.

On sample areas, the following characters were determined for trees and shrubs: ontogenetic stage and absolute age, vitality, origin type (i.e. from seed or from vegetative propagule), height, diameter, crown size. Life history and light tolerance of trees and shrubs were studied both in forest communities and in nurseries where plants were grown without any competition. In five areas, experimental planting of *Quercus robur* L. and *Fagus sylvatica* L. was performed within artificially created gaps in of broad-leaved forest canopy (East European broad-leaved forests, 1994).

Computer modeling was performed as one of the methods of studying species dynamics and age composition of forest ecosystems. On the ground of field data, simulation model of dynamics of multispecies tree synusium (based on the 3-D cellular automata models) was worked out. The following assumptions are the basis of the model: 1) the whole space of modeled ecosystem is subdivided into three-dimensional cells of finite proportions; 2) the biological parameters of trees (i.e. age-dependent light tolerance, growth rate, crown size) change in a discrete way according to the ontogeny periodisation included into the model; 3) transition of each cell from one state to another is determined by both the present state of the cell and the states of neighboring cells (Popadyuk, Chumachenko, 1991; Chumachenko, 1992). The results of model calculations of successional dynamics are given below. Historical cartographic material and commentaries on them are reviewed at Central State Historical Archives (CSHA), Russian State Archives of Ancient Acts (RSAAA), and Russian State Military-Historical Archives (RSMHA).

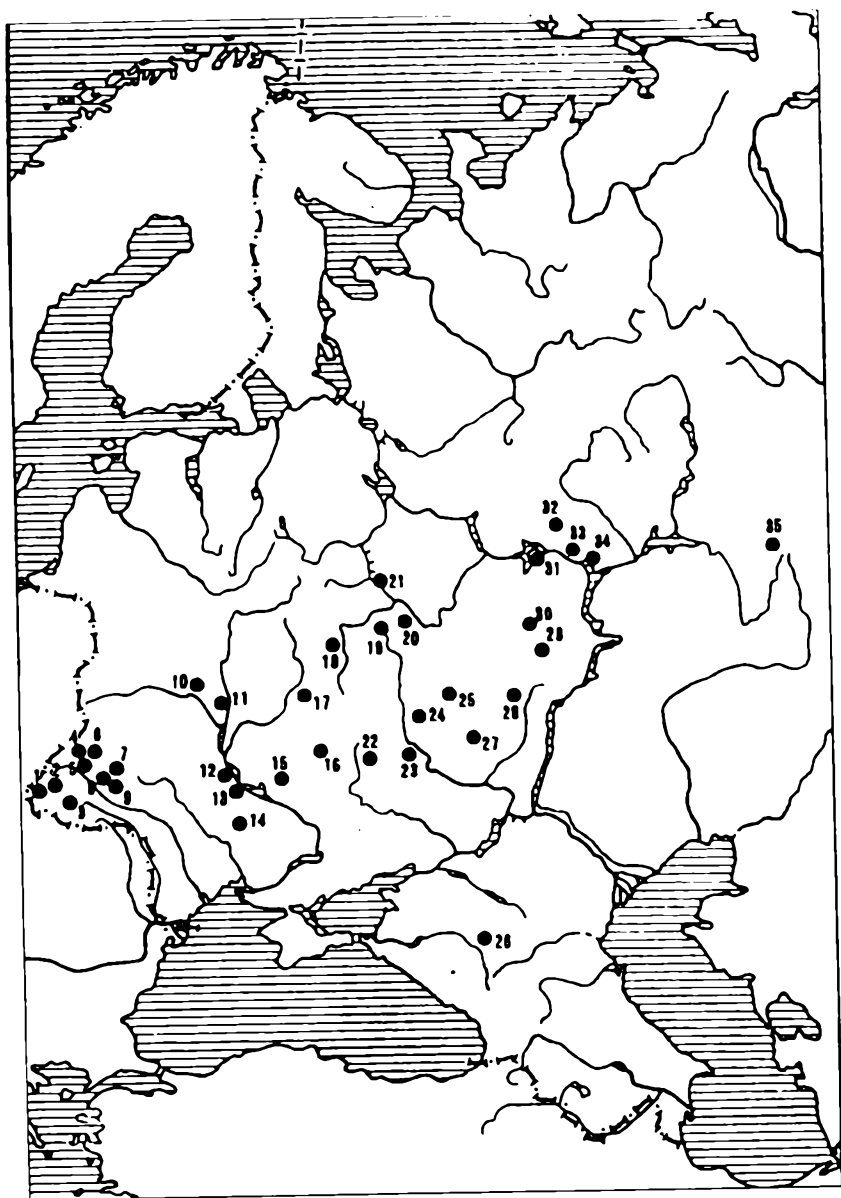


Fig. 1. Location of the research stations.



## **SHORT HISTORICAL REVIEW**

### **Transformations of broad-leaved forests in the Holocene**

Analysis of paleontological, archaeological, florogenetic literature and historical sources makes it possible to reconstruct the area and to estimate, to some extent, the biodiversity of broad-leaved forests. Their broadest geographical distribution coincides with climatic optimum of the Holocene (Neishtadt, 1957; P'yavchenko, 1958; Artyushenko, 1970), that is, 5 - 5.5 thousand years ago (Klimanov, 1978; Borzenkova, Zubakov, 1984). From that time on, areas of dominant species of these forests demonstrate only slight changes (Areas of trees..., 1977 - 1986), but the distribution areas of zonal type forests underwent considerable changes. The southern boundary of these forests continuous distribution moved far northward during the second half of the Holocene while the northern boundary moving to the south. This significant shift of zone borders cannot be explained only by climate changes. The changes showing multiple decreases and increases in temperature during the second half of the Holocene (Il'ves, 1970; Bader, 1974; Kind, 1976; Khotinskii, 1977; Borzenkova, Zubakov, 1984). These climate changes could not be followed by vegetation shifts because of low dispersal activity even of the most widespread tree species (Udra, 1988; Kozharinov, 1994), to say nothing about herb.

Searching for reasons of these changes led to the simple idea. The strongest factor was human activity that transformed the flora and fauna of East European forests (Gorodtsov, 1925; Gozhev, 1929; Komarov, 1951; Krasnov, 1971; Merpert, 1974). This activity was expressed in somewhat different way in different parts of broad-leaved forests zone. Their southern part, first involved in the process of cattle-breeding development, has undergone a strong xerophytization of vegetation cover. The result being the formation of typical steppe landscapes in place of forest-steppe and forest ones (Dohkman, 1968; Dinesman, 1976, 1977, 1992). The same process combined with slash-and-burn and using timber in metallurgy, contributed to the process of open spaces appearing of the central part of broad-leaved forests, so the meadow steppes were formed. Besides, alternation of woody and

non woody spaces in this part of the zone reflect the history of cultural interrelations. The nomads' people were the cattle-breeders and burning down forests to pastures. The farmers' people rather preserving forests, though transformed it, because forests were a necessary element of slash-and-burn agriculture (Saushkin, 1947; Komarov, 1951; Maksimov, 1962; Kirikov, 1966, 1979).

Northern part of broad-leaved forest zone as well as mixed coniferous-broad-leaved forests' one, remained woody for sufficiently long time undergoing the process of economic development. However, long duration of slash-and-burn agriculture in Eastern Europe and preferable use of many broad-leaved tree species in various trades caused considerable change in dominant's composition within tree synusium. As a sequence of that the forests with dominance of competitor species (*Quercus robur* L., *Fraxinus excelsior* L.) were replaced by the forests where ruderal species (*Salix* spp., *Betula* spp., *Populus tremula* L. and *Pinus silvestris* L.) played the dominant role. These species are able to produce a large number of easily flying seeds and therefore can survive on bare substratum. Moreover, the pine and spruce sowing were performed in old ploughed fields in slash-and-burn agriculture cycle (Shelgunov, 1857; Arnol'd, 1880; Gomilevskii, 1897; Essays on the history of Russian village, 1959). Long term slash-and-burn agriculture resulted in serious depletion of soils (Osipov, GavriloVA, 1983). The human impact combined with climate weakening of the broad-leaved species caused a wide expansion of *Picea abies* (L.) Karst. Finally, spruce expansion became stronger in the second half of the Holocene. As a result, the boundary between mixed coniferous-broad-leaved forests and broad-leaved forests moved to the south. Thus, here we may resume the zonal subdivision of East European vegetation was influenced by human activity and climate change, and got a natural-anthropogenic feature at least 2000-3000 years ago.

The agriculture technology was retained almost the same throughout the two last millennia, except the industrial period. During the latter the nature disturbance has undergone qualitative changes namely: the appearance of enormous territories of ploughed fields; water, air, and soil pollution; changes of level and regime of rivers, etc.

The replacing of natural landscapes by strongly disturbed territories where natural components are quite lost could not but influence the biodiversity changes in broad-leaved forests zone. Nowadays, there is no possibility to estimate the extent of biodiversity losses. However, some conclusions concerning key species future can be made. It should be noted the tree species survived on a considerable part of their areas during the second half of the Holocene. Only the position of eastern boundary of *Carpinus betulus* L. area is now the cause of controversies (Gorchakovskii, 1968). Quite different fate had animal key species such as European bison and auroch. They had been eliminated since the beginning till the middle of the present millennium. This fact could not but tell on the composition of the meadow-steppe flora associated with them (Menzbir, 1934; Korochkina, 1969, 1971; Veiberg, 1986).

Other loss became during the last centuries, because number of beaver was reduced to critical size everywhere (Danilov, 1970; Dezhkin, 1970; D'yakov, 1975; Kan'shiev, 1986, 1987; Balodis, 1990). It is worth mentioning that the role of these animals in the ecosystem is not only regulating the hydrological regime. They are also determining species composition of the flora and fauna of wet meadows and waterside-aquatic habitats within forest territories as well (Danilov, 1970). Such considerable difference in the fate of key species of broad-leaved forests should be taken into account when attempting to reconstruct the original state of forest territories.

## **STRUCTURE AND NATURAL DYNAMICS OF CLIMAX FORESTS**

At present time, there are no areas where original (prehistoric) state of forest communities could be directly observed on the territory of Eastern Europe. The study of such forests fragments on protected territories throughout the whole area (Fig. 1.) and the use of the data on ecology and biology of forest species (East European broad-leaved forests, 1994) makes it possible to reconstruct what such forests looked like.

The mosaic-cycle concept of ecosystem organization can be considered as a background for this reconstruction (The mosaic-cycle concept..., 1991). The essence of the concept is the following: stable persistence of communities with maximal species diversity is achieved due to coordinated development of patch mosaics having different spatial and temporal expression. Mosaics of different size and lifetime reflect the features of population life of plants, animals, and other kingdoms' representatives (Viability of populations, 1989). Every species has its population dynamic's pattern (Smirnova et al., 1993); however, in first approximation, population mosaics of key species should be regarded as pivotal for revealing mechanisms of biodiversity preservation. In the case of forests, such key species are, primarily, trees and, to some extent, shrubs. Mosaic-cycle concept of forest ecosystem organization was first introduced in classical works of A.S.Watt (1947), P.W.Richards (1961), and others. Forest mosaics are formed as a result of life and death of tree species. This phenomenon is being known as gap mosaics (Halle *et. al.*, 1978; Brokaw, 1985; Brokaw, Scheiner, 1989; The Ecology..., 1985; Special feature..., 1989; The Mosaic..., 1991). The dimensions of gap mosaic are determined by life history peculiarities of trees and shrubs.

This theoretical framework was the background for ontogeny and life form studying of 15 tree and 10 shrub species in East European broad-leaved forests (Diagnoses and keys..., 1989; Bulanaya, 1985, 1986; Istomina, Bogomolova, 1991). Quantitative limits of individuals demonstrating normal, subnormal, and low vitality was obtained for each ontogenetic stage. For example, ontogeny of *Fraxinus excelsior* L. (Gatzuk et al., 1980) is shown (Fig. 2a). Data on the duration of life cycle of deciduous trees are presented (Fig. 2b).

The life history of plants may be divided into periods or stages. Such ontogenetic stages base on the rise and ceasing of reproductive function and on certain juvenile and adult morphological traits. More details of the ontogenetic stages may be achieved if study development of plant structures (modules), replacement and regeneration of plant tissues or organs. For example, we distinguish eight age stages in the ontogeny of ash. Quantitative characters were taken from Central Russia forest stands.

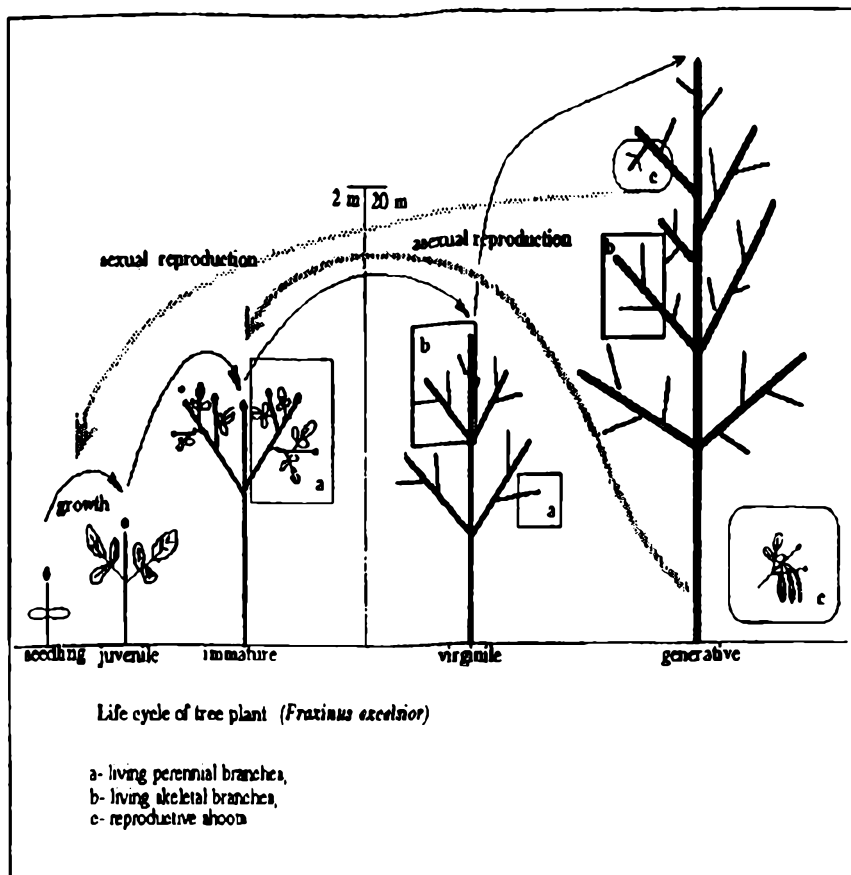


Fig. 2a. Scheme of life cycle of tree plant.

(1) Fruit. A single-seeded outlet, usually germinating only in the year subsequent to shedding.

(2) Seedlings (pl). They appear in late April, and by the end of the first growing season under a forest canopy they possess a hypocotyl, an epicotyl, two cotyledons, a pair of simple leaves, and an unbranched taproot.

(3) Juvenile plant (j). This stage usually possesses calendar age 2 - 15 yr. and is 0.1 - 0.4 m height. It differs from the seedling by the absence of cotyledons and the presence of compound leaves with 3 - 7

leaflets and by unbranched monopodial shoot. The root system consists of a vertical taproot and horizontal lateral roots. The juvenile plant has a high shade tolerance.

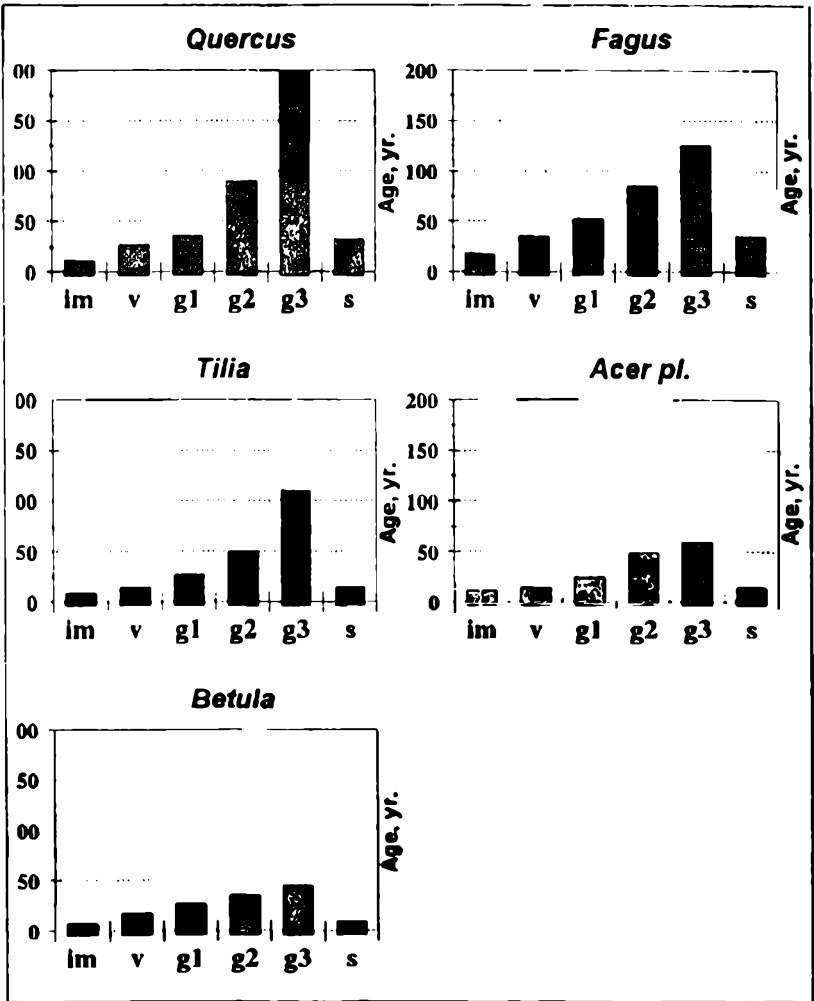


Fig. 2b. Longevity of ontogenetic stages for deciduous trees.

(4) Immature plant (im). This stage possesses calendar age 10 - 20 yr. and is 0.5 - 3.5 m height. At this age stage, mature leaves appear possessing 9 - 13 leaflets, and a monopodial shoot system with second and third order branch develops, though not forming a true crown. The root system is superficial, a taproot being shorter than the second order lateral roots. The light demand increases sharply comparing with the previous age stage, so immature plants may be found only in sunlit areas (gaps) of a forest (for gap size see Table 2).

(5) Virginile plant (v). It possesses calendar age 20 - 30 yr., and is 4 - 10 m height. A typical tree-like habitus appears with a clearly expressed trunk surmounted by a branched crown; the trunk is covered only with periderm. The root system is superficial, with the taproot persisting. Virginile plants neither flower nor bear fruits, but show maximal annual leader shoot growth increments.

(6) Young reproductive plant ( $g_1$ ). This stage possesses calendar age 30 - 50 yr., such trees being 10 - 15 m height. A well-branched fastigate crown appears with maximal width in its lower part. The trunk is covered by rather thin and smooth bark. The root system may demonstrate various structures depending on soil conditions. Flowering and fruiting begin.

(7) Mature reproductive plant ( $g_2$ ). This stage possesses calendar age 50 - 90 yr., the trees being 17 - 25 m height. A large rounded-rhombic crown occurs up to 8 m in diameter, the maximal width being in the middle of its upper part. The trunk is covered by thick bark with small cracks in it. Several processes are indicative for aging occur. They are as follows: reducing annual shoot length if to compare it with the previous age stage; delaying leader-shoot elongation; dying of the bark of weak lateral branches as well as dying of the whole large twigs in the crown, and shifting of the branching zone to the apical parts of shoots.

(8) Old reproductive plant ( $g_3$ ). These plants possess calendar age 100 yr. or more, and are 25 - 30 m height. A more open crown occurs with maximal width being in its upper part. The bark on the trunk is deeply fissured as a result of dead tissues accumulation. Annual shoot's length diminishes sharply comparing with the previous stage, and the occasional death of axillary and terminal buds reduces branching.

Those branches that do form are usually small and twisted. Root system senescence is apparent by the decrease of branching vigor and the dying of root tips and woody roots. A post-reproductive period (subsenile and senile age stages) seems not to occur in ash; old trees are fruiting until death (200 yr. or more).

On the basis of life history studying of all deciduous trees and shrubs of broad-leaved forests, estimation of demographic structure of populations in communities listed above has been made. We carried out the analysis of gap mosaics for many sample plots (Fig. 1; points 1, 2, 4, 14, 18, 19, 27, 30, 35). All these forests have unevenaged stands, because it made possibility to obtain average data of mosaic size that provides the conditions of stable development of each ontogenetic stage of different species (Table 1).

Table 1 shows that birch and oak demands the largest gap size at each ontogenetic stage for their normal development; while ash needs slightly smaller gaps. The minimal demand of light resources is determined for hedge maple. Some time the plants can survive at a low vitality level. It occurs when mosaic size is smaller than necessary for successful development of the species at a certain stage. This vitality state is the so-called quasi-senile state, (Smirnova et al., 1984). The temporal limits of some species survival are given in Fig. 3.

Both normal development and survival duration in the state of "light hunger" are connected with the peculiarities of light demand and shade tolerance inherent to each species. These plant characteristics were estimated according to PhAR intensity in compensation point (shade tolerance) and saturation point (light demand) on the light curve of photosynthesis. The difference between PhAR vales in these points characterizes the amplitude of light perception potentialities of plants (Tsel'niker, 1978).

Special experiments and long-term field observations (Evstigneev, 1991; Evstigneev *et. al.*, 1992) made it possible to work out scales of light demand and shade tolerance for deciduous trees taking into account the ontogenetic stage (Table 2).

The Table shows that factually the position of all species on the scales does not remain constant. For example, we compare two competitive species, *Quercus robur* L. and *Fraxinus excelsior*, on this parameter.



Table 1

Minimum size of ontogenetic loci during life cycle of broad-leaved trees

	<i>Fagus</i>	<i>Quercus</i>	<i>Fraxinus</i>	<i>Tilia</i>	<i>Acer plat.</i>	<i>Acer camp.</i>	<i>Ulmus</i>	<i>Carpinus</i>
Minimum size of ontogenetic locii, m <sup>2</sup>								
immature	20-50	300-500	50-100	200	20	10	50	30
virginile	150-200	1000	250-300	300	70-100	20	250	100
generative	200-400	1500-2500	1000-1500	400-500	400-500	100-200	400-500	400-500
Minimum size of population, hectares	1,0-5,4	12,8-42,5	5,0-13,3	1,1-2,7	1,1-1,8	0,4-1,1	1,0-1,8	0,2-1,2

The first species is characterized by minimal of shade tolerance and maximal of light demand during the greater part of its life history, these features indicating its rather narrow amplitude of light perception possibilities. The second species (*Fraxinus excelsior* L.) is characterized by high level of shade tolerance and by constant growth of light demand during its life history; that is the range of its light perception possibilities constantly increases. Species shift along the scales of light demand and shade tolerance in the course of ontogeny explains species dynamics in the gaps of different size. Large gaps have not limits of lighting for the development of plants. Here the species differentiation is explained by species demands to temperature regime and humidity (Chistyakova, 1991; Evstigneev et al., 1992), as well as by the biological peculiarities (strategy types) (Smimova, Chistyakova, 1980; 1988; Chistyakova, 1988). Quantitative values of some parameters characterizing strategy types of deciduous trees are presented in Table 3. The Table shows that competitive species are characterized by long life span, great size and biomass, moreover high increment of

aboveground biomass per year. It determines their capacity to occupy the largest area in communities and to produce the highest biomass. On the contrary, the species of ruderal strategy (ruderal type according to Grime, 1979) have short ontogeny duration, smaller size and lesser biomass. They demonstrate very high growth rate at early stages of ontogeny and enormous seed productivity. Such characters make it possible for them to occupy new gaps, if light conditions permit their normal development. However, they quickly disappear from the community because of short life span. Stress-tolerant species occupy intermediate position as far as ontogeny longevity, size, biomass, and seed productivity are concerned. They are characterized by the following peculiarities:

1) the greatest variety of life forms (Chistyakova, 1988; Smimova *et al.*, 1991); 2) the lowest ratio between foliage mass and aboveground biomass, that manifests low intensity of physiological processes; 3) a possibility to survive for a long time in quasi-senile state (Smimova *et al.*, 1984).

These species are able to survive within the wide range of ecological and phytocoenotic conditions; they can dominate within ecosystem only when competitive species are absent. On the ground of data on deciduous tree's biology, the following classification of strategies has been introduced (for terminology see Grime, 1979):

### **I: competitive type**

strict-competitive - *Quercus robur* L.;

stress-tolerant- competitive - *Fagus sylvatica* L.;

ruderal-competitive - *Fraxinus excelsior* L..

### **II : stress-tolerant type**

competitive-stress- tolerant *Tilia cordata* Mill., *Acer platanoides* L.;

strict-tolerant - *Acer campestre* L., *A. pseudoplatanus* L., *A. tataricum* L., *Padus avium* Mill..

### **III : ruderal type**

competitive-ruderal - *Carpinus betulus* L.;

stress-tolerant-ruderal - species of *Ulmus*;

strict-ruderal: *Populus tremula* L., *Betula pendula* Roth.

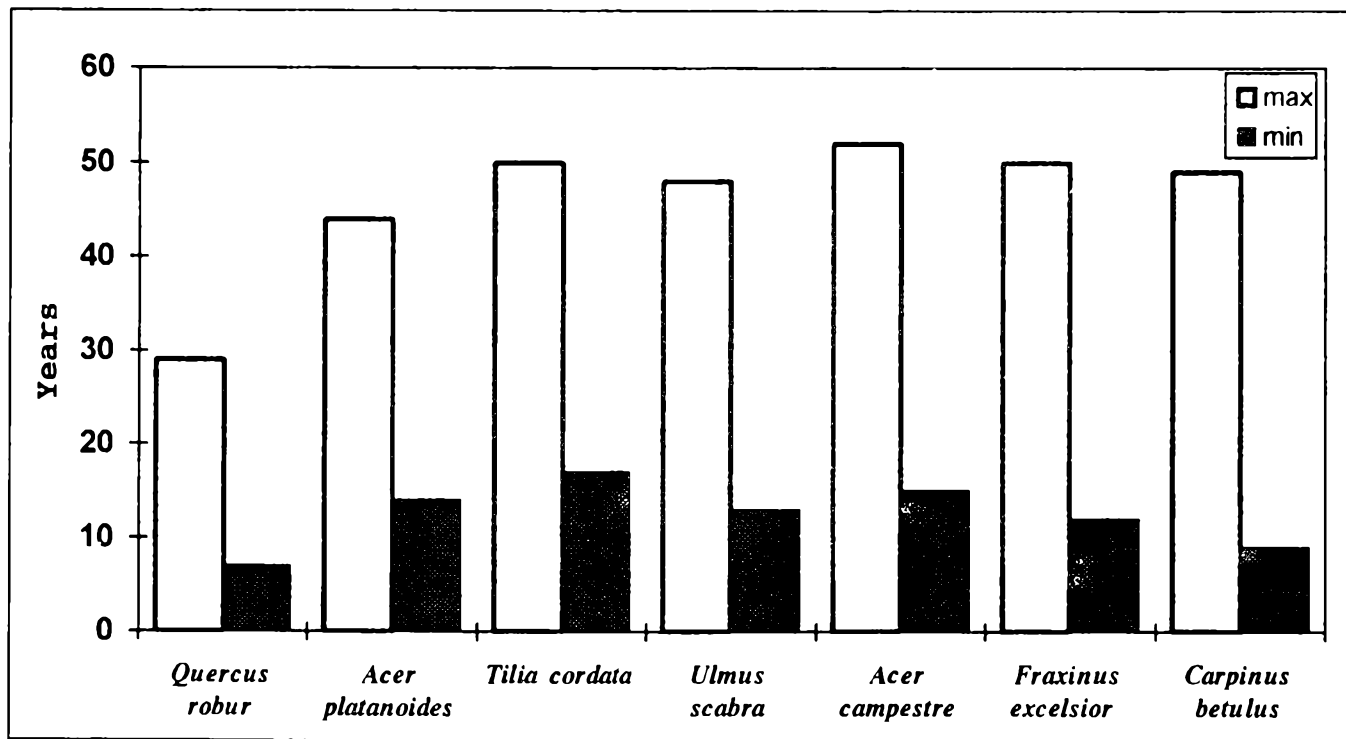


Fig. 3. Longevity of quasisenile stage of trees (max - average of maximal age, min - average of minimal age).

Table 2.

Scales of light demand and shade tolerance for tree dominants of broad-leaved forest.

Light demand j	Shade tolerance j	Light demand im	Shade tolerance im	Light demand v	Shade tolerance v	Light demand 81
<i>Acer platanoides</i>	<i>Acer platanoides</i>	<i>Ulmus glabra</i>	<i>Acer platan.</i>	<i>Populus tremula</i>	<i>Acer platanoides</i>	<i>Populus tremul</i>
<i>Fraxinus excelsior</i>	<i>Fraxinus excels.</i>	<i>Acer platanoides</i>	<i>Acer campestre</i>	<i>Ulmus glabra</i>	<i>Acer campestre</i>	<i>Betula verruc.</i>
<i>Quercus robur</i>	<i>Acer campestre</i>	<i>Fraxinus excelsior</i>	<i>Fraxinus excel</i>	<i>Salix caprea</i>	<i>Ulmus glabra</i>	<i>Ulmus glabra</i>
<i>Ulmus glabra</i>	<i>Ulmus glabra</i>	<i>Betula verrucosa</i>	<i>Ulmus glabra</i>	<i>Betula verrucosa</i>	<i>Tilia cordata</i>	<i>Salix caprea</i>
<i>Tilia cordata</i>	<i>Acer tataricum</i>	<i>Quercus robur</i>	<i>Tilia cordata</i>	<i>Quercus robur</i>	<i>Acer tataricum</i>	<i>Quercus robur</i>
<i>Acer tataricum</i>	<i>Tilia cordata</i>	<i>Salix caprea</i>	<i>Acer tataricum</i>	<i>Fraxinus excelsior</i>	<i>Fraxinus excels.</i>	<i>Fraxinus excel.</i>
<i>Acer campestre</i>	<i>Carpinus betul.</i>	<i>Tilia cordata</i>	<i>Carpinus bet.</i>	<i>Acer platanoides</i>	<i>Carpinus betulus</i>	<i>Tilia cordata</i>
<i>Carpinus betulus</i>	<i>Quercus robur</i>	<i>Carpinus betulus</i>	<i>Quercus robur</i>	<i>Carpinus betulus</i>	<i>Quercus robur</i>	<i>Carpinus betul.</i>
<i>Betula verrucosa</i>	<i>Salix caprea</i>	<i>Populus tremula</i>	<i>Salix caprea</i>	<i>Tilia cordata</i>	<i>Salix caprea</i>	<i>Acer platanoid.</i>
<i>Salix caprea</i>	<i>Populus tremula</i>	<i>Acer campestre</i>	<i>Populus trem.</i>	<i>Acer campestre</i>	<i>Populus tremula</i>	<i>Acer campestre</i>
<i>Populus tremula</i>	<i>Betula verrucosa</i>	<i>Acer tataricum</i>	<i>Betula verruc.</i>	<i>Acer tataricum</i>	<i>Betula verrucosa</i>	<i>Acer tataricum</i>

\*Top row -- species with maximum light demands and light tolerance, bottom row -- species with minimum light demands and light tolerance.

Table 3a..

## General characteristics of competitor trees

Items	<i>Quercus robur</i>	<i>Fagus sylvatica</i>	<i>Fraxinus excelsior</i>
Numer of seeds: thousand/individ	10.2-5	1-10	0.3-80
Cycle of fruiting years	5-10	3-8	2-3
Height increment:cm/yr			
Age:			
from 1 to 5 yr	14.4	10.1	21.8
from 6 to 10 yr	22.8	15.9	38.0
from 11 to 15 yr	32.7	25.6	46.1
Begining of fruitness: yr	50-70	50-70	40-50
Longevity of life: yr maximal	300-400 (500)	250-400 (500)	250-350
Size of adult tree height: m / diameter: cm	40/150	45/150	40/150
Crown areas: sq.m	100-300	150-200	150-300
Productivity vol.m/hectare	550	650	400
Biomass increment kg/yr:			
virginile indiv	0.4	0.45	0.44
generative indiv.	5.0	2.7	2.1
Increment of above ground volume: vol.cm/yr:			
virginile indiv.	525	650	490
generative indiv.	3600	4320	4150
Leaf biomass / aboveground biomass ratio: kg/vol.m:			
virginile indiv.	0.07	0.08	0.07
generative indiv.	0.04	0.02	0.05
Type of asexual reproduction			
Root sprouting			
Xylorhizome sprouting			+ /subadult
Stem sprouting			+ /subadult
Stump sprouting	+ /subadult	++ /subadult + /adult	++ /subadult + /adult

\* + low intensity of vegetative propagation, ++ high intensity of vegetative propagation / subadult - into the first half of life cycle, adult - into the second half of life cycle.

Table 3b.

## General characteristics of stresstolerant trees

Items	<i>Acer plata-noides</i>	<i>Tilia cordata</i>	<i>Acer psedoplat.</i>	<i>Acer cam-pestre</i>
Numer of seeds: thousand/individ	10-90	0.2-20	20-80	10-60
Cycle of fruiting years	3-4	3-6		2-3
Height increment:cm/yr				
Age:				
from 1 to 5 yr	19.2	10.1	12.3	9.0
from 6 to 10 yr	24.3	23.5	15.1	21.5
from 11 to 15 yr	29.1	38.5	22.2	32.0
Begining of fruitness: yr	30-50	30-50	30-50	30-50
Longevity of life: yr	150-200	150-200	150-200	100-160
maximal		(300)		(200)
Size of adult tree height: m / diameter: cm	35/80	35/100	35/80	27/60
Crown areas: sq.m	100-300	100-300		50-150
Productivity vol.m/hectare	250	250	250	150
Biomass increment kg/yr:				
virginile indiv	0.2	0.2	0.18	0.15
generative indiv.	1.6	1.6	1.2	1.1
Increment of above ground volume: vol.cm/yr:				
virginile indiv.	280	470	290	270
generative indiv.	2470	3280	2500	1790
Leaf biomass / aboveground biomass ratio: kg/vol.m:				
virginile indiv.	0.21	0.18	0.22	0.22
generative indiv.	0.05	0.05	0.07	0.07
Type of asexual reproduction				
Root sprouting				
Xylorhizome sprouting	+ / subadult	++		++
Stem sprouting		++		++
Stump sprouting	+	++	+	++

Table 3c..

## General characteristics of ruderal trees

Items	<i>Carpinus betulus</i>	<i>Ulmus scabra</i>	<i>Betula pendula</i>	<i>Populus tremula</i>
Numer of seeds: thousand/individ	10-500	30-200	30-8000	> 10000
Cycle of fruiting years	1-2	2-3		
Height increment:cm/yr				
Age:				
from 1 to 5 yr	19.5	18.9	27.3	32.0
from 6 to 10 yr	32.4	26.9	65.5	86.7
from 11 to 15 yr	40.1	42.9	90.0	108.4
Beginning of fruitness: yr	20-40	20-40	20-30	20-30
Longevity of life: yr	100-120	80-120	80-120	80-100
maximal	(300)	(300)	(150)	(150)
Size of adult tree height: m / diame- ter: cm	30/60	30/50	30/80	30/110
Crown areas: sq.m	70-100	120-300		
Productivity vol.m/hectare	160	130	190	220
Biomass increment kg/yr:				
virginile indiv	0.3	0.1	0.2	0.2
generative indiv.	1.7	0.7	2.0	1.8
Increment of above ground volume: vol.cm/yr:				
virginile indiv.	470	200	500	560
generative indiv.	2670	1300	3550	4550
Leaf biomass / aboveground biomass ratio: kg/vol.m:				
virginile indiv.	0.10	0.18	0.14	0.11
generative indiv.	0.05	0.06	0.03	0.02
Type of asexual reproduction				
Root sprouting		+ / subadult		++
Xylorhizome sprouting	+ / subadult	+ / subadult		
Stem sprouting	+	+		
Stump sprouting	++	+	+ / subadult	+ / subadult

Besides trees, the biology of shrubs (Istomina, Bogomolova, 1991) and herbs (Smirnova, 1987) have been studied in detail in East European broad-leaved forests. As in the case of trees, the variety of shrub strategies is connected not only with quantitative limits characterizing size and growth reactions, but with the characters of growth forms as well. The examples are given in Fig. 4.

The Figure shows that maximal variety of growth forms in shrubs, is manifested by stress-tolerant species; it is just the same picture we have obtained for trees (Chistyakova, 1982, 1988). Interaction of tree and shrub synusia becomes noticeable on the initial stages of gap development. The generative shrubs compete with immature and virginile trees for light and other ecological factors because of their faster rate of ontogeny stages passing. The strongest competitor within shrub synusium proves to be *Corylus avellana* L.. Also for trees of the earliest stages of life history ( $j$ ,  $im_1$ ), herb synusia are competitively significant. This synusia are also heterogeneous because of the different strategies of species constituting them. Classification of strategy types in herb synusia is based on such parameters as ontogeny longevity, biomass, productivity of seeds and vegetative propagules, vegetative mobility, duration of the occupied territory keeping, etc. (Smirnova, 1987). At the same time, spatial structure and patch dynamics in herb synusia are determined by gaps that are appearing after of tree death and soil perturbations connected with tree falls.

Study of ontogeny, ecological and biological peculiarities as well as strategy types of climax forest leads to the conclusion that tree, shrub, and herb synusia include species of all strategy types. In all synusia, stable existence of populations is connected with constant patch mosaic formation. The differences between the synusia concerning patch mosaics manifest themselves by the fact that both patch size and life span decrease from tree to herbs synusia. Within one patch formed as a result of tree death, several mosaic patches of shrub populations and a great number of those of herb populations can exist. Strict correlation in individual distribution of different synusia is absent in uneven-aged broad-leaved forests. It appears due to the differences of spatial and temporal scale of the population life of plants. Precise maps also show this lack of the correlation, because population patterns do not coincidence for the cohorts of tree, shrub, and herb species.










Species	Strategy	Tree form	Acroxylic form	Geoxylic form	Dwarf form
<i>Corylus avellana</i>	Competitor				
<i>Euonymus verrucosa</i>	Stress-tolerant				
<i>Sambucus racemosa</i>	Ruderal				

Fig. 4. Life forms and life strategies of shrubs.

## GAP STRUCTURE AND DYNAMICS

Gaps in forest community may differ in size and orientation. The factors influencing this differentiation are obvious, i.e., size of a separate tree, the number of synchronously died individuals, and the direction of their fall.

Subdivision of gaps according to their size is rather conventional. However, in climax forest there is always a set of gaps of different size sufficient for the complete realization of all the tree's ontogeny. The broad-leaved trees commonly have not the possibility to start fruiting in small gaps (200 - 500 m<sup>2</sup>), that is, the gaps that are commensurable with the crown projection of 1 - 2 trees. Even the most shade-tolerant of them (*Fagus sylvatica* L., *Acer campestre* L.) settling in such gaps, remain in pregenerative state for a long time. Full ontogeny of shadetolerant species (*Fagus sylvatica* L., *Acer* spp., *Tilia-cordata*) is possible in medium-sized gaps (20 - 600 m<sup>2</sup>). The trees with high light demand (*Quercus robur* L., *Fraxinus excelsior* L., *Betula pendula* Roth., *Populus tremula* L.) can occur only in large ones, i.e., 1500 - 2500 m<sup>2</sup>.

In large gaps, all age stages can be observed not only in the case of high light demanders, but of less light-requiring species as well. That is why tree microcommunities forming within them are, as a rule, polydominant. In gaps larger than 2500 m<sup>2</sup>, conditions of forest environment are considerably different from that of the neighbor forest sites. Such gaps form in the most cases as a result of exogenous influence, as far as tree population life is concerned. Formation of large gaps occurs in several stages. When the increase in gap size coincides with increase in PhAR demand of trees, fruiting comes without any delay. If it is not so, there is either a pause in development of young tree regrowth being in depressed state, or the latter dies. Its fate is, largely, determined by the degree of species shade tolerance, which changes during the development of woody plant (see Table 2). The free area is settled by regrowth that has been under tree canopy before, as well as by new germs. Originally, young plants (seedlings, juvenile individuals) get an accidental distribution within the gap. But when young trees overgrow herbaceous plants, i.e., reach immature state, the regrowth distribution already becomes

clearly dependent on light regime, humidity, and soil fertility. The analysis of maps has shown that viable regrowth and adult trees of *Quercus robur* L. are most often found in the north of a gap. On the contrary, *Fraxinus excelsior* L. occurs in the southern and western parts. As to the regrowth of *Populus tremula* L., *Betula pendula* Roth., and *Salix caprea* L., it can be found near the gap center. Young individuals of birch, aspen, mountain elm, and goat willow survive on rotten trunks and stumps of trees or on sites with disturbed herb layer (ungulate diggings). Besides lighting, they are also very sensitive to air humidity and soil moisture. Having little stock of nutrients in seed, they can grow rapidly only on substrata with high humus content. Besides environmental, the local habitats, and the presence of shrub layer (tall shrubs) affect distribution of tree regrowth in gaps. Thus, in plain broad-leaved forests, the size of tree microcommunities may correspond to gap area, or they can occupy only part of it, this part being much smaller than light conditions permit. In the latter case, the area free from regrowth is occupied by *Corylus avellana* L. In mountain forests of the Carpathian Mountains, slope exposure and steepness have considerable influence on light regime and microcommunity size in the gap (Chistyakova, Parpan, 1991; East European broad-leaved forests, 1994).

#### DIFFERENTIATION OF GAPS INTO ZONES ACCORDING TO TREE AND SHRUB COMPOSITION

(links Nemorion and Fagion)

Gap differentiation becomes mostly apparent in the case when gaps are large. Gaps more than 30-50 m wide can be divided into three zones, the first (central) one covering 10 - 15 % of the area. This zone in broad-leaved forests with the dominance of *Quercus* is usually occupied by tall shrubs of *Corylus avellana* L., tightly adjoining each other. In beech forests, the central zone is as a rule occupied by tall herbs.

The second (marginal) zone (24 - 45% of the overall area of the gap), is occupied by scattered stunted shrubs of hazel, as well as by tree regrowth. The third one (that is, border zone or the zone of double overlapping) is shaded by the crowns of adult trees adjoining

the gap and by crowns of hazel shrubs sparsely distributed within the zone. This zone size is about 40 - 60% of the overall gap area. Spreading out within a gap, hazel prevents excessive soil oxidize and penetration of herbs non-inherent to forest communities. At the same time, hazel restrains the development of tree regrowth. In beech forests, shrubs do not seriously suppress tree reproduction; here, the function similar to that of hazel is performed by beech regrowth which, before treefalls, found itself under old tree canopy.

In small and medium-sized gaps, as well as in large, but not very wide ones (up to 30 - 50 m in diameter), the central zone is missing. The most favorable conditions for tree regrowth to survive take place in marginal zone that is stretching out the gap. Its width does not exceeding 1 - 2 heights of adult trees. Gap size as well as its configuration and orientation on cardinal points is, largely, determined by chance factors. Moreover, local topography, wind rose, and community history play a certain part in their formation too. Yet, distribution of viable regrowth within a gap is determined only by the correspondence between environmental conditions and species biology.

#### **DYNAMICS OF AGE STRUCTURE AND SPECIES COMPOSITION OF TREES AND SHRUBS WITHIN THE GAPS IN BROAD-LEAVED COMMUNITIES** (link Nemoria)

The study of age and spatial structure of communities showed that stable community capable of selfmaintenance must comprise age mosaic elements of different size and of all age classes (East European broad-leaved forests, 1994). The communities located in different parts of broad-leaved forest zone (the center of the Russian plain and the north-east of the zone) have some similar regularities. There are the rates of patch mosaic elements, their size, and proportion of species in ecosystem composition. Intracommunity dynamics of broad-leaved forests can be characterized as cyclic, consisting of stages consecutively replacing one another eventually. The duration of periodically repeating cycles is commensurable with that of the ontogeny of the most long-lived edificator, i.e., *Quercus robur* L.

Secondary succession cycle consists of five consecutive stages (Fig. 5). Shrubs (most often *Corylus avellana* L.) predominate at the

first stage, its duration being about 20 - 30 years corresponding to the life span of hazel skeleton axis.

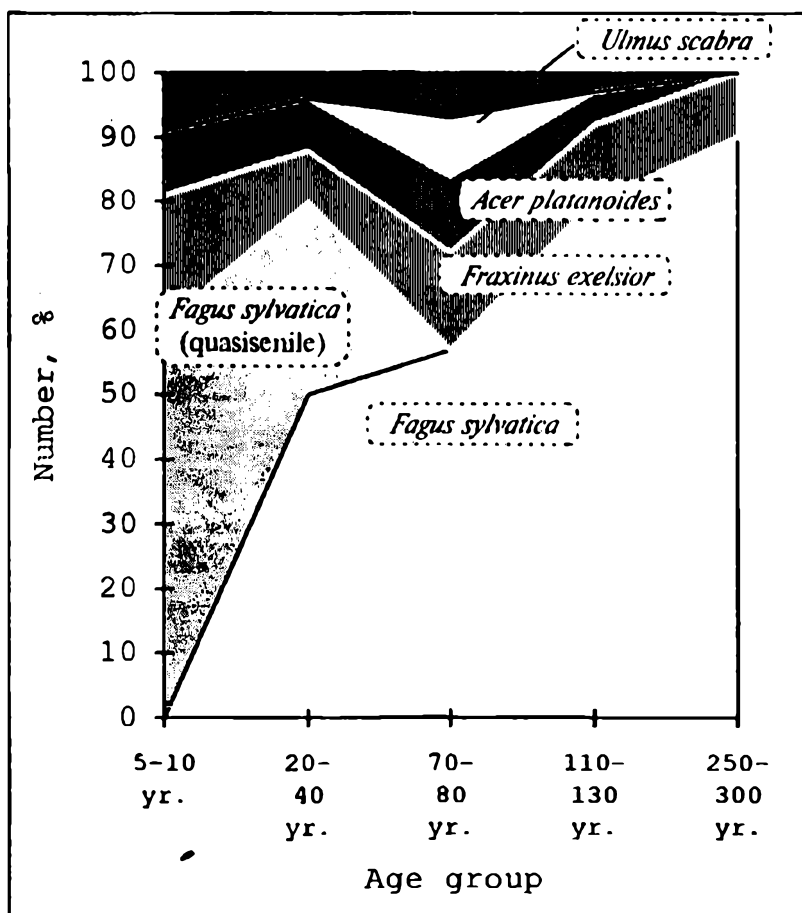


Fig. 5a. Proportion of trees within different age groups in *Fagetum*.

Codominance of shrubs and trees characterizes the second stage (30 - 40 years). It ends in senescence and dying of hazel shrubs. At the same time tree regrowth is going out from shrub layer. Trees of

different life span predominate at the third stage. This is a stage of maximal species diversity; it lasts about 30 - 60 years.

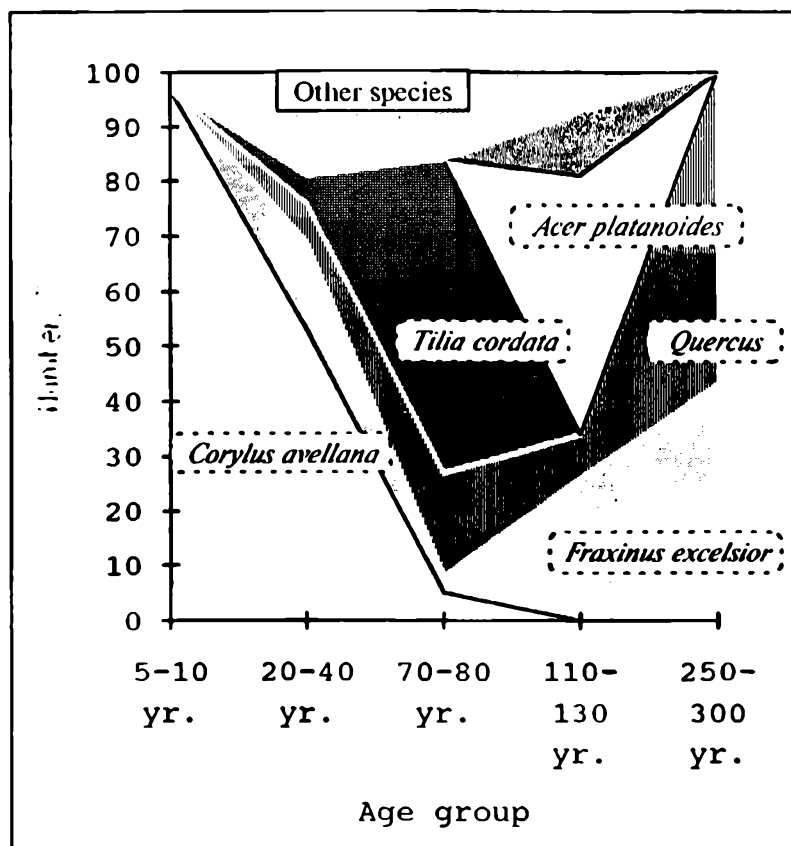


Fig. 5b. Proportion of trees within different age groups in *Tilieto-Nemoretum okense*.

Trees with both long and middle life spans predominate at the fourth stage; its duration is 30 - 90 years. By this time, species like *Betula spp.*, *Populus tremula L.*, *Sorbus aucuparia L.*, and *Padus avium Mill.* are lost from the microcommunities in oak forest. The fifth stage is characterized by dominance of trees with long life span (*Quercus*, *Fraxinus*); it lasts 100 - 150 years.

In the end of each cycle in age-heterogeneous communities, species replace each other moving within the ecosystem area. Due to different life span of trees, two or three medium-sized gaps or several small ones can fuse forming one large gap thus the prior cycle being "missing".

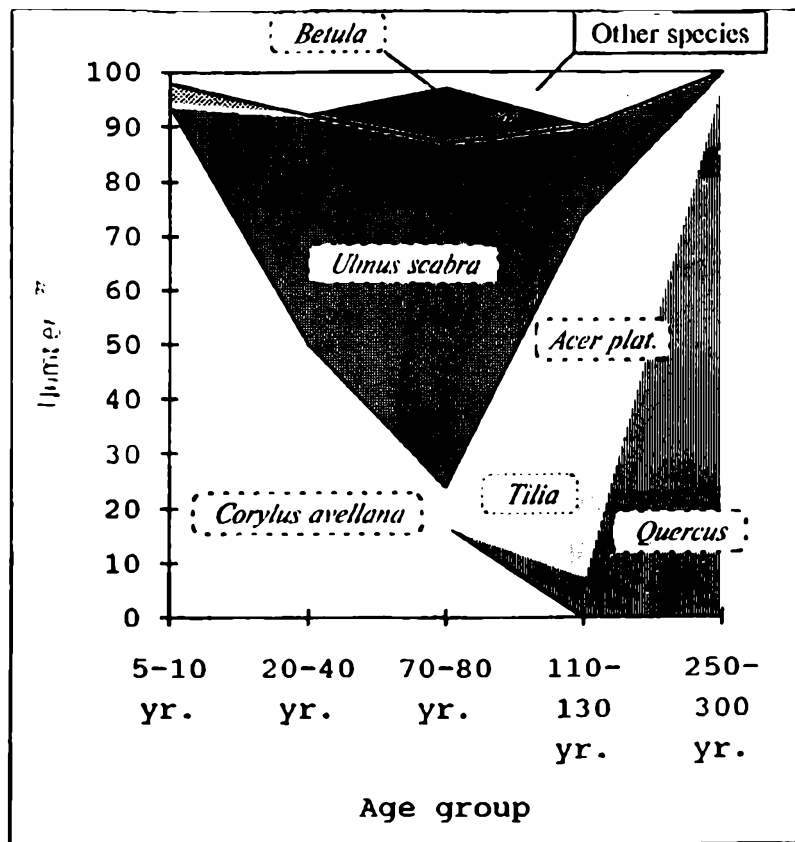


Fig. 5c. Proportion of trees within different age groups in *Mixto-Nemoretum praeuralense*

**DYNAMICS OF AGE STRUCTURE AND SPECIES COMPOSITION OF TREES  
WITHIN THE GAPS IN BEECH COMMUNITIES**  
(link Fagion)

Four stages are typical for mosaic successions in communities of *Fagetum podolicum* association (Fig. 5a). Beech regrowth that has overgrown under forest canopy predominates at the first stage (20 - 30 years).

Different tree species with different life spans codominate in the second stage (30 - 100 years); this is the stage of maximal age states and species diversity. Trees of long and middle life span predominate at the third stage (80 - 120 years). As a rule, elm and hornbeam disappear from microcommunities by the beginning of this stage. Trees with long life span (beech, oak, ash) predominate at the fourth stage (100 - 200 years). The analysis of patches of different size and life span in broad-leaved forests from different syntaxa shows that floristic completeness of tree and shrub synusia is retained. It occurs if the gaps necessary for normal ontogeny of competitive species (oak, beech, ash) appear in a natural way during the development cycles. Calculations made by the authors (Smimova et al., 1990) showed that for *Quercus* the minimal area where patch mosaic can completely appear is about 50 ha. For other species from *Nemorion* link, this area is considerably smaller. Yet, if forest communities occupy the territory of 50 ha, its stable persisting cannot be guaranteed because of the possible unfavorable influence of disturbed neighboring territories. Scraps of broad-leaved forests with clearly pronounced patch mosaics that have survived by the present time are often even smaller and happen to be on the brink of destruction. In case of beech, the minimal patch mosaic area is much smaller (Table 1). However, pure beech forests are anthropogenic variants either of broad-leaved forests with beech, oak, and ash or of mixed coniferous-broad-leaved forest with spruce and fir. In both cases, stable mosaic structure can become apparent on areas commensurable with those of stable communities of *Nemorion* link.

Now we have the first result of simulation modeling of population dynamics of the three woody species. They represent population dynamics of three strategy types (oak as a competitive species, Norway



maple as a tolerant one, and birch as a ruderal one). Moreover, these species differ on the light demand. The models show that stable coexistence of all the species is possible if proportion of young individuals is of 30 to 65% in all populations (Fig. 6).

Successful development of regrowth occurs only in gaps, and their total areas are being about 40% of the overall community territory. It may be considered as threshold value for estimating the degree of disturbance of demographic and spatial structure of the real communities. This pattern of tree numbers dynamics and of the territory occupied by them has been obtained as a result of a 4000-year period of stationary regime in the model.

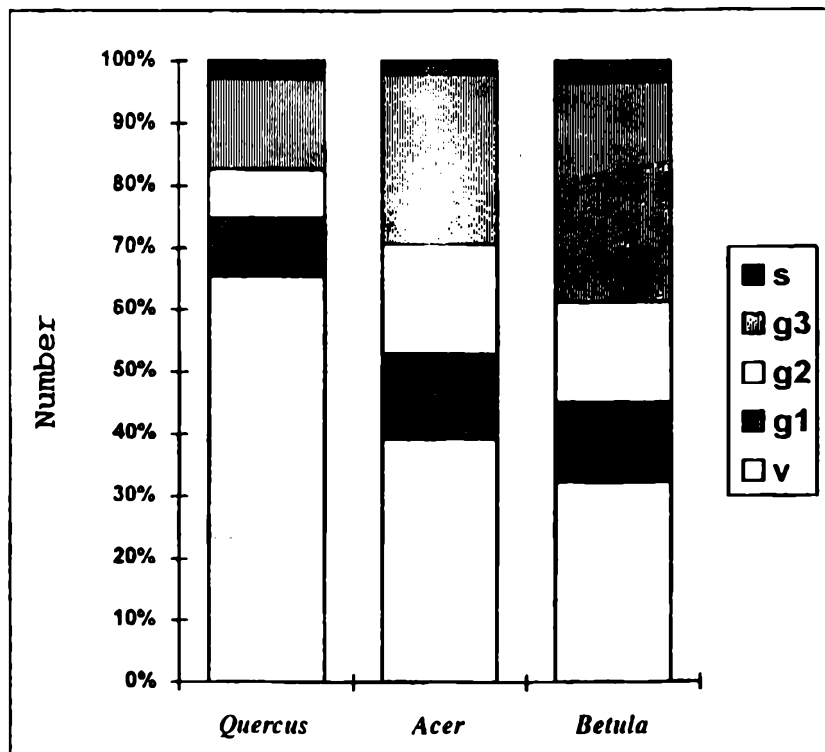


Fig. 6. Simulated ontogenetic spectra of trees.

Different ratio of ontogenetic groups in different species is the sequence of biological and ecological peculiarities of these species. Their proportion in community is not directly connected with age state's spectrum type, though, in this case, the species with most numerous virginile group predominates in all layers.

## **GAP DIFFERENTIATION ACCORDING TO DISTRIBUTION OF HERBS AND REGROWTH OF TREES AND SHRUBS**

It has been shown above that development of trees and shrubs in gaps are slightly interdependent. However, not only gap size and woody vegetation within the gaps are important for herbs, but soil perturbations connected with treefalls as well (Skvortsova et al., 1983). As a result of this process, the following elements of habitat are formed: hillocks, where deep soil horizons are exposed to day light; pits; fallen tree trunks. In climax forests, each piece of surface has at a certain time suffered soil perturbation. The period of existence of treefalls outer trace is commensurable with tree ontogeny.

The study of the herb's distribution pattern and tree regrowth in communities of *Tilieto-Nemoretum okense* association showed that, in case of soil perturbations, the resulting microsites differ according to moisture regime. Pits are places where water stagnates due to the disturbance of capillary soil structure. Hillocks are characterized by somewhat low moisture and better aeration; rotten trunks are notable both for sufficient moisture and high humus content. These differences are strengthened by vital functions of ungulates (wild boars) making the soil in pits more compact. The latter leads to long water stagnation in them. The analysis of abundance and frequency of occurrence of herb species in different habitat elements connected with treefalls manifested the presence of slightly fragmented continuum. A group of species related to pits happens to be more clearly distinguished. They are common inhabitants of black alder forests: *Ranunculus repens* L., *Lysimachia nummularia* L., *Chrysosplenium alternifolium* L., *Filipendula ulmaria* (L.) Maxim., *Cardamine pratensis* L.. Hillocks and flat sites lack clearly pronounced specificity of species composition and abundance. The only thing to be mentioned is that in the investigated

community, the species inherent to relatively dry broad-leaved forests namely *Carex pilosa* Scop. is to be found only on hillocks. Newly formed hillocks are the sites where herbs of ruderal strategy demonstrate high abundance.

Seed reproduction of many herb species of competitive and tolerant strategy, as well as that of trees of ruderal strategy, also often occurs on these hillocks. However, within small and medium-sized, the seedlings die quickly. Herbs and shrubs of ruderal strategy (*Impatiens noli-tangere* L., *Geranium robertianum* L., *Rubus idaeus* L., *Urtica dioica* L., *Sambucus racemosa* L.) may be usually found on rotten trunks. Seedlings of trees with easily flying seeds (species of *Salix*, *Betula*, *Ulmus*) grow there too. The study of distribution of *J* and *im* individuals of deciduous trees in *Tilieto-Nemoretum okense* association (the "Kaluga zaseki" reservation) showed that seed reproduction of ash happens to be abundant in all habitat types.

The reproduction of Norway maple is the most abundant on microelevations (treefall hillocks). Flat sites are the only place for reproduction of linden. Seedlings of goat willow and birch occurs only on rotting trunks (Fig. 7).

The investigation of regeneration in communities of *Carpineto-Nemoretum ucrainicum* association (Korotkov, 1990) has revealed main dynamic processes at early stages of fallen trees decay. It should be stressed that in the first 3 years after treefall regrowth of ruderal species (*Salix caprea* L., *Populus tremula* L., *Betula pendula* Roth.) appears in bulk on hillocks. Its number is about 30 - 50% of the total number of tree seedlings. As far as shrubs are concerned, *Sambucus nigra* is the one of the earliest species to appear during the first years. The total number of vascular plant species on hillocks and pit slopes is three times higher than their number on sites lacking treefall mosaic.

We studied herb and tree regrowth distribution in communities of *Fagetum podolicum* association located in the lower mountain belt of the Carpathian Mountains. Here, unlike communities of *Tilieto-Nemoretum okense* association, pits are sufficiently well drained and only slightly differ, from flat sites as far as soil moisture is concerned. Due to that, the presence of mesohygrophilous species has not been recorded. In monodominant beech forests, a layer of slightly rotting

litter of several dozen centimeters thick accumulates in pits; this proves to be a serious obstacle for plant settling. Usually they are free from vegetation for a long time. The main body of herbaceous species occupies flat sites. On hillocks and pit slopes, seedlings of *Acer psuedoplatanus* L., *Fagus sylvatica* L., *Ulmus scabra* L. usually occur in bulk; sometimes also regrowth of *Sambucus nigra* L. develops in these sites.

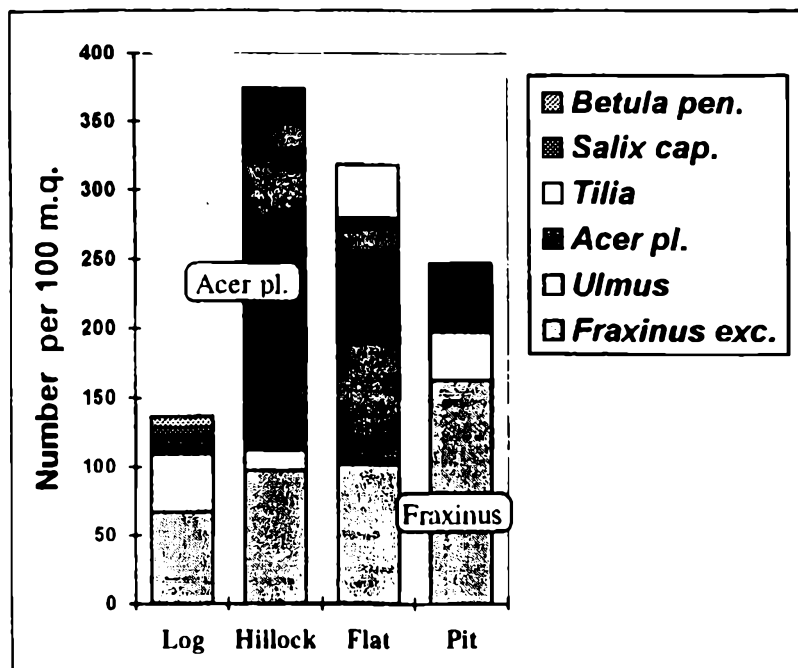


Fig. 7. Number of seedlings on the habitat elements associated with treefall.

Thus, brief description of tendencies of herb and regrowth distribution pattern in broad-leaved forests shows the presence rather close correlation between the habitat elements and the spatial structure and dynamics of herb synusia and regrowth.

The study of patch mosaic in different synusia shows those age-heterogeneous multispecies broad-leaved ecosystem functions as a complex of mosaic successions of different scale. The unidirectional development of populations age-homogenous loci of tree edificators is a large-scale mosaic succession. The similar development of herb populations' loci within variants of treefalls associated with soil perturbation demonstrates the different variants of small-scale mosaic successions. Climax forest exists as a system of multitude of mosaic successions of different scale. However, it should be noted that the whole variety of mosaics is determined by ontogeny of one or few dominants.

### **ANIMAL-DEPENDENT PATCH MOSAICS**

All the things mentioned above represent the description of mosaic scaling connected with plants' life. Yet, in prehistoric broad-leaved forests, there occurred forest animals, whose activity led to gap formation. Their size was commensurable with the one of gaps formed as a result of big trees dying off or even exceeded them. The largest group of key species in broad-leaved forests were big herbivores (aurochs, the European bison) eliminated by now. The experiments on reintroduction of the European bison in different parts of broad-leaved forests (the "Belovezhskaya pushcha," Khoper, Prioksko-Terrasny, Central Caucasus nature reserves) demonstrate significant changes. New communities of sparse forest and meadow with steppe species appeared at stands of these gregarious animals as well as in watering-places and on paths. The size of zoogenic glades with meadow flora varied from 0.1 to 3 - 5 ha. Stand's exploitation for one or two dozen years led to the strong soil compression and to the development of bunch grasses. At the same time, animals damage big trees and foraging regrowth and destroy tree and shrub vegetation. Large gaps connected with watering and foraging places appeared in the forests. Herbaceous plants prevailed over woody ones in the ration of these animals. It is confirmed by the fact that, in food ration of European bison, meadow species constitute 90%, with grasses prevailing among them. Analysis of fodder species lists of bison (Korochkina, 1969, 1971) and comparison of them with the present flora of meadow hay-

glades and pastures of domestic animals revealed considerable similarity. Both archaeological and historical data are the evidence of wide and abundant spreading of these large herbivores which caused the patch mosaic's formation in prehistoric times. All these things make it possible to consider zoogenic glades as an obligatory element of broad-leaved forests. These facts are helpful for reconstructing the structure of prehistoric forests.

Another key species of broad-leaved forests of prehistoric type was the European beaver. It has persisted in several isolated sites in forest regions throughout the last millennium. In the middle of the XX th century European beaver was reintroduced in the large part of East European territory (Danilov, 1970; Dezhkin, 1970; D'yakov, 1975; Lavrov, 1981). Environmental impact of this animal is so significant that his dwelling places have got the name of "beaver landscapes". Below we give the extents of some patches of these landscapes. In literature, we found descriptions how a beaver family use trees for building dams on rivers and streams with considerably steep banks. This activity is leading to the formation of riverside glades of 0.1 to 3 ha. Vegetation of such glades in broad-leaved forest zone is represented by meadow, forest-edge, and steppe species (Barabash-Nikiforov, 1950; Danilov, 1970; Dezhkin, 1970; Feklistov, 1984; Kan'shiev, 1986, 1987). These glades exist till beavers leave this site due to food exhaustion. Then the glades become again afforested, at first, with ruderal strategy trees. On the rivers with sloping banks, dam-building leads to flooding of a large forest territory (the size of beaver ponds ranges from 0.2 - 0.5 to 20 - 30 and more ha). Woody vegetation dies in the zone of under flooding; lowland meadows and bogs form at pond outskirts. After beavers leaving to the another site along the river, the dam gradually goes to ruin, and recovery of woody vegetation, with *Alnus glutinosa* (L.) Gaertn. being the leader, begins on baring substratum. Vital functions of beavers not only determine mosaic-cyclic successions of vegetation in which the flora of light habitats is presented, but also form microsites giving refuge and food for many animals, both vertebrate and invertebrate. It should be mentioned that a practically complete elimination of beavers by the end of the XIX th -- the beginning of the XX th century has led to considerable decrease

in biodiversity on certain territories. Artificial settling of beavers does not always lead to recovery of correlated flora and fauna within "beaver landscapes". The fall appears due to "island" pattern of the recent forests and the absence of migration channels for many species.

Apart the above-mentioned zoogenic mosaics of great size, forests expose a considerable influence on plant composition and mosaic's density due to selective foraging (East European broad-leaved forests, 1994). Thus, density of Norway and hedge maple is connecting with foraging activity of small rodents and hares on a large extent. Without these animals, shade-tolerant maple species, in some cases practically completely suppress the regrowth of other tree species.

Simulation of selective damage of young generation of Norway maple determines the threshold level of elimination of immature plants, which corresponds to frequently observed ratio of adult trees of oak and maple. In simulation experiment, stable ratio (80% for oak and 20% in case of Norway maple) in the upper layer occurs when, at each modeling step (10 years), from 70% to 85% of maple regrowth die. The obtained values of selective damage of one of the modeled species correspond to field data for Central Russia oak forests (Dinesman, 1961). Thus, theory of tree fall mosaic is not sufficient for the reconstruction of a prehistoric forest' structure. In these forests treefall mosaics occurred together with animal-dependent patch ones.

By the beginning of the present millennium bison and auroch was eliminated in Eastern Europe (Kirikov, 1966, 1979). The abundance of the other species of ungulates had been greatly reduced, and they could not cause the great patch mosaics any more. As a result, intraforest glades became incapable to self-maintenance in a natural way. As big animals forming zoogenic mosaics were eliminated; their ecological niche in the forest zone was occupied by cattle. Traditions of forest pasturing were retained till the middle of the XX th century (Gomilevskii, 1987). Besides pasturing, small-contour mosaic of slash-and-burn with the alternation of woody and non woody territories made it possible for a large set of plant species of open habitats to survive.

The traditional methods of land-use, described by A.V.Sovetov (1867), created the size of ploughed fields and hayfields not strongly differing from that of natural phyto- and zoogenic patch mosaics. However, in the XX century these methods were replaced by industrial agriculture. This led to considerable reduction of agrolandscape biodiversity. Enormous homogeneous agricultural and silvicultural lands appear on the forest areas, i.e., large fields, sown meadows, woody plantations, *etc.* The changes became a severe obstacle for reproduction of many species due to the diminution of "reproductive potential" of areas (Udra, 1988; Korotkov, 1992).

## **SECONDARY SUCCESSIONS OF BROAD-LEAVED FORESTS**

Structure and dynamics of broad-leaved forests described in the previous part were studied in isolated fragments of slightly disturbed forest tracts belonging to the associations listed above. Both slightly and strongly disturbed communities were examined in associations.

Our study showed that it is just secondary mono- or oligodominant communities. In these forests some species can predominate namely birch, pine, aspen, lime, oak, maple, beech or hornbeam. According to D.V.Vorob'ev's (1953) (data concerning the European part of the former USSR), 54 of 56 types of natural broad-leaved forest types are able to transform into birch forests. While 45 forest types could be transform into pine ones, and 43 types into aspen forests. Lime, mountain elm, and maple forests appear much more rarely. The frequency of secondary forest formation instead of polydominant broad-leaved forests in connection to the type of external influence are given in the Table 4.

The Table 4 shows that the prevalence of birch forests is obviously not accidental, for practically all types of forest using promote birch spreading. Therefore, secondary birch forests distinguish from each other not only due to causes of geographical character.



Table 4.

Number of forest types that occur into secondary stands due to different landusing (data from Vorob'ev, 1953).

	Haying	Tillage	Bur- ning	Clear cutting	Selective cutting
Birch forest	3	23	30	39	
Pine forest		15	19	5	3
Aspen forest			1	29	
Spruce forest					23
Oak forest				7	15
Lime forest				10	7

Unlike secondary aspen forests appear mainly after cuttings. As the sequence of that they are more homogeneous in their origin (stump sprouts). Most birch forests as well as pine ones connected with agrosylvopastoral impacts or crown fires. So they sharply differ from postcutting birch forests by species composition of all synusia especially herbaceous one.

It is convenient to recognize the degree of anthropogenic digression caused by various ways of forest exploitation in the past (Rudzskii, 1899) according to two large groups of methods.

1) Method of floristic comparison. Here the completeness of species lists and diversity of species composition in communities (real flora) is compared with potential flora; i.e., ecological-floristic description of non disturbed forests.

2) Ontogenetic method. Here the evaluation of real ontogenetic population structure of woody plants is made regarding ontogenetic spectra's completeness.

Ontogenetic characteristics are more sensitive to the disturbances in comparison with ecological-floristic ones. They are less inertial:

their disturbances are more rapidly revealed as well as more rapidly "wiped out". Even slight change such as selective cuttings causes considerable changes of ontogenetic structure of tree synusium. Their results are especially evident in the cases of high frequency of selective cuttings. In these cases the replacement of the community dominants occurs not only in lower layers, but in main upper canopy as well. In all associations and in different ecotopes within an association, populations of stress-tolerant species forming abundant stump sprouts begin to prevail in tree synusium. The ruderal species (except hornbeam that can form traumatic sprouts in all ontogenetic stages) almost completely disappear. Such redistribution of species of tree synusium throughout the area of broad-leaved forests can be illustrated with the help of three examples. Such forests belong to the associations geographically remote from each other (Fig. 8).

In the east of the area where species composition of tree synusium is impoverished, oak is ousted in the upper layer by lime and Norway maple and completely disappears from the second layer (Fig. 8a). Here the selective cuttings performed for a long time caused an absolute absence of regrowth of the main edificator in spite of the presence of still fruiting trees of parental generation. In the southern part of the broad-leaved forest area, oak populations ousting occur due to hedge maple. Absence of maple in the upper layer is explained only by the fact that its individuals even in their oldest age do not reach the size of oak or ash (Fig. 8b).

In the western part of the broad-leaved forest, the upper layer is the most diverse. Here, the oak participation is strongly reduced due to the influence of more shade-tolerant competitive species (ash, beech). Hornbeam populations prevail in the second and lower layers (Fig. 8c). Strong sprout reproduction of this species in all ontogenetic stages suppresses the young regrowth of all competitive species, but oak regrowth is the one to suffer most.

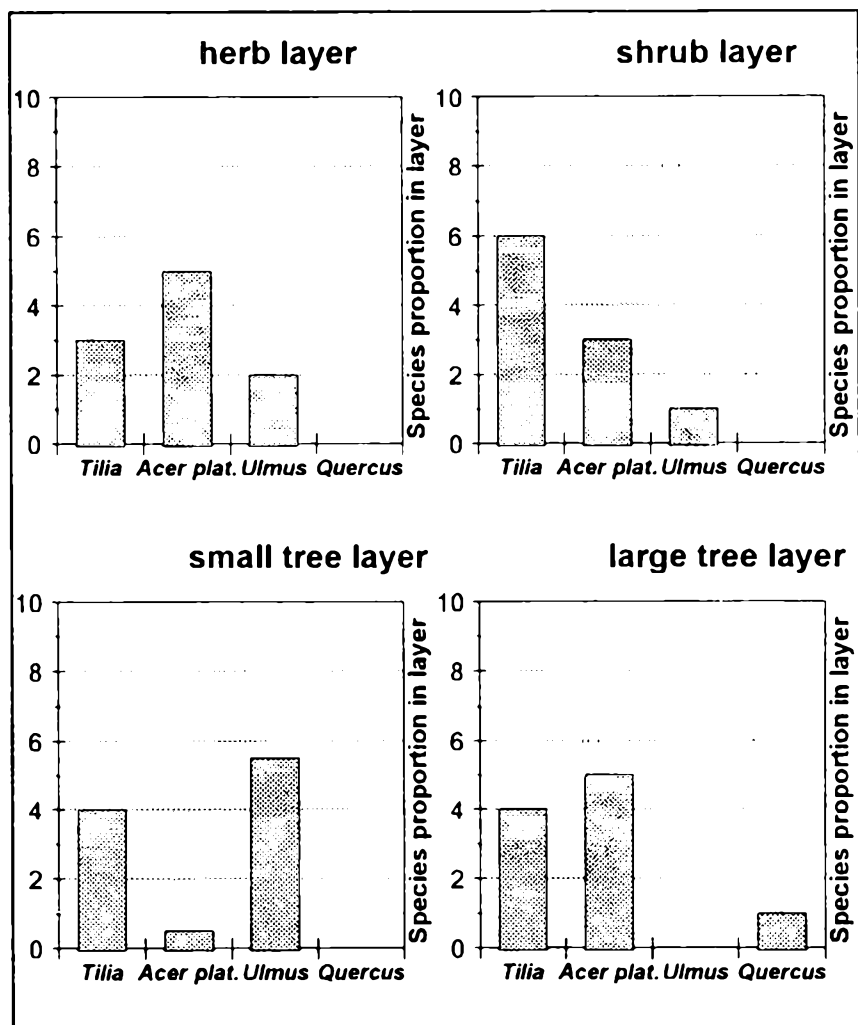


Fig. 8a. Layer distribution of tree species in *Tilietum uralense*.

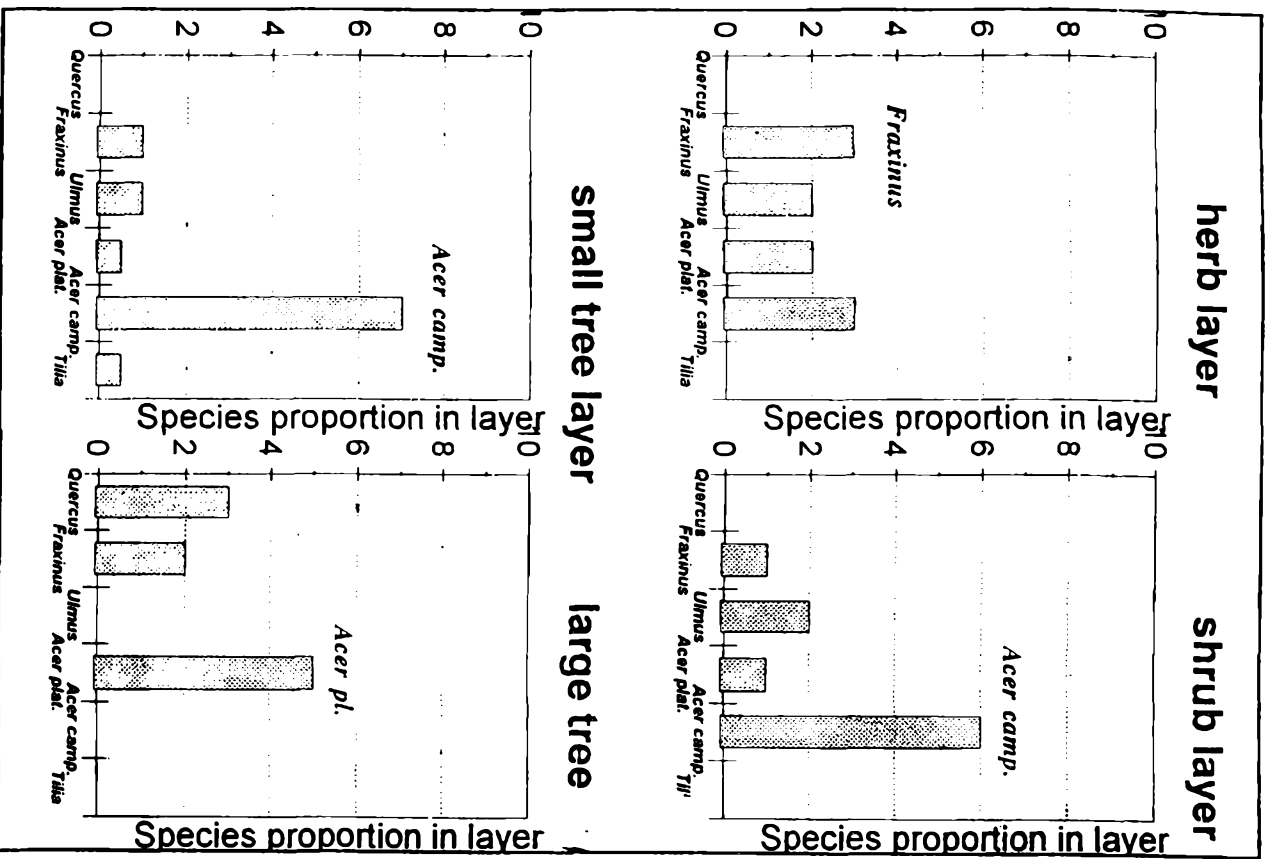


Fig 8b Layer distribution of tree species in *Mixto-Nemoraetum tanaiticum*.

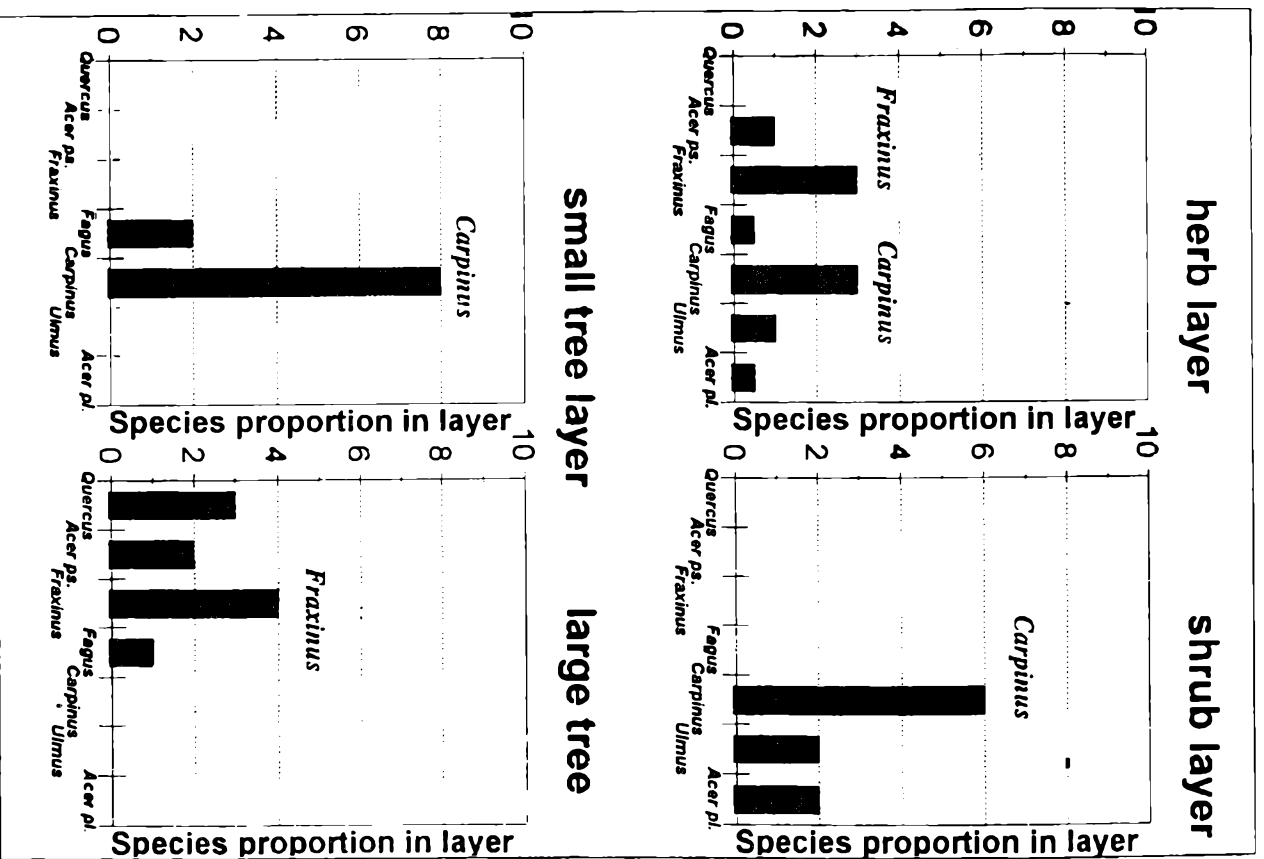


Fig. 8c. Layer distribution of tree species in *Carpineto-Nemorenum ucrainicum*.

Weakening of the role of competitive species begins with the disappearing of the youngest ontogenetic groups (immature and virginile). In the most cases young generative competitor's trees are depressed by adult ruderal and tolerant trees due to the light competition. The incompleteness of oak and ash populations becomes stronger if the vegetative offspring of tolerant species increases. Their ontogenetic spectra is becoming fragmentary. In such spectra, only the youngest and the oldest ontogenetic groups can be found. Restoration of completeness of fragmentary populations even in favorable situations will require now many dozen years, as oak or ash trees need about one hundred years to reach young generative state. On the contrary, slight disturbances (i.e., selective cuttings of large periodicity and low intensity) are unlike strong influences in that they are not always accompanied by the loss of ontogenetic completeness. In some communities, tolerant species retain stable dynamic equilibrium of generations, while community as a whole possesses age-heterogeneous mosaic structure. Unfortunately, there are no absolutely age-heterogeneous oak populations in the modern forests. As to the other deciduous tree species, their ontogenetic spectra are much more close to the stable (complete) one; these spectra are shown in Fig. 9.

Within the whole area of East European broad-leaved forests, the state of oak populations happened to be the worst among main representatives of tree synusium. They often do not include immature and virginile regrowth even in the presence of considerable number of fruiting trees of different ages. Relatively mild influence of selective cuttings changes the species ratio in tree synusium and, to a lesser extent, tells on the species of other synusia. However, the transformations (described below) can be observed in them as well. Strong disturbances such as clear cuttings, ploughing, fires, and haying cause the death of adult trees and regrowth of all species.

Moreover, species composition of subordinate synusia changes sharply as a rule. Afforestation of ploughed fields, hayfields, and cuttings is accompanied by appearance and prevalence of meadow, forest-edge, and ruderal species. If such disturbances embrace large area and/or are too often repeated, many forest nemoral species cannot settle again on disturbed territory. Essential transformations of

broad-leaved forests on the territory now covered with forest, are revealed with the help of floristic method. Detailed statistics of forest distribution on categories, species composition, and age of dominant tree species are to be found in the materials of "The USSR forest inventory". It should be also noted here that the majority of forest landscapes is represented by age-homogenous stands with poor flora in all synusia. Besides broad-leaved communities, considerable area within the broad-leaved forest zone is occupied by pine and spruce forests. With rare exceptions, they have formed after silvicultures.

Mixed stands, in some cases, can be considered as the remnants of natural variants (according to other vegetation classifications they may be treated as forest types), depending on ecotope. Review on their composition peculiarities and geographical distribution is to be found in voluminous works of V.P.Vorob'ev (1953) and S.F.Kurnayev (1980). Already now anthropogenic transformations of landscapes in the broad-leaved forest zone are taking place in enormous scale. Further use of modern schemes of forest exploitation would unlikely change the typological diversity of secondary communities. Changes would affect on the age structure of forests but their floristic composition would not change considerably. The nature reserves established on intensively exploited lands play rather specific role in the general picture of recent forest dynamics. Secondary stands excluded from economic exploitation begin to restore natural (i.e., age-heterogeneous) ontogenetic structure of tree populations. However, rate and direction of secondary successions depend largely on economic prehistory of forests and on the recent structure of landscapes.

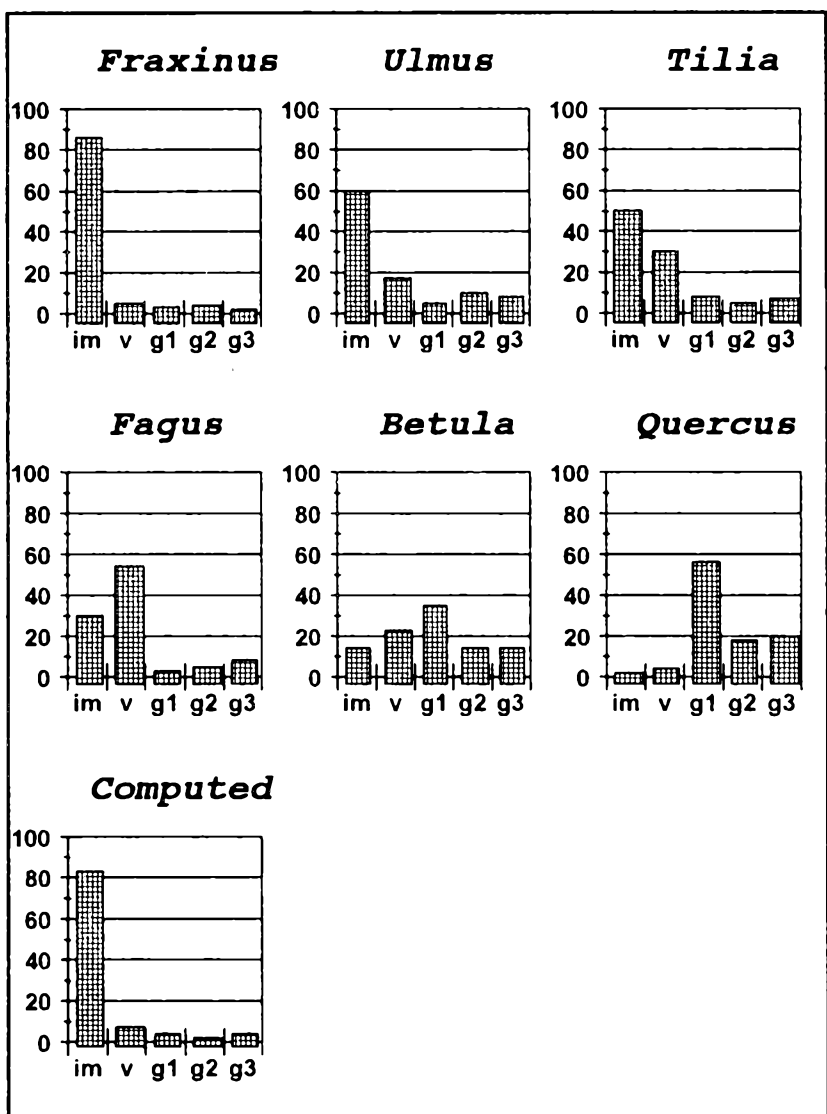


Fig. 9. Ontogenetic spectra of tree populations in the best present forests.



Ontogenetic and floristic laws of forest transformations and restoration after different kinds of exploitation may be easily observed in the "Kaluga zaseki" nature reservation. Here one may find areas of various fates and history. There are slightly disturbed broad-leaved forests (fragments of former abatis line ("zaseki")) (Ponomarenko *et al.*, 1992). Areas that had suffered cuttings of different type and size, afforested agricultural lands, and silvicultures of different age. In this reservation, forests are growing on soils of either heavy or light mechanical composition and with different degrees of fertility. This soil diversity also increases the number of ecosystem variants looking like the *Tilieto-Nemoretum okense* association. The wide spectrum of anthropogenic transformations of broad-leaved forests in European Russia can be traced on the protected territory (about 5000 ha).

Successional processes in the reservation may be treated as the expressions of the main laws inherent to the vegetation cover of forest landscapes within the broad-leaved forest zone. The diversity of habitats, secondary forests and disturbance types is summarized in Table 5. We show detailed description of disturbed forests by twelve variants of communities from "Kaluzskiye zaseky" reserve. The least disturbed fragment of age-heterogeneous broad-leaved forest is characterized by age completeness of populations for the majority of tree species. Their age spectra are shown in Fig. 10. This fragment corresponds to variant (1), e.g., broad-leaved forests suffering rather small and rare cuttings.

The occurrence of a large number of tree species (11 species in a single community) is ensured by seed and vegetative reproduction in most of their populations. However, the main edificator species (*Quercus robur* L.) performs exclusively seed reproduction while *Populus tremula* L. population persists only by vegetative way (root sprouts).

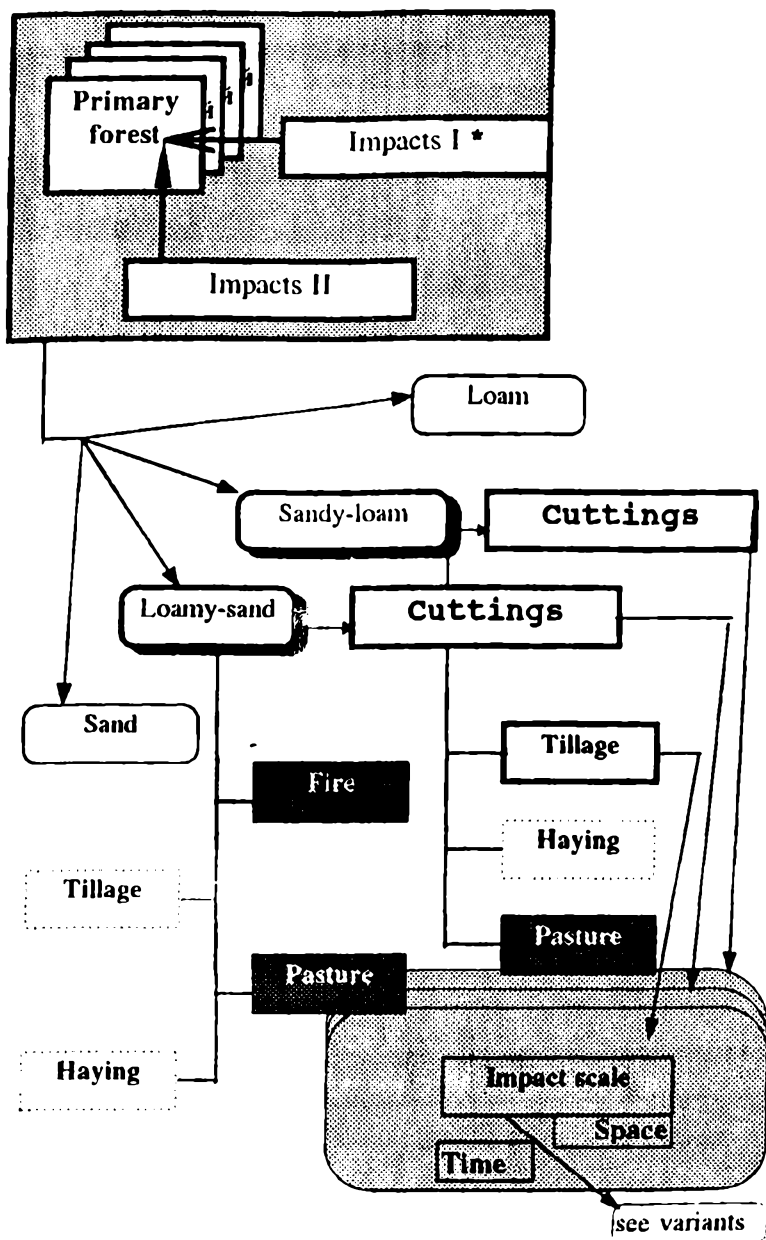


Table 5. Types of disturbances, habitats and secondary forests diversity

\* Impacts I -- disturbance without soil change; impacts II -- disturbance with soil change.

Continuing of Table 5 (land-use causes and diversity of variants)

	Postcutting community		Postcutting community	
	sandy-loam		loamy-sand	
	Small scale of cutting ***	Large scale of cutting	Small scale of cutting	Large scale of cutting
Large rotation age **	Unevenage broad-leaved forest (variant 1)	Aspen-broad-leaved forest (variant 3)	Unevenage broad-leaved forest (variant 1)	Aspen-broad-leaved forest (variant 3)
Short rotation age	Broad-leaved forest withuot oak (variant 2)	Aspen or birch forest withuot oak (variant 4)	Broad-leaved forest withuot oak (variant 2)	Aspen or birch forest withuot oak (variant 4)

**\*\* Large rotation age:** *the time between sequent impacts is more than half of key species ontogenesis; short rotation age: the time between sequent impacts is less than half of key species ontogenesis.*

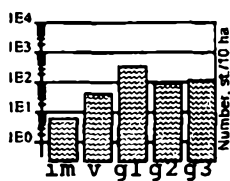
**\*\*\* Small scale:** *the size of created mosaic is smaller than the size of the largest elements of the primery forest mosaic; large scale: the size of created mosaic is bigger than the size of the largest elements of the primery forest mosaic.*

Continuing of Table 5 (land-use causes and diversity of variants)

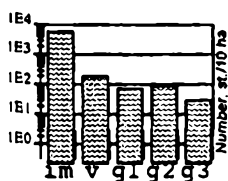
	<b>Secondary forests on oldfields</b>		<b>Secondary forests on oldfields</b>	
	<b>Sandy-loam</b>		<b>Loamy sand</b>	
	Small field	Large field	Small field	Large field
<b>Large rotation age</b>	Birch-broad-leaved forests (variant 5)	Birch forests with oak (variant 7)	Mixed pine forests (variant 9)	Pine forests (variant 11)
<b>Short rotation age</b>				

	<b>Posthayfield communities</b>		<b>Posthayfield communities</b>	
	<b>Sandy-loam</b>		<b>Loamy sand</b>	
	Small field	Large field	Small field	Large field
<b>Large rotation age</b>				
<b>Short rotation age</b>		Maedows with small trees (variant 8)	Birch forests (variant 10)	Meadows (variant 12)

*Quercus robur*



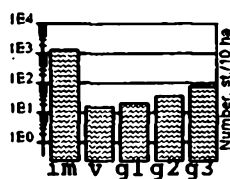
*Fraxinus excelsior*



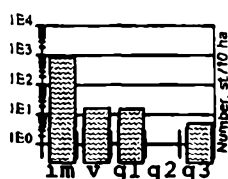
*Tilia cordata*



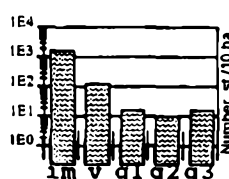
*Acer platanoides*



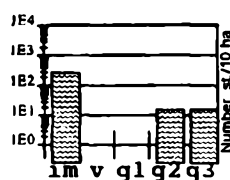
*Acer campestre*



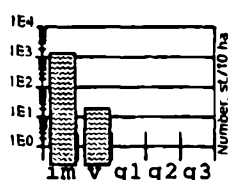
*Ulmus scabra*



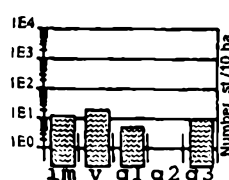
*Betula verrucosa*



*Padus racemosa*



*Malus silvestris*



*Sorbus aucuparia*

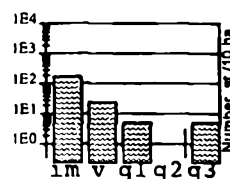


Fig. 10a. Ontogenetic structure of oak old-growth in "Kaluzskiye zaseky" reserve (seeded generations).

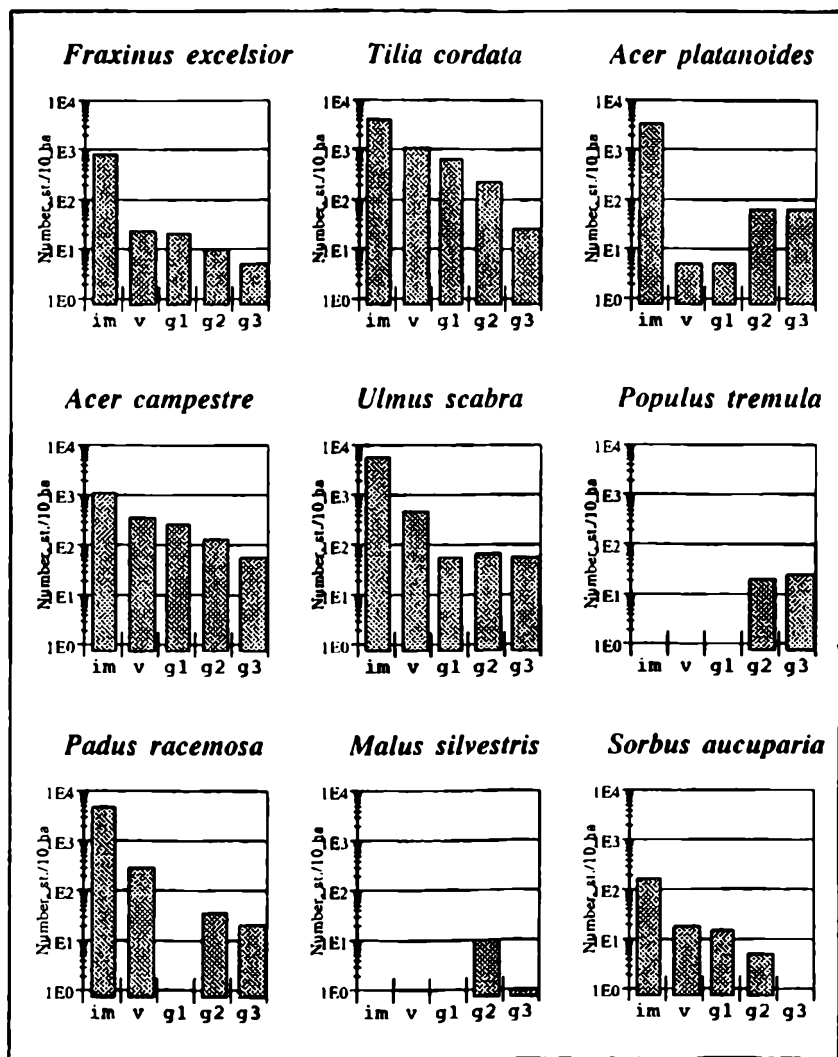


Fig. 10b. Ontogenetic structure of oak old-growth in "Kaluzskiye zaseky" reserve (vegetative generations).

Conservation of a such fragment will not cause changes in species composition of tree synusium, at least in the nearest future,

nevertheless certain redistribution of species percentage in different layers is possible. In tree (upper) layer, due to prevalence of old and middle-aged birch and aspen trees, these species decrease percentage. At the same time, the dying off the old generation of birch and aspen can improve the conditions of oak reproduction. As the sequence, oak would be represented by more abundant young generation within lower layers (those of herbs and shrubs). Shrub synusium (7 species) in age-heterogeneous broad-leaved community is represented factually by all shrub species inhabiting in the given region (*Corylus avellana* L., *Euonymus europaea* L., *E. verrucosa* Scop., *Lonicera xylosteum* L., *Viburnum opulus* L., *Ribes nigrum* L., *Frangula alnus* Mill.). These species are highly constant. *Corylus avellana* L. (a species of competitive strategy) prevails among them, significantly worsen the conditions of reproduction for light-demanding tree species. Herb synusia (both tall herbs and ephemeroids) include a set of typical species of broad-leaved forests. More than a half of species list is represented by species of nemoral ecological-coenotic group. Among tall herbage, the following species have the highest constancy in such forests: *Aegopodium podagraria* L., *Dryopteris filix-mas* (L.) Schott, *Galeobdolon luteum* Huds., *Urtica dioica* L., *Pulmonaria obscura* Dumort., *Asarum europaeum* L., *Glechoma hirsuta* L., *Viola mirabilis* L., *Stellaria holostea* L., *Geum urbanum* L., *Milium effusum* L., *Carex sylvatica* Huds., *Polygonatum multiflorum* (L.) All., *Mercurialis perennis* L., *Galium odoratum* (L.) Scop. Among ephemeroids *Allium ursinum* L., *Corydalis cava*, *C. marschalliana*, *C. solida* (L.) Clairv., *Anemone ranunculoides* L., *Gagea lutea* (L.) Ker.-Gawl., *G. minima* (L.) Ker.-Gawl. and *Ficaria verna* Huds. prevail. It should be noted that both high species diversity and high abundance and constancy of ephemeroids in the early spring sward are observed in the ephemeroid synusium.

Second variant (2), i.e., age-heterogeneous broad-leaved forests without oak does not occurs in the territory of the reservation. According to our studies in other regions (East European broad-leaved forests, 1994) we can say, such forests are very alike variant (1). However, they have, to some extent, depleted species composition of tree synusium.

Variant (3) is the most widespread throughout the whole territory. It is represented by age-homogenous stands from 40 to 120 years old which have appeared after clear cuttings of old growth stands in the forest tract. Species diversity remains unchanged in the composition of the tree synusium (the same 11 tree species as in the variant (1)). Percentage of species with ruderal strategy does not change either (about 30% of the number of tree species). The greatest difference between this variant and age-heterogeneous forest lies in ontogenetic structure of tree populations and in degree of species dominance. In cut-down stands, only 4 - 5 species form the framework of canopy in all layers; the resting ones are merely present as auxiliary so they are not shown on the diagram (Fig. 11). Shrub synusium also retains species diversity, but projective coverage of shrub layer is usually not very high. Herb synusia factually do not differ from those in age-heterogeneous forest: 56% of the overall species diversity (100 species) are represented here by species of nemoral group. Comparison of old-growth communities growing on clayey and loamy-sand substrata shows that their species composition slightly reacts to substratum differences. Coefficient of sample similarity of T.Sorensen ( $C_s = 2j/(a + b)$ ) for two spatially adjacent plots on loam and loamy-sand was 0.67; while in the case of two spatially remote plots on loamy-sand soil it was 0.64. Comparison of lists of species with high constancy (23 species for three plots) shows higher similarity for spatially close plots. 16 of 17 forest species growing on loam have been also recorded for neighboring plot on loamy-sand. Only 8 of them are found on the plot on loamy-sand, but at a distance of several kilometers. The total number of species on each plot varies from 100 to 136.

Variant (4) is represented by plots that have appeared after multiple clear cuttings of stands that is not reached maturity age. Species composition of tree synusium is somewhat poorer (7 species) than that in previous variants, but ontogenetic structure of tree populations is more favorable for complete populations to develop (Fig. 12). As in the previous cases, population recovery occurs both by seeds (oak, maple, birch) and by vegetative sprouts (lime, aspen, goat willow). For this variant, it can be mentioned that, in the case of oak, vegetative reproduction is observed together with seed reproduction.



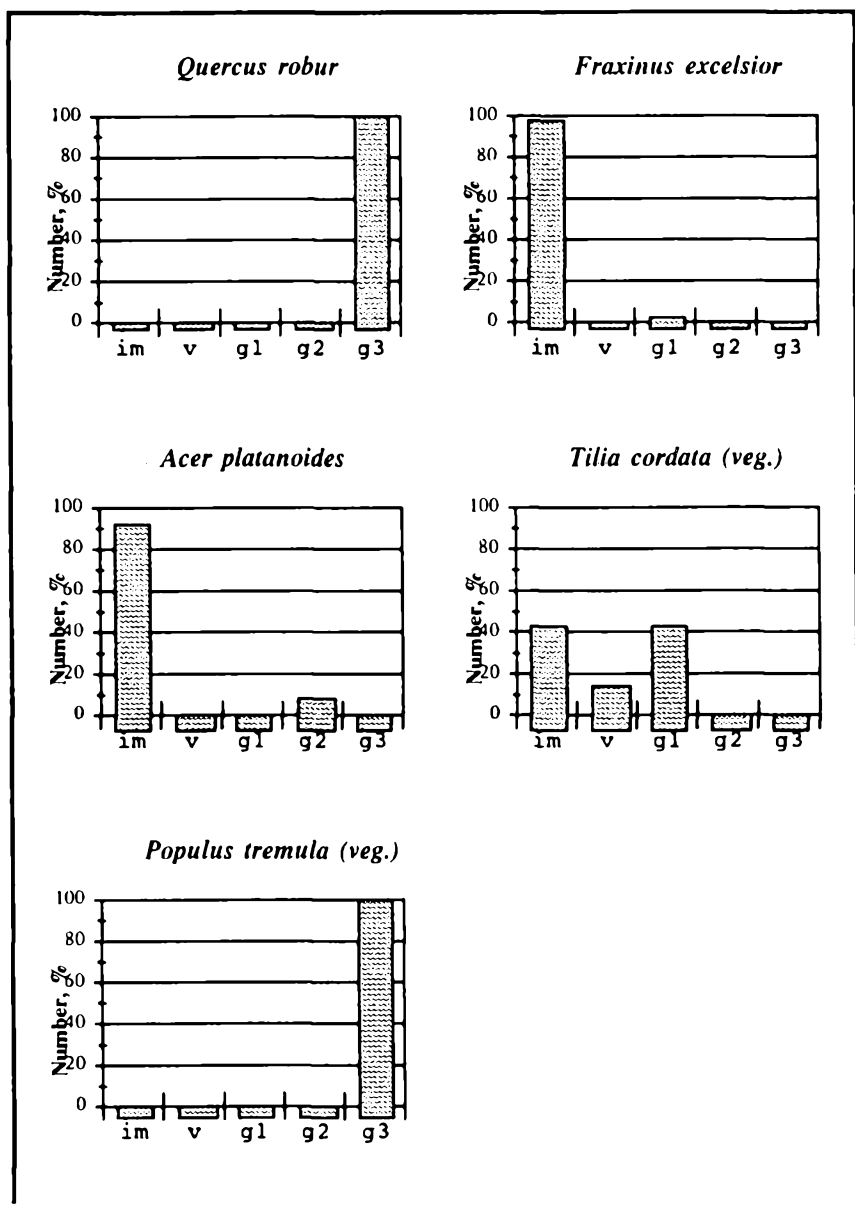


Fig. 11. Ontogenetic structure tree population in secondary forests (variant 3).

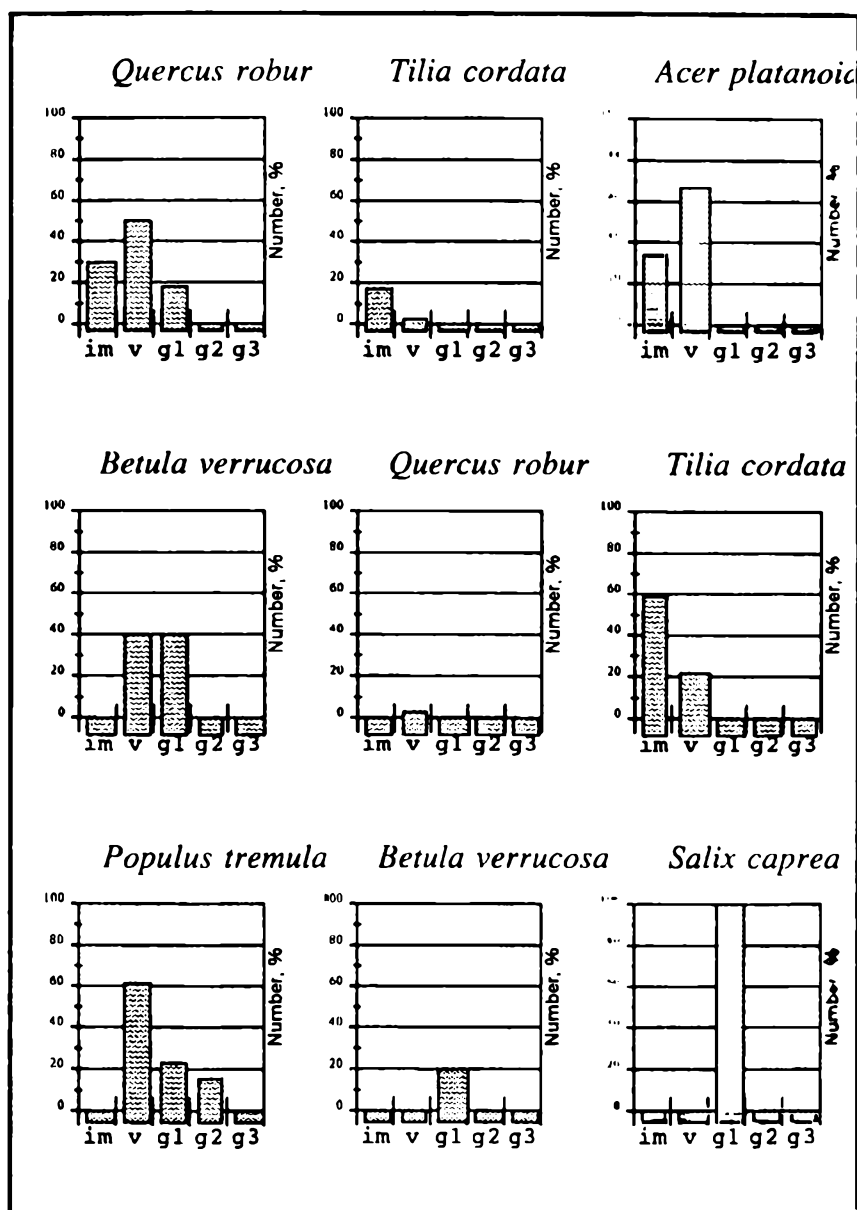


Fig. 12. Ontogenetic structure tree populations in coppices (variant 4).

Shrub synusium is considerably poorer than one in the age-heterogeneous forest, but species composition of the whole community is not poorer (total of 96 species). The synusium of tall herbs consists of half of species of nemoral group, as well as of species of meadow, forest-edge, and boreal groups. At the same time, nemoral (*Galeobdolon luteum* Huds., *Pulmonaria obscura* Dumort., *Viola mirabilis* L.), and meadow, and forest-edge species (*Geranium sylvaticum* L., *Glechoma hederacea* L., *Veronica chamaedrys* L., *Hypericum maculatum* Crantz.) are characterized by high constancy.

Ephemeroids have high constancy in spring sward, though their abundance is somewhat lower than in the case of old-growth forests. However, disappearance of the species with the highest demand in soil richness (*Corydalis cava* and *C. marschalliana*), occurring almost everywhere can be noted.

The next group of variants strongly differs from those considered above. All of them have appeared on the places of agrosylvopastoral system, and tree layer (if present) is formed by individuals of the first generation. Ontogenetic spectra of tree species are similar to those of variant (4), but with the only difference that there are not factually trees appeared by vegetative propagation (till the first cutting). Difference of loamy and sandy-loam substrata is not important for all synusia in habitats with undisturbed soil.

Variant (5) appears on former ploughed fields and hayfields up to 50 ha in size, neighbor to the forest communities and, therefore, rarely experiencing the deficiency in seeds of typical forest species. The tree layer of such communities is not always dense, but lists of tree species are practically complete (about 11 species), and oak and lime have high constancy among them. Other deciduous species (mountain elm, maples) are considerably more rare, ash is practically absent, in spite of relatively favorable conditions of growing. The most constant species are birch, aspen, goat willow (the percentage of species with ruderal strategy in tree layer reaches 65%). Shrub synusium is represented by all common species. The synusium of tall herbs is not seriously depleted in these forests. The group of nemoral species takes 37.8%. The synusium of ephemeroids practically completely disappears. In some cases, wild flower or pilewort can be met, but with low

abundance. The reduction of nemoral flora and disappearance of ephemeroids are compensated by the appearance of many meadow and forest-edge species and weeds. Species composition of communities is somewhat richer (up to 140 species) than in age-heterogeneous forest.

Variant (7) differs from the previous one by considerable (about 10 km) remoteness of these communities from large tracts of broad-leaved forests. Small fragments of forest vegetation surviving during the period of agricultural exploitation ensure a flow of seeds or vegetative diaspores, and, therefore, species composition of tree and shrub synusia is sufficiently complete. Unlike variant (5), only aspen has here high constancy; oak, birch, and goat willow are met somewhat more rarely. Deciduous species typical to age-heterogeneous forest become rare, while ash being completely absent. The synusium of tall herbs is similar to that of variant (5), but it is rather poorer. Ephemeroids are practically completely absent.

Variant (8) represents open meadow communities in the place of former ploughed fields or hayfields. Isolated trees never form a canopy (even a sparse one), though almost all species are present (but with very low constancy). Similar situations are observed in shrub synusium. Sharp decrease in the number of species of nemoral group is compensated in plenty by meadow and ruderal herbs. Total list of species numbers 282 species.

Variants (9) and (10) are analogous in their origin to variants (5) and (6), but they are located on soils of light composition (sands and loamy sands). During the of agrosylvopastoral impact, soil depletion reaches such a degree that the majority of deciduous species cannot grow on these sites. Oak, notable for the highest tolerance to soil richness and acidity, is an exception. Spindle-trees (*Euonymus spp.*) disappear from shrub synusium, but willows appear instead. The group of nemoral species is reduced to 18 - 20% of the total number of herb species. Species of meadow-steppe flora possessing more xerophytic ecology start playing a greater part in species composition, and species list of the whole communities numbers 120 - 140 species.

Variant (11) represents large fragments of pine forests in the degraded fields on sands (humus horizon of 2 - 3 cm is laid under by

thick red-colored sand layer). Only two species namely *Betula pendula* Roth. and *Pinus sylvestris* L. are present in tree synusium. Occasionally spruce and aspen may be occurred. Shrub synusium is absent, too. The total species list numbers 50 species, nemoral group making only 13%.

The diversity of variants of secondary communities presented in the scheme (Table 5) does not show a linear trend of degradation of broad-leaved forests. Thus, the first four variants, in spite of ontogenetic differences and, correspondingly, different dynamic of reorganizations in tree and shrub layers, are very alike as far as total species composition is concerned. All of them can be considered as the initial stage of degradation. The degradation result in maximal species losses in the synusium of tall herbs due to the loss of light-demanding species because of extremely dense forest canopy. The estimation of species composition of these communities according to D.N.Tsyganov's (1983) scales of light demand show the ways of loses. The species of forest-edge and light flora, whose persistence in forests was earlier maintained on large glades by large ungulates. They are absent in the communities under consideration. Variants (5), (7), and, probably, (6) make a group of communities demonstrating the second stage of degradation. Not only ontogenetic completeness of tree populations is disturbed here, but replacement of species of nemoral group by meadow and forest-edge ones occurs also. Restoration of age-heterogeneous structure in tree synusium is not necessarily followed by restoration of previously lost of herb species belonging to the nemoral group. Variants (9) and (10) can be considered as even deeper level of degradation, as losses of nemoral species in all synusia are considerable. Such a deterioration of state is caused not so much by the specific methods of land-use, but moreover by the peculiarities of the habitats themselves. More rapid degradation of light soils also causes more serious degradation of forest.

Variant (11) is the last link in the chain of communities growing on light soils, but it will never be such a link in the chain of communities on clayey substrata. Variant (12) expresses complete loss of forest vegetation; it is represented by upland meadows on former woody lands.

The performed analysis of degradation of broad-leaved forests touched on two aspects of human influence on forest ecosystems (spatial and temporal ones). However, just one more aspect, happened to have stayed beyond the analysis, namely the intensity of community transformation. To some extent, the problems of influence intensity are touched upon when dividing secondary variants into groups namely with or without soil cover disturbance. Such a differentiation has to do with very strong transformations, but disturbance intensity is often milder character and it is manifested in different levels of stand exploitation. Selective cutting of adult or young trees also significantly changes the dynamics of populations and of the whole community. To retrace degradation trends connected with selective forestry; the materials of long temporal series together with data on the quantity of the cut-down trees are required. There are no reliable documentary sources with such information to be found; thus, simulation happens to be an indispensable instrument.

An experiment with a model of multispecies' stands demonstrates the trends of change of quantitative participation for species with different biology and ecology at different levels of timber withdrawal and frequency of cuttings (Table 6).

Table 6.

Simulation of the disturbance regimes for two species stand

Selection , %	Years between impacts			
	10	50	100	200
10	56*/14**	75/10	75/12	83/6
25	28/21	66/16	75/12	84/5
50	7/14	55/30	64/27	79/9
75	1/4	33/53	40/54	71/13
100	0/0	5/90	10/88	62/28

\* Abundance (total crown area) of oak trees. \*\* Abundance of birch trees.

Two species (oak and birch), four variants of cutting periodicity, and five levels of cutting intensity were presented in simulation experiment. All calculated values are obtained for stationary regimes of the model's behavior. The table shows that prevalence of birch in tree layer is achieved in the case of high intensity of cuttings, i.e., cuttings occurring not less than once hundred years. The greater in the period between cuttings, the less noticeable is the prevalence of birch at all intensity levels. In the broad-leaved forest zone, cutting rotation of 50 - 60 years (commonly used in Russian forestry) has caused non-accidental prevalence of birch forests with poor presence of oak. A model with a 50-year period of clear cutting gives a similar ratio of oak and birch. The possibilities of the model considerably increase with the proper provision with field data on the ecology and biology of tree species. So this model may be used for forecasts of the forest development with diverse species composition and in different soil-climatic conditions.

The corollaries made by model calculations are as follows: theoretically, populations of *Quercus robur* L. could persist throughout many centuries in the composition of birch forests which have undergone cuttings; but this is true only in condition of full provision of the whole community area with viable seeds. In real forests, oak regrowth is often not sufficient for self-maintenance of its coenopopulations. That is why many forestry specialists try to work out technologies ensuring successful reproduction of this economically valuable species. Nowadays, the problem becomes still more complicated since it is necessary not only to preserve a certain species, but to provide conditions for self-maintenance of the whole complex of forest plants as well.

One of the ways of compromise solving the tasks of economy and nature protection is the technology of group-selective cuttings aimed the imitation of natural mosaic structure of age-heterogeneous forests (Methods recommendations..., 1989). These group-selective cuttings with subsequent planting of oak have given the best results in the age-homogenous stands of the *Carpineto-Nemoretum ucrainicum* association (the Kanev nature reservation, Ukraine) (Korotkov, 1990). The same result was obtained in secondary age-homogenous birch forests

previously replacing the communities of the *Tilieto-Nemoretum okense* association (the Bogdanovo park forest, the Moscow region). In birch forests, abundance of tree and shrub regrowth has increased more than 10 times during five years after cutting on the plots from 1200 to 2000 m<sup>2</sup>. At present time, oak prevails among the young generation (9800 individuals per ha). The height of six-year-old oak trees is from 100 to 170 cm, the increase in height being from 38 to 47 cm per year. Planting of oak trees was done by separate biogroups, each biogroup covering the area from 40 to 750 m<sup>2</sup>; in five years, the crowns in the biogroups closed up, and there was no need in annual weeding.

According to the technology proposed, cutting does not diminish the expenses on the following care of the regrowth; at the same time, it creates favorable conditions for the restoration of plant populations in all synusia. The number of species sharply increases in the composition of depleted age-homogenous stands (in birch forests, from 35 - 40 to 50 - 60 species per 100 m<sup>2</sup>). The increase of species richness occurs mainly due to natural species of light habitats.

## CONCLUSIONS

As our historical analysis has shown the broad-leaved forests were the main vegetation type in Eastern Europe. The forest zone transformation in the second half of Holocene is the result of anthropogenic influence or even almost complete destruction. Due to the human activities the south part of broad-leaved forest's zone was transformed into steppe-like valley with small islands of forest-like vegetation. These forests cover only 5--10 % of this territory, and in some regions even less. Most of these forest "islands" have in the recent time long ecotone-like borderlines so their structure and taxonomic diversity depend upon the neighboring areas lacking forests. In the northern part of the broad-leaved forests zone the taxonomic structure of tree layer is nowadays highly transformed; trees with reactive strategy are here the dominants. However, the forests cover



here up to the 50% of the area and in some regions even more. The main body of recent forests is large continuous stands that are factually independent of human agricultural activity in both their structure and dynamics.

Our detailed analysis of such broad-leaved woods shows that:

1) The high taxonomic diversity in tree and shrub synusia is well preserved in the areas which have suffered only rare and slight cuttings. These were mostly state (i.e., not private) forests that not used for agriculture. On the contrary, forests which were cut many times as well as forests grown on the areas of agricultural fields have very poor tree synusia. Here, in most cases only three or four dominants occur namely birch, aspen, and pine.

2) Age structure of tree populations is transformed in all forest variant. However, in slightly disturbed forests the tolerant species populations have as a rule the complete ontogenetic spectra (i.e., they are age-heterogeneous). The populations of both competitive and ruderal species have incomplete ontogenetic spectra, only one of the age stages usually prevailing. In the forests that have undergone strong disturbance (cuttings and/or ploughing) all the species represent the incompleteness of population age spectra.

3) The floristic composition of herbaceous synusia in slightly disturbed forests are changed towards the prevalence of shade-tolerant species of the nemoral group. Most of light-demanding species persist only in forest edges and in meadows. Only in this forest variant one can observe the ephemeroid synusium represented by maximal species number. In forests replacing the former agricultural areas the light-demanding herbaceous species are mostly widespread; ruderal species also occur here. Ephemeroid synusium is absent in these forests as a rule.

The law of forest structure and dynamics revealed for great stands permit to recognize the main trends of their possible changes. Once the protective regime is established, the restoration of complete ontogenetic structure of populations is the most rapid for tolerant species. As a sequence of that, the flora becomes poorer because of the loss of light-demanding species within all the synusia. In the tree synusium this trend expresses as a regression of oak populations. All

the modern methods of forest exploitation also do not allow self-maintenance populations for the most species. The most of sufferers are the species incapable to reproduce vegetatively as well as species with feeble seed dispersion, i.e., small radii of reproductive activity. The new alternative technology of forest exploitation is proposed using the imitation of small-scale mosaics inherent to age-heterogeneous forests.

In the south regions of broad leaved forests zone with relatively small areas covered by forests the floristic and demographic degradation of "island" forest communities are large. The most necessary way of preservation activity would be the preservation of all the areas with native woody flora. These "islands" have to be used further for the expansion of tree species populations.

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