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**CURRENT STATE OF CONIFEROUS-
BROAD-LEAVED FORESTS
IN RUSSIA AND UKRAINE:
historical development, biodiversity, dynamic**

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The article contains several sections. The first one is devoted to classifying forests into subzones and geographical variants. Two subzones marked out traditionally: a subzone of coniferous-broad-leaved forests and a subzone of south taiga. The subzones are distinguished by positions of broad-leaved trees and nemoral herb species. The whole zone contains 6 geographical variants that differ one another by the species' richness of tree synusia, the dominant tree species, vertical and horizontal structure of communities.

The second section concerns the syntaxonomy of Russian mixed forests, and a floristic composition of intact old-growth forests. The complete syntaxonomy is absent, because different sources were used just as a previous prodromus of syntaxa.

The floristic composition and structure of mixed forests are very heterogeneous. Nevertheless, the group of nemoral species is represented well in all the variants, and they are relatively constant there. The proportion of boreal species increases from south to north and from west to east, but this group is poorly represented in south variants.

The third section contains a brief review of Holocene history of mixed forests. The northern border of broad-leaved forests shifted to the south on 300-700 kilometers. There are two of causes of this phenomenon: climatic changes, and land-use. The last one includes shifting cultivation, cattle grazing, planting of pine and spruce on clear-cuttings and oldfields.

The fourth section describes structure and natural dynamics of old-growth forests. The dynamics of mixed forests as whole depends simultaneously on: the longevity of trees; the light condition for seedlings; the structure of herb layer; and the quantity of decay wood.

The last section describes the secondary successions. We show the significance of two ways of forest transformations. The first one is shifting -- cultivation; the second -- selection and clear cuttings.

INTRODUCTION

Modern forests in any geographical zone possess rather complicated habitus and structure in which the following aspects are picked up:

- 1) taxonomic composition and communities structure inherent to preagricultural biota;
- 2) features and ways of land-use in the past;
- 3) present-day industrial influences (East-European broad-leaved forests, 1994; Hengeveld, 1994).

In order to maintain the sufficient biodiversity level as well as to organize the sustainable land-use it is necessary to evaluate the contribution of every factor mentioned above in the structure and dynamics of modern forests in concrete geographical regions. To do this, it proves to be necessary to solve the following problems:

- 1) the problem of reconstruction of taxonomic composition, structure and dynamic traits inherent to the forests of pre-agricultural type;
- 2) the problems of analysis of methods and technological means of land use which have formed the recent plant communities;
- 3) the last problem is to reveal the directions and rates of successional dynamics in communities which are transferred from the human usage regime to the reserve one.

The present work is the first attempt to solve all the problems mentioned above for the vegetation of coniferous-broad-leaved forests zone in the European part of the former USSR. The work is supported by International Science Foundation (grant N.1 No.300), by State

DISTRIBUTION OF CONIFEROUS-BROAD-LEAVED FORESTS

Forests with the presence of both broad-leaved and coniferous species may be subdivided into two subzones. Namely, there is the subzone of mixed coniferous-broad-leaved forests in the strict sense of the word, and other is the subzone of southern taiga. In the first subzone, broad-leaved and coniferous tree species occupy similar positions. Both broad-leaved and coniferous species reach the first layer here, while, in the lower layers, the community basis (in relation to numbers and biomass) is formed by nemoral herb and tall herb species. In the second subzone, the position of broad-leaved tree species is a subordinate one, and their number decreases considerably. They reach only the second layer or exist merely in the form of understory. The example of it can be *Tilia cordata Mill.* in the Central Ural (Vegetation cover of the USSR, 1956; Vegetation of the European part of the USSR, 1980).

The comparison of the areas of tree species (Areas of trees..., 1977, 1986) and zonal maps of vegetation cover shows that the northern boundary of mixed forests coincides with the northern borderline of *Tilia cordata Mill.* area for a great length while the southern boundary corresponds to the southern borderline of *Picea abies Karst.* and *P. obovata Ledeb.* areas (Tsinzerling, 1931; Yakovlev, Voronova, 1959; Bogachev, 1964). The northern boundaries of continuous areas of *Acer platanoides L.* and *Quercus robur L.* coincide in their western part with the northern borderline of mixed forests. In the east, a continuous area of oak and maple is located southward of this boundary. However, isolated locations of these species are marked far northward (up to latitude 60° North) (Kurnaev, 1973).

Taking into account that the boundary between mixed coniferous-broad-leaved forests (in the strict sense of the word) and southern taiga is relatively conventional, there is no further distinguishing of subzones in the text. All data are given for mixed forests in the wide sense of the word.

Using the physiognomic and floristic signs the mixed forests may be subdivided into the following geographical variants.

1) Beech-fir-spruce forests of the Carpathian Mountains. These are forests with very rich tree flora. *Picea abies* (L.) Karst. and *Abies alba* Mill. predominate among conifers. Trees reach big size (the height being 30-35 m, the diameter exceeding 1 m) and live for 300-400 (600) years. Among deciduous species, *Fagus sylvatica* L. is usually the predominating one; it can reach the first layer, but more often forms the second layer, where *Acer pseudoplatanus* L., *A. platanoides* L., *Tilia cordata* Mill., *Ulmus glabra* Huds, and *Carpinus betulus* L. can also occur (Kozii, Stoiko, 1958; Golubets, 1978).

2) Beech-hornbeam-spruce forests of the Kaliningrad Region and the Baltic states. They are also multispecies communities comprising *Picea abies* (L.) Karst., *Fagus sylvatica* L., *Tilia cordata* Mill., *Fraxinus excelsior* L., *Acer platanoides* L., *A. pseudoplatanus* L., *Ulmus glabra* Huds., etc. (Vimba, 1959; Rasin'sh, 1964; Bobrov, 1971).

3) Broad-leaved-spruce forests with *Carpinus betulus* L. in the Baltic states and the Central Belarus (Kairyukshtis, 1966; Vegetation cover of Byelorussia, 1969).

4) Broad-leaved-spruce forests of the center of the Russian Plain, including forests of Bryansk Poles'e and of the Oka Poles'e (Rybakov, 1935; Bulokhov, 1973). They comprise the above-mentioned broad-leaved tree species except *Fagus sylvatica* L., *Carpinus betulus* L., and *Acer pseudoplatanus* L. (Vegetation of the European part of the USSR, 1980). Beginning with this geographical variant, latitudinal differences of the forests under consideration are revealed most clearly. In the forests of the first four variants *Picea abies* (L.) Karst. is observed (Pravdin, 1975). Further, on the left bank of the Volga, there begins introgression zone where numerous hybrids of *P. abies* (L.) Karst. and *P. obovata* Ledeb. are marked.

5) Broad-leaved-fir-spruce forests of the Volga left bank where *Picea abies* (L.) Karst., *P. obovata* Ledeb., *Abies sibirica* Ledeb., and *Tilia cordata* Mill. predominate. The abundance of oak in tree layer is low (Zhilkin, 1928; Vasil'ev, 1935; Porfir'ev, 1947, 1961, 1970).

6) Lime-fir-spruce forests of the Western Ural. Only few of broad-leaved species play the significant role here namely: *Tilia cordata* Mill. and, to some extent, *Ulmus glabra* Huds. In these forests, the presence of *Betula pubescens* Ehrh. and, here and there, of *Populus tremula* L. is also noticeable (Zubareva, 1967, 1975; Terinov, 1967; Firsova, Rzhannikova, 1972; Turkov, 1979a, 1985). In the geographical variants listed above the number of species in tree sinusium decreases from west to east and from north to south. The stand density also decreases in these directions. As an example, some characters of stands on sample plots are given in Table 1.

Table 1.
Some characters of sample plots along geographical gradient.

| Locality | Carpathian National Park | Bryansk forests Reserve | CFBR | Kilemery Protected Area | Sabar Protected Area |
|--------------------------------|--------------------------|-------------------------|------|-------------------------|----------------------|
| Number of species of high tree | 6 | 10 | 3 | 5 | 3 |
| Crown projection, % | 80 | 80 | 50 | 60 | 50 |
| Maximal diameter, cm | 130 | 80 | 60 | 60 | 80 |
| Density of adult trees, st./ha | 277 | 722 | 540 | 433 | 337 |

The decrease of stand density is connected with increasing proportion of herbaceous plants in the total assimilative surface (biomass) in this communities.

Herb layer of coniferous-broad-leaved forests consists of four species groups namely nemoral, boreal, nitrophyte, and a group of tall

herbs. The first two groups were separated by the floristic criteria, the last ones -- by the morphological traits of species. The ratio of species number differs, to some extent, in different geographical variants.

Along the south-north gradient, besides the above-mentioned changes in tree sinusium, the size of broad-leaved trees suffers a considerable decrease. Many edificators become as small as the species of the second layer or even of understory (shrub) (Zubareva, 1967, 1975; Environmental conditions in forest..., 1973; Information materials, 1975a, b, 1976, 1977; Karpov et al., 1983).

In the southern part of mixed forests, communities with noticeable proportion of *Picea spp.* and *Abies sibirica Ledeb.* (geographical variants 4 and 5) occupy the most highly moistened habitats, i.e. the lower position on slopes and ravine valleys. Both broad-leaved and coniferous tree species here reach the first layer (25-30 m), and species from nemoral group predominate in the herb layer (Zhilkin, 1928; Konovalov, 1936; Timofeev, 1936; Grozdov, 1950; Porfir'ev, 1947, 1961; Kurmaev, 1973). Further to the north, conifers occupy watersheds while broad-leaved species gradually become subordinate. They are found only in the second tree layer (15-20 m) or in the understory. In herb layer, species of nemoral group (such as *Galium odoratum (L.) Scop.*, *Galeobdolon luteum Huds.*, *Mercurialis perennis L.*, etc.) still predominate (Smirnova, 1936; Byleeva, 1966; Yurkevich et al., 1971; Chertovskii, 1978; Turkov, 1979, 1985; Karpov, Shaposhnikov, 1983; The Kologrivskii forest, 1986). At the northern borderline of coniferous-broad-leaved forests (southern Karelia, surroundings of Onega Lake, northern Valdai Hills, upper reaches of the Vyatka, Vetluga, Kama, and Pechora rivers, and others), species of nemoral floristic complex may be found only in the understory and herb layer (Sokolov, 1931; Sukachev, 1931; Tsinkerling, 1932; Alekhin, 1936; Bobrovskii, 1957; Yakovlev, Voronova, 1959; Nitsenko, 1960). With the transition from the central parts of mixed forests to northern ones, the tracts of these forests shift from watersheds to steep and well-drained slopes of the southern exposure. Then they begin to occupy river valleys only (Porfir'ev, 1947, 1961; Denisov, 1970; Orlov et al., 1974, 1980; The Kologrivskii forest, 1986). In the northern part of the center of the Russian Plain, spruce forests with dominance of nemoral

species in herb layer are at present time closely related to well-drained habitats. In regions with plain relief, these are river and stream valleys. On each concrete territory, there exist certain differences in the composition and structure of forests growing at different mesorelief elements. These differences will be considered with reference to the Central Forest Biosphere Nature Reserve (CFBR). Large tracts of mixed forests are located on rugged watershed plain here where river and stream valleys possess steep banks, and carbonate moraine is lying close to surface (0.6-0.8 m). Spatial distribution of forests along catena are quite regular. In the upper parts of relatively steep slopes nemoral-wood-sorrel spruce forests grow on weak-soddy and pale-yellow podzols with different humus richness. On upper dry parts of these slopes, rather small sections of weasel-snout spruce forests with maple are marked. Middle parts of slopes are occupied by the communities of woodruff spruce forests with lime. Soil are soddy brown podzols and pale-yellow podzols here. On the lower parts of slopes directly adjoining riverbeds, communities of mercury spruce forests with mountain elm are located. The soils under these spruce forests are soddy weak podzols with the presence of gleying layer.

In the northern part of mixed forests of the Volga left bank, communities with broad-leaved species (mainly of *Tilia cordata* Mill.) are situated on the upper parts of slopes of southern exposure on carbonate moraine bedrock (Gorchakovskii, 1968; Orlov et al., 1974). Detailed description of such communities' distribution according to the relief elements is given in some case studies (The Kologrivskii Forest, 1986).

In the northern part of mixed forests zone of the Western Ural, communities with presence of lime and mountain elm are situated on the middle parts of the western slopes. This position provide favorable temperature regime due to inversion processes in the atmospheric circulation. Detailed descriptions of such communities have been made in the Visim reserve, Sverdlovsk region (Information material..., 1975a, b, 1977; Shevelev, 1977; Turkov, 1979b, 1985).

Mixed coniferous-broad-leaved forests have been carefully investigated on the territory of the European part of the former USSR during the last 50-60 years. Nevertheless, the comprehensive research

methods are absent, and we have to collect additional field data. New data are dealing with demography and spatial structure of tree populations, and also with floristic diversity of relatively non-disturbed forest communities.

METHODS

The ontogenetic and geobotanic researches were carried out in the Ukraine and Russia (Fig. 1). Sample plots were located in the forests that have protected status or in the managed forests that were exploited during a long period.

The largest sample plots (from 1 to 4 ha) were located in the protected forests with complicated stand structure and rich species composition. For such plots we compiled maps (scale 1:100, 1:200) which fix location of all trees (DBH > 2 cm), adult shrubs, and herb aggregations. For research of small herb mosaics we used the maps of scale's 1:10 and 1:20. Special attention was made for the mosaics of habitat elements connected with tree falls.

On the sample plots we recorded calendar and ontogenetic age, vitality, origin (seeded or vegetative), height, diameter at breast height (DBH), and crown size for tree and shrub individuals.

The historic information was collected in the Central State Historical Archives (CSHA), Russian State Archives of the Ancient Act (RSAAA), and Russian State Military-Historic Archives (RSMHA).

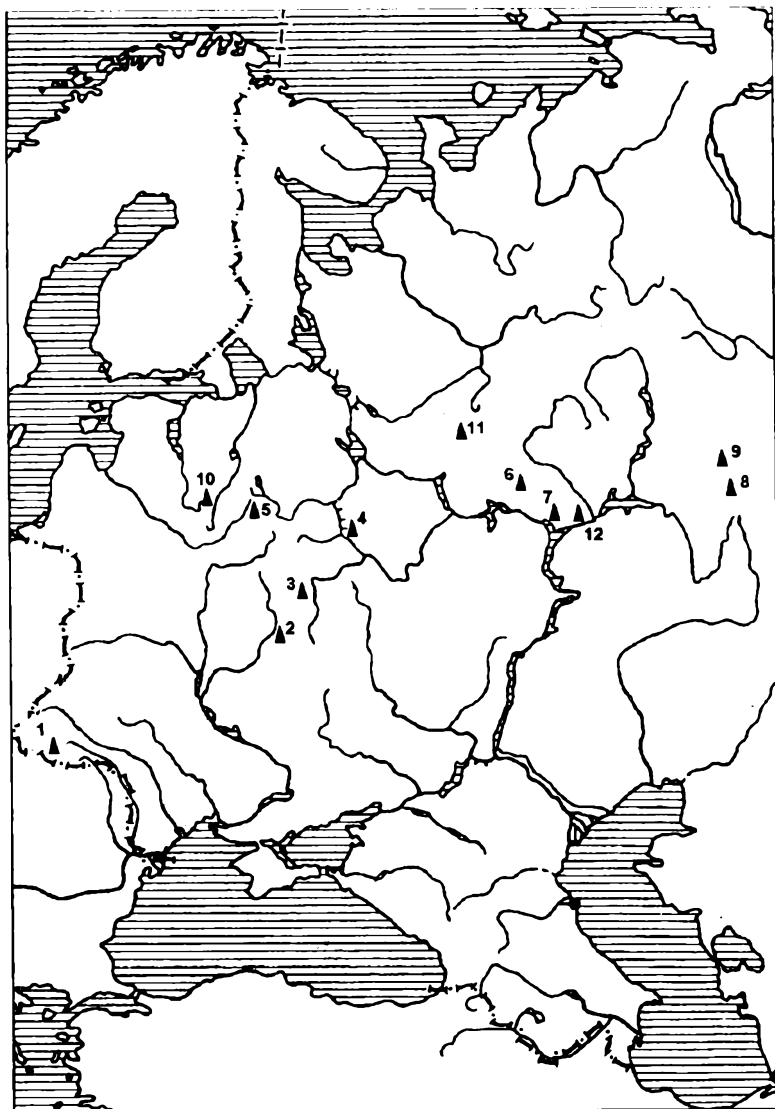


Fig 1. Locations of the research stations in the coniferous-broad-leaved forests.

SYNTAXONOMY OF THE EAST EUROPEAN CONIFEROUS- BROAD-LEAVED FORESTS

A transitional character of mixed forests, as well as considerable changes of their species' composition due to different land use patterns (cuttings, ploughing, silvicultures) complicate their syntaxonomic analysis strongly. There is no monograph works on these forests analogous to that of Yu.D.Kleopov (1990) devoted to the broad-leaved forests of the European part of the former USSR. Because of that, data of different authors were used for a floristic analysis of the concrete regions. For western regions we used the work of W.Matuszkiewicz (1981), for central and northern ones the publications of several authors (Korotkov, 1986, 1991; Korotkov, Morozova, 1988; Bulokhov, 1990; Shaposhnikov et al., 1988). In the case of eastern regions we used the work of R.Schubert et al. (1979). The transitional character of the territory is revealed by the fact that northern variants within the coniferous-broad-leaved forests zone are traditionally referred to the class *Vaccinio-Piceetea* Br.-Bl. 1939. The southern variants are commonly attributed to the class *Quercu-Fagetea* Br.-Bl. et Vlieger in Vlieger 1937. A preliminary prodromus of mixed broad-leaved-spruce forests according to these data is given below.

Class *Vaccinio-Piceetea* Br.-Bl. in Br.-Bl., Siss. et Vlieger 1939.

Order *Vaccinio-Piceetalia* Br.-Bl. 1939 em K.-Lund 1967.

Union *Vaccinio-Piceion* Br.-Bl. 1938.

Subunion *Melico-Piceion* K.-Lund 1981.

Ass. *Quercu-Piceetum* (Mat 1952) em Sokolowski 1968.

Subass. *Quercu-Piceetum galeobdoletosum* Minaeva 1988
(described in the Southern Valdai Hills, in the CFBR)

Class *Quercu-Fagetea* Br.-Bl. et Vlieger in Vlieger 1937 em Klika 1939.

Order *Fagetalia sylvaticae* Pawl. in Pawl., Sokol., Walisch 1928.

Union *Carpinion betuli* Issler 1931 em Mayer 1937.

Ass. *Rhodobryorosei-Piceetum abietis* Korotkov 1986 (Broad-leaved-spruce forests of the northern part of the center of the Russian Plain).

Subass. *Rhodobryo-Piceetum typicum* (distinguished at the Northern Valdai Hills); variant *Carex pilosa Scop.* (described in the Moscow Region).

Subass. *Rhodobryo-Piceetum asperuletosum* Minaeva 1988 (distinguished at the Southern Valdai Hills, the CFBR).

Ass. *Tilio-Carpinetum* Tracz. 1962.

Subass. *Asperuletosum odoratae* (Morozova et al., 1992) - broad-leaved forests with the spruce in the center of the Russian Plain (the Kaluga and Bryansk Regions). We studied a number of forests of the Desna river basin (the Bryansk Region) which had been described in detail by A.D. Bulokhov (1979; 1990). However, we failed to reveal sufficient correspondence of our data to any of vegetation units distinguished by him. So we use meaning of the association here as a term *sensu lato*. Broad-leaved forests with spruce in the Kaluga Region differ slightly from forests of the Desna basin. They are characterized by more depleted species composition. Forests of the Klyaz'ma river flood lands (the Moscow Region) can likely be referred to the same association, but as highly depleted variant due strong human impact. However, we haven't enough data even for preliminary distinguishing of a separate unit.

Ass. *Tilio-Piceetum* Schubert et al. 1979 (broad-leaved-fir-spruce forests of the Volga left bank and lime-fir-spruce forests of the Western Ural and of the Middle Ural). We have not developed special syntaxonomic investigations of this region, but the following units may be preliminary distinguished within the association.

Subass. *Chrysosplenietosum* - coniferous-broad-leaved mountain forests of the Western Ural (the Sverdlovsk Region) - more humid and less disturbed variant as compared with the *Typicum* subassociation.

Subass. *Typicum* - plain forests of the Volga left bank.

Subass. *Chrysosplenietosum var. Abies* - lime-fir-spruce forests of the Middle Ural (more depleted subassociation variant concerning nemoral elements).

Union *Galio-Abietion* Oberd 1961.

Ass. *Galio-Abietum* Oberd 1962 (fir-spruce-beech forests of the Carpathian).

Floristic composition and ecological structure of coniferous-broad-leaved forests are very heterogeneous. They reflect, first, geographical displacement of the forest section and, second, its habitat conditions. In geographical aspect, north-south gradient is expressed more distinctly than west-east one. Thus, among species with high constancy, there are only two ones specific for the Carpathian and one specific for the Ural Mountains (Table 2).

In general, ecological-coenotic spectra of the Ural and Carpathians communities manifest much similarity. There are no specific southern or northern species either, but ecological-coenotic spectra of the northern (CFBR) and southern (the "Bryansky Les" Reserve and the "Kaluzhskie zaseky" Reserve) communities differ greatly. In the northern variant (the CFBR), the number of boreal species is a little higher than that of nemoral ones, while in the extreme southern variant (the "Bryansky Les" Reserve) the percentage of boreal species is very low. In another southern variant (the Ul'yanovo forest of the "Kaluzhskie zaseky" Reserve) among species with high constancy, there are no boreal species at all because soils are richer than in Bryansk. Generally, in the species composition of herb layer of the coniferous-broad-leaved forests, the leading role belongs to the species from nemoral group. For all investigated points the total number species with high constancy (IV and V class) are 87, and there are 42 nemoral and 28 boreal ones. This proportion may be some evidence for the assumption that the broad-leaved forests had a larger extension in the past. The continuous areas of it were shifted at the south sufficiently during last millennia.

Analysis of full species lists gives a more uniform picture of boreal and nemoral species distribution. In two "northern" (to the north from Moscow) variants of the investigated forests (CFBR and Kilemary Protected Areas), the number of boreal species is higher than the number of nemoral ones. In the east variant (Sabar Protected Areas), these quantities are approximately equal, but in all other points, nemoral species are more numerous.

It should be mentioned that, besides two main groups (nemoral and boreal), a significant role in the species composition of herb layer is played by species of nitrophyte ecology. Their constancy reflects

Table 2

List of species with high frequency within areas of mixed forest zone.

| <i>Species</i> | Carpath | Bryansk | CFBR | Zaseky | Klyazma | Kilemary | Kazan | Sabar | Visim |
|-------------------------------------|---------|---------|------|--------|---------|----------|-------|-------|-------|
| <i>Aconitum excelsum</i> | | | V | + | | + | IV | V | IV |
| <i>Adoxa moschatellina</i> | + | + | + | + | + | + | V | V | IV |
| <i>Aegopodium pentagraria</i> | | V | V | V | V | V | V | V | + |
| <i>Ajuga reptans</i> | | | | | V | + | | | |
| <i>Asarum europaeum</i> | | V | + | V | V | IV | V | V | + |
| <i>Athyrium filix-femina</i> | V | + | V | + | + | + | + | V | + |
| <i>Calamagrostis arundinace</i> | | | + | | + | | + | IV | |
| <i>Carex pilosa</i> | | V | + | V | IV | + | IV | | |
| <i>Chamerion angustifolium</i> | | | IV | | | | | + | + |
| <i>Chrysosplenium alternifoium.</i> | + | + | V | | | + | + | V | IV |

| <i>Species</i> | Carpath | Bryansk | CFBR | Zaseky | Klyazma | Kilemary | Kazan | Sabar | Visim |
|-------------------------------|---------|---------|------|--------|---------|----------|-------|-------|-------|
| <i>Cicerbita uralensis</i> | | | | | | | + | V | + |
| <i>Cinna latifolia</i> | | | V | | | + | | V | IV |
| <i>Cirsium oleraceum</i> | | | IV | | | | | | |
| <i>Convallaria majalis</i> | | V | | + | IV | | + | | |
| <i>Crepis paludosa</i> | | | IV | + | + | | | | |
| <i>Dentaria glandulosa</i> | IV | | | | | | | | |
| <i>Dryopteris austriaca</i> | V | | + | | + | | | + | + |
| <i>Dryopteris filix-mas</i> | + | + | | IV | V | + | V | IV | IV |
| <i>Dryopteris carthusiana</i> | | V | + | IV | V | V | + | + | |
| <i>Equisetum pratense</i> | | | IV | + | IV | IV | + | + | |
| <i>Equisetum silvaticum</i> | + | + | V | + | + | + | IV | + | |
| <i>Filipendula ulmaria</i> | + | | IV | + | + | + | | | |

| <i>Species</i> | Carpath | Bryansk | CFBR | Zaseky | Klyazma | Kilemary | Kazan | Sabar | Visim |
|--------------------------------|---------|---------|------|--------|---------|----------|-------|-------|-------|
| <i>Galeobdolon luteum</i> | V | V | V | V | V | + | | | |
| <i>Galium odoratum</i> | + | V | V | + | | V | V | V | |
| <i>Galium schultesii</i> | | + | | | IV | | | | |
| <i>Geum rivale</i> | | | V | + | V | | + | | |
| <i>Geum urbanum</i> | | V | | + | + | + | + | + | |
| <i>Glechoma hederacea</i> | | + | | V | + | + | V | IV | |
| <i>Gymnocarpium dryopteris</i> | + | | V | | + | IV | | | + |
| <i>Impatiens noli-tangere</i> | | | | | V | | | V | |
| <i>Luzula pilosa</i> | | + | V | + | | + | + | | + |
| <i>Maianthemum bifolium</i> | + | V | + | | | V | IV | + | + |
| <i>Mercurialis perennis</i> | + | V | V | IV | | | V | | |
| <i>Milium effusum</i> | + | V | + | IV | V | IV | V | V | IV |

| <i>Species</i> | Carpath | Bryansk | CFBR | Zaseky | Klyazma | Kilemary | Kazan | Sabar | Visim |
|--------------------------------|---------|---------|------|--------|---------|----------|-------|-------|-------|
| <i>Moehringia trinervia</i> | | V | | | | | | | |
| <i>Myosotis sylvatica</i> | | | | | | + | + | IV | IV |
| <i>Oxalis acetosella</i> | V | + | V | | + | V | + | IV | V |
| <i>Paris quadrifolia</i> | + | + | + | + | | + | + | IV | + |
| <i>Phegopteris connectilis</i> | + | | V | | | + | | + | |
| <i>Polygonatum multiflorum</i> | | V | | IV | | | IV | + | |
| <i>Pulmonaria obscura</i> | | V | V | V | | V | V | V | + |
| <i>Ranunculus cassubicus</i> | | | + | | IV | + | | | |
| <i>Ranunculus repens</i> | + | | IV | + | + | + | | | |
| <i>Ribes nigrum</i> | | + | | | | + | | + | + |
| <i>Rubus idaeus</i> | + | + | V | + | | IV | + | V | IV |
| <i>Rubus hirtus</i> | V | | | | | | | | |

| <i>Species</i> | Carpath | Bryansk | CFBR | Zaseky | Klyazma | Kilemary | Kazan | Sabar | Visim |
|----------------------------|---------|---------|------|--------|---------|----------|-------|-------|-------|
| <i>Rubus saxatilis</i> | | V | V | + | IV | IV | + | | |
| <i>Stachys sylvatica</i> | | | + | + | + | | + | IV | + |
| <i>Stellaria holostea</i> | | V | V | V | V | IV | V | V | + |
| <i>Stellaria nemorum</i> | + | + | V | + | IV | | IV | V | V |
| <i>Thalictrum minus</i> | | | | | | | + | IV | |
| <i>Trientalis europaea</i> | | + | V | | | IV | + | | |
| <i>Trollius europaeus</i> | | | | | V | | | | |
| <i>Urtica dioica</i> | + | V | V | + | V | + | V | V | IV |
| <i>Viola mirabilis</i> | | V | | + | | + | IV | + | + |
| <i>Viola selkirkii</i> | | | | | | IV | | + | IV |

* **Carpath** - Carpathian National Park, **Bryansk** - "Bryansky Les" Reserve, **CFBR** - Centralno-Lesnoj Biospheric Reserve, **Zaseky** - "Kaluzskye zaseky" Reserve, **Klyazma** - "Klyazma" Protected Area, **Kilemary** - "Kilemary" Protected Area, **Kazan** - Volzsko-Kamskv Reserve, **Sabar** - "Sabar" Protected Area, **Visim** - Visim Reserve.

habitat humidity rather than geographical gradient. The role of the nitrophyte species is quite insignificant only in the driest and the most southern variants. These species are rare for the coniferous-broad-leaved forests on sands of the "Bryansk Les" Reserve, and for oak forests with spruce in the "Kaluga Zaseki" Reserve. Really, nitrophyte species do not demonstrate high constancy (IV-V frequency class) in the forests of the Kilemary Protected Areas; though, this group is represented by 13 species from the full species list of the areas. Low constancy of the nitrophyte plant may be explained by poor soils of the Kilemary. On the contrary, their role is the highest in the CFBR forests, where dense moss layer keeps constant high moisture on the rich soils. In other variants, their percentage is a little lower than in the CFBR, but near the average one. Total number of species with high constancy (considering all stations) equals 17 for nitrophyte group, while for boreal and nemoral groups it is, correspondingly, 28 and 42. Species of other groups are almost absent (Table 2).

BRIEF HISTORY OF CONIFEROUS-BROAD-LEAVED FORESTS IN THE HOLOCENE

According to spore-pollen data (Neishtadt, 1957; P'yavchenko, 1958; Serebryanyi, 1971, 1973; Kozharinov, 1994), mixed forests in the middle Holocene occupied a large area of the European part of the former USSR. This forest belt is extending from the existing northern boundary of broad-leaved forests to the northern edge of taiga. According to spore-pollen data, the existing contour of northern taiga forests may be subdivided into two parts. In the northern part even traces of pollen of broad-leaved tree species are not presence; in the southern such pollen traces are only in a few sample cuts. In the middle taiga, the pollen is found in each sample cut. In the southern taiga, the amount of broad-leaved trees' pollen in spore-pollen spectra is 5-10%, while in coniferous-broad-leaved forests it reaches 50% and more.

The northern boundary of pollen of broad-leaved trees in the middle Holocene coincides with present northern boundaries of the areas of these trees (Neishtadt, 1957; Khotinskii *et al.*, 1966; Serebryanyi, 1971, 1973; Areas..., 1977, 1986). However, the area's contours of the key broad-leaved species retained till the present time, the vegetation of this territory changed significantly in the late Holocene. Coniferous-broad-leaved forests which were growing in the north of the present tundra zone of Eastern Europe in the middle Holocene, since then shifted southward up to 300-700 km. Broad-leaved trees have almost disappeared from the zonal vegetation, having been retained in separate refuges. Climate changes (the decrease of average annual temperatures and the increase of humidity) are indicated as one of the causes of such a state (Kind, 1976; Klimanov, 1982; Borzenkova, Zubakov, 1984). They have strengthened the advantages of conifers in comparison with broad-leaved trees.

According to the spore-pollen data conducted in the CFBR and to analysis of flora' composition, two stages of the vegetation cover were fixed during the Holocene on this territory (P'yavchenko, 1953, 1955; Minyaev, Konechnaya, 1976). The first stage is dated by the Atlantic Period (7700-4500 years ago), when forest area with *Picea abies* (L.) Karst. decreased, and they occurred in separate locations. This process took place due to increase of the areas occupied by broad-leaved and spruce-broad-leaved forests with *Tilia cordata* Mill., *Ulmus laevis* Huds., *U. scabra* Huds., *Acer platanoides* L., *Fraxinus excelsior* L. Oak had appeared on the territory of the CFBR only by the beginning of more drier Subboreal Period (4500-2500 years ago).

The second stage is dated by the Subatlantic Period (2500-0 years ago). It was a period of the destruction of broad-leaved and spruce-broad-leaved forests. Spruce forests spread widely again and occupied practically the whole territory of the Reserve. Besides climate changes, traditional land use patterns (i.e., slash-and-burn agriculture, forest pasturing, storage of deciduous tree, branches for fodder) played the significant role both in forest area decrease and in complete disappearance of mixed forests. The forest burning was an obligatory stage of slash-and-burn agriculture cycle. It is recording by archaeologists for all territories occupied by Finno-Ugric, Baltic, and

Slavic tribes more than 3000 years ago (Tret'yakov, 1932; Krasnov, 1971; Dolukhanov, 1973; Bader, 1974; Merpert, 1974).

Repeated burning down of forests changed their species composition: species with easily flying seeds (pine, birch, willow, and spruce) spread widely. The present strengthening of conifer positions in old-growth stands of this zone is probably connected with the fact that there was a practice of pine and spruce sowing on old ploughed fields. This action being legalized by the Decree of Peter the Great "On afforestation" (Shelgunov, 1857; Gomilevskii, 1897).

Investigations conducted in the Middle Ural showed that, beginning with the period dating back to 7000-6000, broad-leaved tree pollen is constantly present in spore-pollen spectra. Its maximum occurred 4500 years ago. Pollen of hornbeam (not growing now in this territory) was recorded up 2500 years ago. Studies in the Visim Reserve (northern part of the Ural mixed forests) also manifest stable presence in spectra of lime and elm pollen, and during the climate optimum of oak and hazel pollen (Panova, Makovslii, 1979).

A significant role of a human impact in losses of broad-leaved species from the mixed forests is confirmed by the data on their wide use in the X-XIII centuries. These species were used for building and utensil making in the regions of Novgorod, Yaroslavl', and Kostroma (Essays on the history..., 1959). At present, broad-leaved trees are virtually absent here. According to many authors' opinions, complete disappearance of broad-leaved species in the northern part of mixed forests during the last millennium was caused by anthropogenic influence (Gorchakovskii, 1968; Porfir'ev, 1975; Dyrenkov, 1984). Thus, according to A.K.Denisov's (1970) data, the northern boundary of *Quercus robur* L. has shifted 100-200 km southward in the Vyatka Region during the last millennium.

On the contrary, the increase of the role of broad-leaved species has been recorded for communities in the last decades in the northern part of mixed forests. Observations show that the main cause of such increase is an almost complete cessation of traditional forest use. Selective cuttings, litter gathering, pasturing were abandoned after World War II due to serious decrease in rural population in these regions (Rechan et al., 1993). It is interesting that under similar climate

conditions the opposite tendency is noted for Sweden mixed forests. Here, strengthening of spruce populations has occurred over large areas for the last 2000 yr., but approximately since XVIII century spruce begun to predominate in the stands. The extension of spruce populations closely correlates with cessation of burning and progress of silviculture practice that have recently occurred (Bradshaw, 1993, p. 764).

STRUCTURE AND SPONTANEOUS DYNAMICS OF NON-DISTURBED MIXED CONIFER-BROAD-LEAVED FORESTS

Mosaic-cycle regularities of dynamics of the remnants of non-disturbed mixed forests are just the same as in the broad-leaved forests (Falinski, 1978; Hibbs, 1982; Beatty, Stone, 1986; Foster, Reiners, 1986; Hytteborn et al., 1989; East-European Broad-Leaved Forests, 1994).

In the early published the "Eastern Broad-leaved forests" (1994), it is shown that the size of intracommunity mosaics is determined, primarily, by specific traits of tree and shrub ontogeny. Investigations in mixed forests confirmed that the main features of conifer (*Picea* and *Abies*) ontogeny does not differ in their main traits from those of broad-leaved trees. However, characters of crown structure in spruce and fir determine the specificity of vertical structure of tree canopy in forests with their presence (Serebryakov, 1962; Kozhevnikova, 1982). The description of *Picea obovata* Ledeb. ontogeny based on study of sample trees from the Sabar Protected Areas is given below as an example. /

Absence of vegetative reproduction is the main peculiarity of the coniferous trees. These species can not enrich their populations by the vegetative offspring as it is commonly for leaved trees. The latter ones bear rooted shoots on xylorhizomes (*Tilia cordata* Mill., *Acer campestre* L., *Ulmus* sp.), stump sprouts (*Tilia cordata* Mill., *Acer* sp., *Fraxinus excelsior* L., *Fagus sylvatica* L., *Quercus robur* L.), and root sprouts (*Populus tremula* L.).

Picea obovata Ledeb. ontogeny always starts with seed germination, as the species is incapable to reproduce vegetatively. This is one of the main distinctions between coniferous and deciduous species. The latter have an opportunity to considerably replenish young generations due to vegetative offsprings. They are grown from rooting shoots on xylorhizomes (lime, hedge maple, elms), from dormant buds on stump (lime, maples, ash, beech, oak) or from sprouts on roots (aspen).

Seedling (p). By the end of the first growing season a plant has a hypocotyl, epicotyl, 6-8m cotyledons, and rather small (2-3 mm) primary shoot with needles of juvenile type, and an unbranched taproot. The juvenile needles are short, thin, and lighter than needles of mature type.

Juvenile plant (j) possesses calendar age 3-7 yr, and height 4-8 cm. A plant has an unbranched monopodial shoot (the first order of branching); cotyledons are absent yet. Needles are of juvenile type. Lateral roots appear in root system.

Immature plant (im). A plant possesses calendar age 4-21 yr, and height 0.1-1.4 m. At this ontogenetic stage, there appear needles of mature type, inherent to all the subsequent ontogenetic stages. Lateral branches develop on the main axis (on monopodial shoot); these branches also demonstrate monopodial growth. The order of crown branching is 2-5. Crown diameter may reach 100 cm. Annual terminal elongation is up to 10-15 cm. Lateral growth is comparable with the terminal elongation in size; this leads to the formation of sparse primary crown. At this ontogenetic stage as well as at the previous ones, the plant has high shade tolerance, and many individuals survive even in highly shaded conditions. Superficial root system begins to form due to branching and fast growth of lateral roots.

Virginile plant (v). A plant possesses calendar age 10-40 yr, and height 1.1-13 m. This ontogenetic stage is characterized by maximal annual elongation. The terminal elongation of the first and second order axes considerably exceeds those of higher order shoots. On sunlit sites, the elongation of the main axis can reach 70-80 cm per year. This stage is characterized by considerable decrease in shade tolerance. Young trees develop a crown resembling in shape that of adult trees.

The order of branching is 5-7; crown diameter reaches 3 m. The basal diameter of trunk ranges from 1-3 to 20 cm. The height of the first alive branch's attachment is about 50 cm (i.e. the crown is rather close to the ground). At this ontogenetic stage, monopodial growth of leader axis may be disturbed. On the branches of the second and higher orders new shoots appear from dormant buds. These shoots will form the main part of assimilatory biomass at later ontogenetic stages. The root system is superficial and resembles that of immature plants, but is of greater size.

Young reproductive plant (g_1). A plant possesses calendar age 25-68 yr, and height (5)15-25 m. At this ontogenetic stage, fruiting begins (the first cones appear in the upper part of the crown). Trunk retains a monopodial type of growth (except the cases of periodic exogenous damage of terminal bud). Elongation of the main axis exceeds that of the second-order branches (axes). At this time, the main axis grows faster than the second-order axes. In turn, the second-order branches grow faster than branches of higher orders. Tree crown becomes of narrow pyramidal shape and has distinctive asymmetry in the development of the main axis and of lateral branches. This is distinction from crowns of the majority of deciduous trees which often form several branches slightly different in their diameter in young reproductive state already. In future, this feature makes it possible for deciduous trees to form crowns of great diversity of shapes depending on local light conditions. Retention of narrow pyramidal form of crown during the long time leads to the fact that the lower layers under adult conifer trees are in much better light conditions than those under deciduous trees.

The order of branching at this ontogenetic stage is 6-8, the crown diameter being up to 5 m. In crown, there appear more and more thin shoots developing from dormant buds, and in its lower part the monopodial growth becomes more and more often disturbed. The height of attachment of the first alive branches of the second order increases reaching 3 m, but crown length remains very high (more than 3/4 of total trunk length). This fact being not observed in deciduous trees of the same ontogenetic stage. In the lower part of the trunk, the

crust is already well formed and begins to crack. The height of the cracked crust area along the trunk reaches 1.5 m.

Mature reproductive plant (g_2). A plant possesses calendar age 60-130 yr, and height 21-34 m. The tree gets the shape of an adult well formed ("mature") organism with maximal ability for fruiting. Cones are located in the upper and middle part of the crown. At this ontogenetic stage, the growth of the main axis slows down. Crown shape approximates that of a cylinder with a small cone on the top. Crown diameter is up to 7 m. Practically along the whole crown, shoots developed from dormant buds are abundant. The maximal order of branching may vary from 7 to 10. The basal diameter of trunk reaches 70 cm. The trunk devoid of the second-order alive branches has the height from 2 to 6 m and is covered by thick, strongly cracked crust. The cracked crust area is recorded up to 9 m height.

Old reproductive plant (g_3). Its calendar age is 120-200 yr, its height being 30-34 m, crown diameter reaching up to 9.5 m. The basal diameter of trunk reaches 120 cm. The crown has a cylindrical shape with very obtuse cone on the top. The main axis completely loses a monopodial growth, and there is practically no increase in height. The elongation of the second order branches is also very small. On crown top, shoots are short and thick with shortened, almost rounded needles. At this stage, the assimilatory biomass of the tree almost completely consists of secondary crown, i.e., of shoots developing from dormant buds. The same fact was recorded for *Picea abies* (L.) Karst. in the CFBR forests (Karpov et al., 1983). The main axis replacement leads to formation of 2-3 and more equally developed orthotropic terminal shoots. Fruiting is periodically abundant, but less so than in case of mature trees. Order of branching remains the same as before. Strong flexure of the lower branches is often observed. The height of alive crown attachment is retained at the same level. The crown remains highly extensive, though not so dense, till the very old age. The trunk is covered with thick, highly cracked crust. The cracked area of the trunk spreads almost along its whole length. The process of crown withering in spruce is rather fast in comparison with deciduous trees. Only 1-2 years may pass since the moment of withering of few sparsely distributed branches in the upper part of the crown till the

death of the whole tree. Due to fast dying-off of old reproductive individuals, subsenile (ss) and senile (s) trees (i.e., trees lacking the ability to make seeds) are observed very seldom. The short duration of a postreproductive period in spruce is a distinction between conifer edificators and many deciduous ones. The latter are characterized by gradual crown dying-off and, in some cases, by clearly manifested postreproductive period. Due to this fact, light conditions under the canopy of adult deciduous trees change more gradually than under conifer canopy. This is the cause of different conditions for regrowth development in deciduous and mixed forests.

Abies sibirica Ledeb. ontogeny is very similar to that of *Picea obovata* Ledeb. described above, and its main stages are shown in Fig. 2a, 2b).

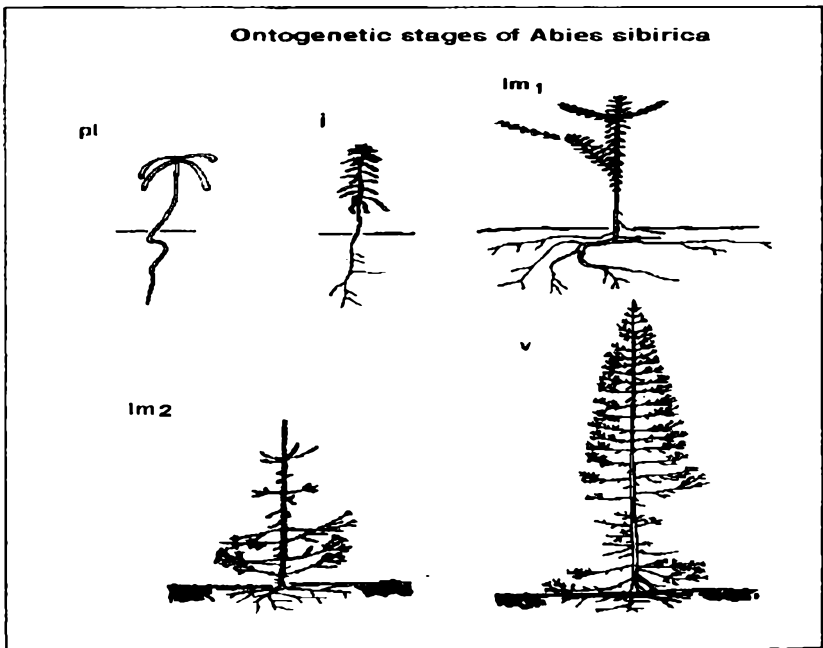


Fig. 2a. First half of ontogenesis of *Abies sibirica* Ledeb. (according to I.D.Makhatkov's (1991) data).

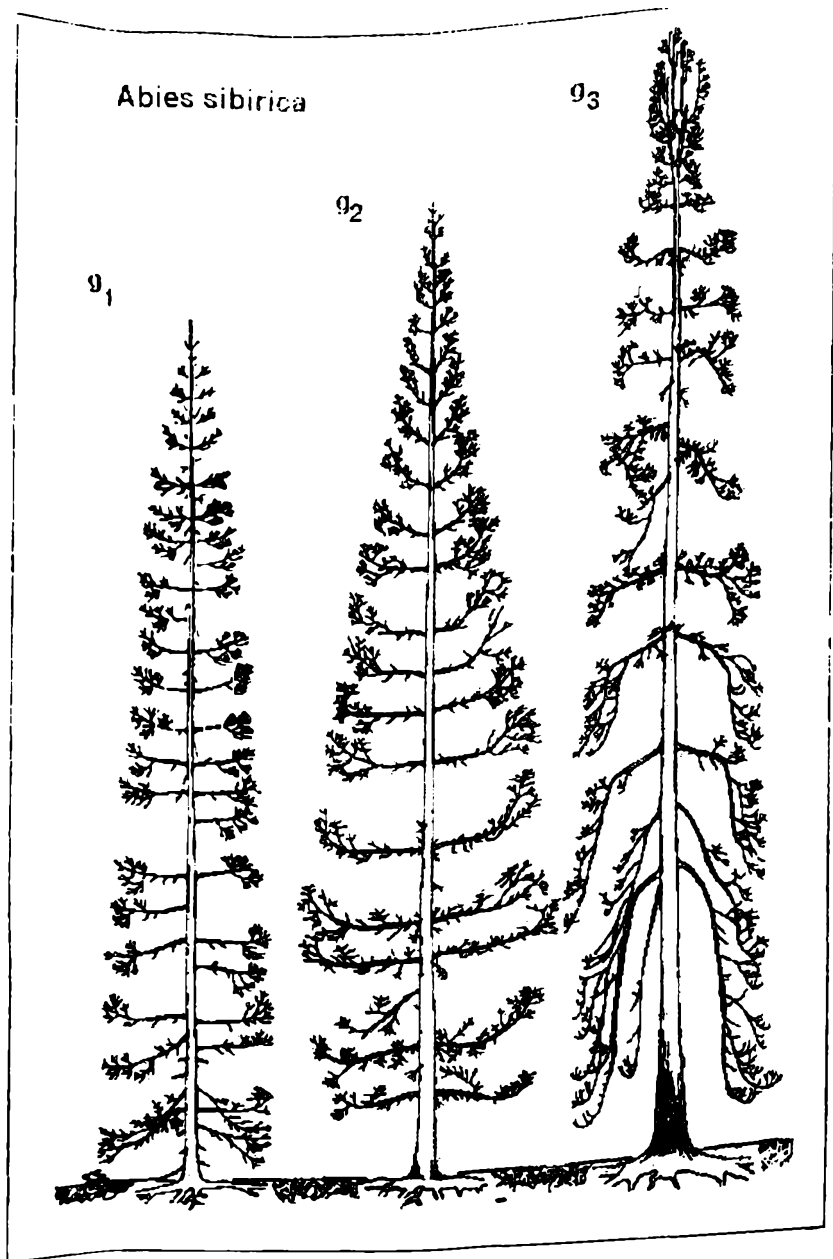


Fig. 1b. Second half of ontogenesis of *Abies sibirica* Ledeb.

In the work (East European broad-leaved forests, 1994) is shown that the structure and spontaneous dynamics of uneven aged stands are mainly determined by light regime in gaps of different size. Though, mixed coniferous-broad-leaved forests are similar to the broad-leaved ones by their floristic composition, they are depending on their dynamics on wider spectrum of factors. Besides light supply, habitat elements forming due to windfalls (Skvortsova et al., 1983), abundance of rotting wood, and extents of herb layer influence the tree regrowth. Examples of significance of each of the above-mentioned factors in the dynamics of mixed forests from different geographical variants are given below.

The most western of mixed forest variants under consideration (communities of *Abieto-Piceon* union) was described in the Carpathian National Park on brown loamy-cobble soils (Popadyuk, Ripa, 1989). These are forests of the middle-mountain belt where tree sinusium comprises 5-7 species. The basis of tree layer is formed by mature and old reproductive trees of *Abies alba Mill.* and *Fagus sylvatica L.* Other species occur in many fewer numbers, but they also have ontogenetic complete populations (Fig. 3).

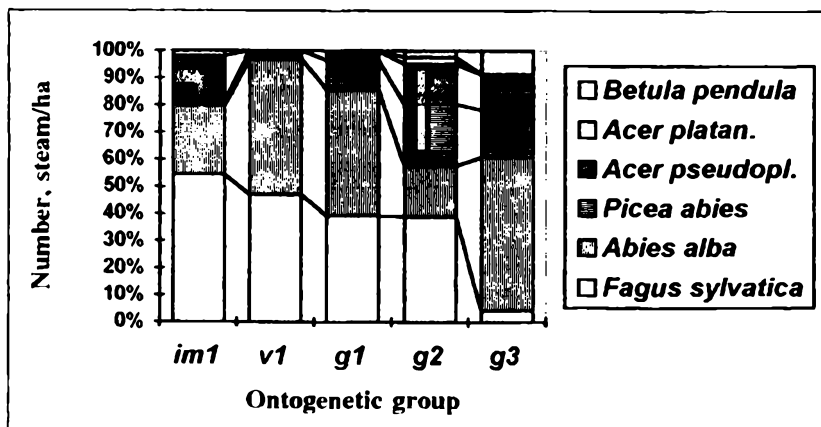


Fig. 3. Ontogenetic structure of population of the fir-beech forest in the Carpathian National Park.

Maximal fluctuations in ontogenetic spectrum are noted in populations of a ruderal species *Betula pendula* Roph. Fragmentary populations are also typical for *Ulmus glabra* Huds.; this fact being connected with mass death of the species because the outbreaks of the Dutch elm disease were recorded in the Carpathian Region in the 1930-40 th. and the 1950-60 th.

As in broad-leaved forests, ontogenetic completeness of tree populations is possible only if gap mosaic which provide favorable conditions for young generations on the place of tree-falls exists. Shade-tolerant species of tree synusium (fir, spruce, beech) have successful reproduction within the gaps of small size (about 100 m²). Gaps of such size are clearly insufficient for light-demanding species (in particular, for birch); because of that, birch populations are so scanty in the Carpathian mixed fir-spruce-beech forests. One can record less than 10 adult trees, and less than 50 trees of juvenile and immature ontogenetic stage on a 1 ha plot.

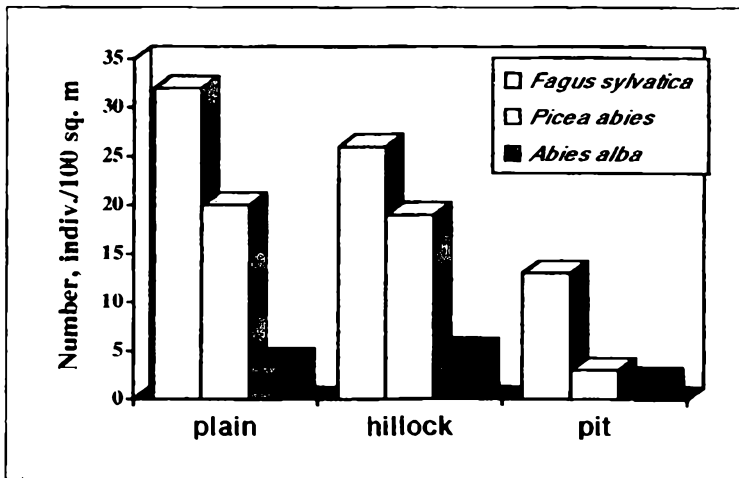


Fig. 4. Number of seedlings on the habitat elements in the fir-beech oldgrowth (Carpathian National Park).

The analysis of tree species reproduction in gaps shows that young generation in edicator populations successfully develops on quite different habitat elements connected with tree-falls. Among these elements, the lowest regrowth density is noted in deep tree-fall pits characterized by accumulation of thick layer of slowly rotting litter. The litter impedes rooting of seedlings of all species including steadfast seedlings of beech (Fig. 4). Due to poor herb layer and good soil drainage, reproduction of all tree edicators is successful both on flat sites and on tree-fall hillocks.

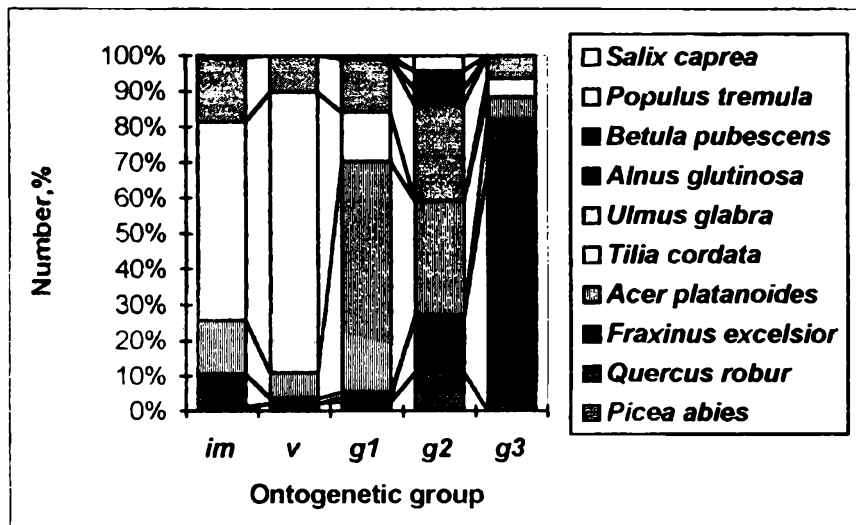


Fig. 5. Ontogenetic structure of spruce-oak forest in Bryansk Forest Reserve.

The fourth geographical variant has been described in several points of broad-leaved-spruce forests of the center of the Russian Plain. The southern types of the forests (*Querceto-stellariosa* group of associations) have been described in the "Bryansk Forest" and "Kaluga Zaseki" Reserves on sandy, sandy loam, and loamy soils. They are

characterized by very high species diversity of tree synusium. In the composition of tree layer, broad-leaved species (according to the strategy type: *Quercus robur* L. -- competitive, *Acer platanoides* L. -- stress-tolerant, and *Ulmus glabra* Huds. -- ruderal) have the largest proportions. Other species (among them *Picea abies* (L.) Karst.) are present merely as an admixture, though their populations also consist practically of all ontogenetic groups (Fig. 5). In this variant, unlike the Carpathian mixed forests, ontogenetic completeness in populations of some tree species (*Tilia cordata* Mill., *Populus tremula* L.) is ensured by vegetative offspring.

The gap size and, consequently, the light regimes determine here as well as in the Carpathian coniferous-broad-leaved forests a possibility of successful reproduction for species different strategy type and different light demand.

A detailed analysis of light regimes on a permanent sample plot in uneven aged mixed forest showed that lighting is ten times higher in gaps than in shaded sites under big tree's crowns (Fig. 6).

However, the maximal values of light flow in the lower layers can be noted only in certain hours. In the given example, lighting on the transect was sufficient for growth and development of regeneration of all species of tree synusium on the twelfth plot from 10:00 till 12:00 a.m only. For comparison, there is shown that lighting changes over a day under the crowns of adult trees in aspen forest appearing after cutting of an uneven aged forest. In dense stand evened by cutting, mosaic of light spots is almost unnoticeable. Maximal values do not exceed 6% of full lighting in an open place; it leads to considerable decrease in number of species whose regrowth can develop under the canopy. As in the Carpathian forests, in communities of the "Bryansky Les" Reserve on depleted sandy soils, almost all tree species successfully germinate and survive on all habitat elements in sites provided with sufficient lighting level. Spruce is the exception, and its regeneration being almost completely connected with rotting tree trunks.

The observation made in the southern variants of mixed forests of the Central Russia showed an interesting regularity. Presence of large decaying trunks is necessary condition for successful self-maintenance of spruce populations.

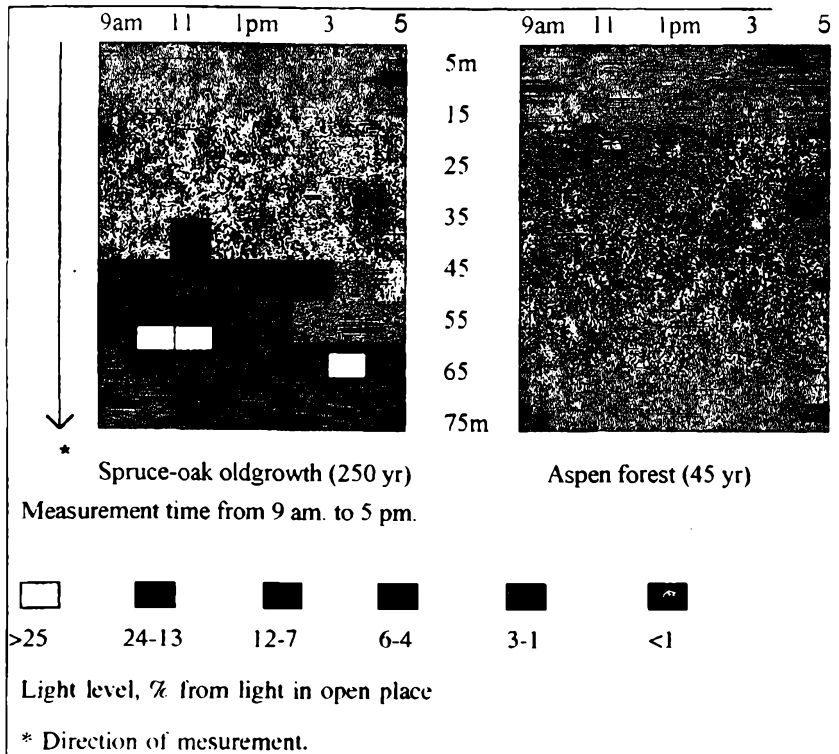


Fig. 6. Light dynamic during the day in mixed oldgrowth and aspen community.

It is right for the wide range of environmental conditions (from humid habitats on loamy soil to relatively dry forests on sands). The same conclusions were made in the investigations throughout the whole area of mixed forests in Russia (Dekotov, 1931; Vasil'ev, 1935; Obnovlenskii, 1935; The Kologrivskii Forest, 1986), as well as in Northern Europe (Hofgaard, 1993). Artificial elimination of debris from mixed forests (selective cutting system) leads to quick replacement of spruce by shade-tolerant deciduous species due to disappearance of large gaps and absence of the substratum favorable for spruce reproduction. Besides debris elimination, regular thinning cuttings lead to smoothing of habitat elements connected with tree-falls occurred earlier (Fig. 7).

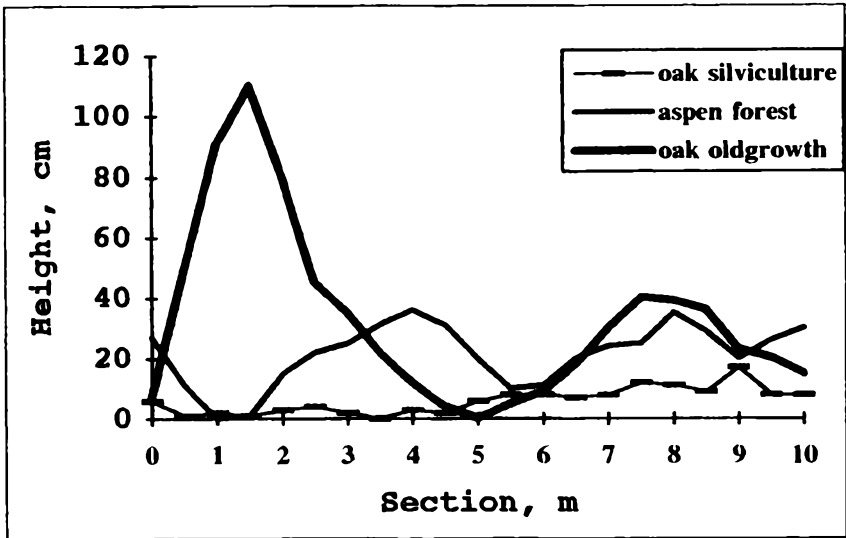


Fig. 7. Loss of habitat elements associated with old forest in secondary forests

Interrelations between surface mosaic and soil heterogeneity in deep horizons and soil fertility is analyzed in detail in publications of soil scientists (Ponomarenko et al., 1993). Here, we stress that only the whole variety of the structural and functional mosaics of uneven aged stands can ensure self-maintenance of a maximal number of species in tree synusium as well as other synusia during an indefinitely long time.

Northern communities of broad-leaved-spruce forests of the center of the Russian Plain (*Quercus-Piceetum galeobdoletosum* and *Rhodobryorosei-Piceetum abietis* associations) are described in the CFBR. Contrary to southern and western variants, they are characterized by dominance of *Picea abies* (L.) Karst. in all layers. Ontogenetic spectrum of spruce manifests left-side asymmetry which is typical for tree species (most numerous are young ontogenetic groups). Broad-leaved species occupy subordinate positions in tree layer while the edificator of broad-leaved forests *Quercus robur* L. is either completely absent or its populations are fragmentary. *Tiliacordata* Mill. populations keep in better state than other

species due to vegetative reproduction of lime (Fig. 8). In populations of maple and mountain elm (species of stress-tolerant strategy), old reproductive trees are missing. Populations of one of ruderal species (*Betula pubescens* Ehrh.) are practically devoid of young generation at present, while populations of another species (*Populus tremula* L.) are represented by all ontogenetic groups.

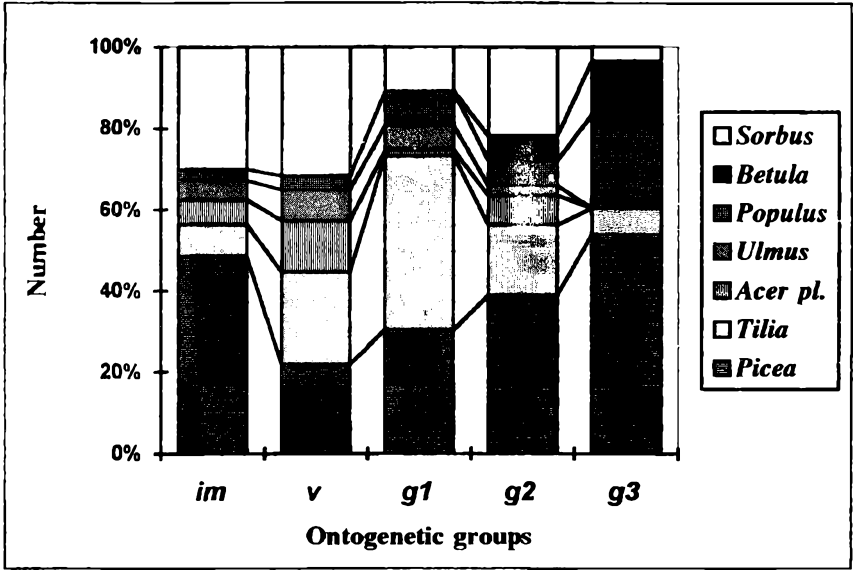


Fig. 8. Ontogenetic structure of tree population in spruce oldgrowth (the CFBR).

A detailed analysis of age structure of spruce populations shows complicated dynamics of young generation survival and dying off in different age groups. Despite the undulated character of age spectrum, spruce population retains the dominant position and, at the same time, does not prevent the reproduction of other species of tree synusium (Fig. 9).

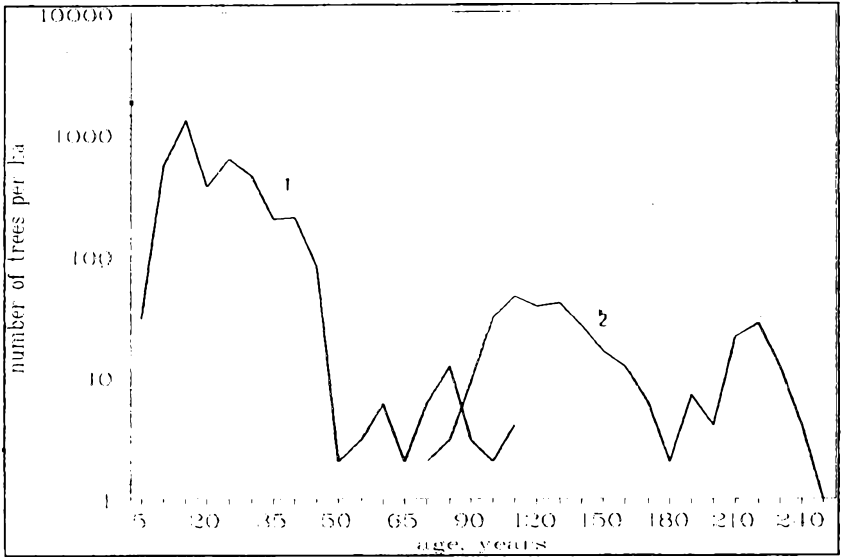


Fig. 9. Age spectra of spruce stands in the woodruff spruce forest with lime (subass. *Quercus-Piceetum galeobdoletosum*): 1 - DBH < 6 cm; 2 - DBH > 6 cm.

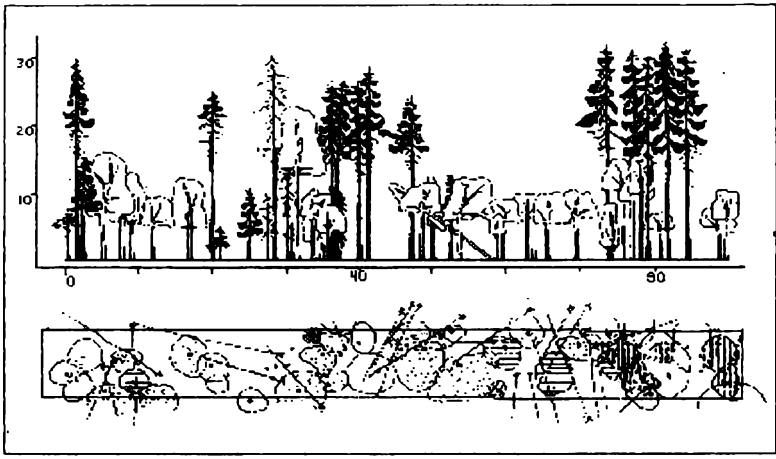


Fig. 10. Cross section of oldgrowth spruce forest in CFBR.

Mosaic-layer organization of the northern variant of mixed coniferous-broad-leaved forests with distinctly expressed gaps is clearly seen on the profile diagram of uneven aged mixed forest in the CFBR (Fig. 10).

On a 90 m transect, alternating aggregations of adult spruce trees and the regrowth of conifers and of broad-leaved trees can be traced. Adult generation of spruce is notable for its low density, but population as a whole consists of individuals of any age. Constant replenishment compensates old trees dying off, though the numbers of age cohorts vary widely.

The presence of two clearly expressed maximums of numbers is a characteristic feature of age structure of the examined population of spruce (Fig. 9). They correspond to the ages of 110-140 and 200-220 years. Because of the absence of long temporal series, it is impossible to determine the cause of a gap formation between the two peaks of adult individuals numbers. It may be connected both with unfavorable conditions of reproduction 180-200 years ago and with mass reproduction of phytopathogens or maybe with some other causes.

On the transect, mosaic of spots of different composition and age alternate each other. Aggregations with single generation (adult) spruce and big trees of mountain elm in the second layer are one type of spots. Aggregations with two spruce generations and sparse second layer of mountain elm and maple are second types of spots. Moreover, there is a new gap with tree layer of 20-30-year old maple and mountain elm. Aggregations with relatively age-heterogeneous spruce trees (maximal age of spruce is 230-240 years) and lime trees in the second layer are one more types of spots.

Investigations carried out in the CFBR on the transect of more than 40 km length (Georgievskii, 1992) made it possible to distinguish gaps of different age (from 5 to 80 years and more) and to reveal the way of gap's origin. According to these data, new gaps are annually forming on 0.4-2% of the forested area. Average gap size is 50x70 m. A complete cycle of microsuccessions from settling till dying off trees performed throughout the whole area of community lasts for about 500 years. In North American mixed forests, the time of establishing of

structural features that are inherent to uneven aged stands is close to the time of establishing the equilibrium between birth rate and dying off in tree populations (Tyrrell, Crow, 1994).

Understory actively responds to changes in the upper layers and soil conditions. Species diversity of the lower layers, maintained due to cyclic disturbances, ensures the stability of species composition and regeneration potential of populations of all species. In sparse uneven aged stands, parental generation only partly limits reproduction in populations of tree species. The shading of young trees by adult ones as the main limiting factor of tree population's self-maintenance is weakened in such forests. Other causes determine a possibility of tree species to reproduce new generations.

The structure of soil cover acts as one of such factors. In uneven aged communities of the CFBR, the structure of the ground layers is determined by a combination of several elements of mosaic. They mark different stages of microsuccessional processes occurring in gaps: (1) windfall depressions with the dominance of pioneer species; (2) aggregations of big ferns and raspberry connected with elevated and flat sites in old gaps; (3) windfall hillocks with a group of forest-edge species; (4) transition microrelief depressions with nitrophyte species; (5) closed old windfall pits with sphagnum mosses; and (6) flat surfaces with boreal species near stump hillocks and nemoral species between hummocks. Temporal sequence of the listed spots in herb layer is connected with habitat element's transformations. This process is shown on the following scheme (Fig. 11).

In these conditions, seedling of birch and aspen occur sporadically on windfall hillocks, while that of maple, mountain elm, and elm takes place on flat surfaces with nemoral species. Lime vegetative offspring near parental trees is usual. Successful reproduction of spruce is found only on decaying trunks. It should be mentioned that, in the northern variant of mixed forests, many habitat elements -- pits with sphagnum mosses, transition microrelief depressions, *etc.* -- are unfavorable for regeneration of all tree species. To the north of the CFBR near the boundary between the Novgorod and Pskov Regions (the Rdeya and Polistovo Reserves), uneven aged mixed forests exist on rather small islands (less 20 ha each ones).

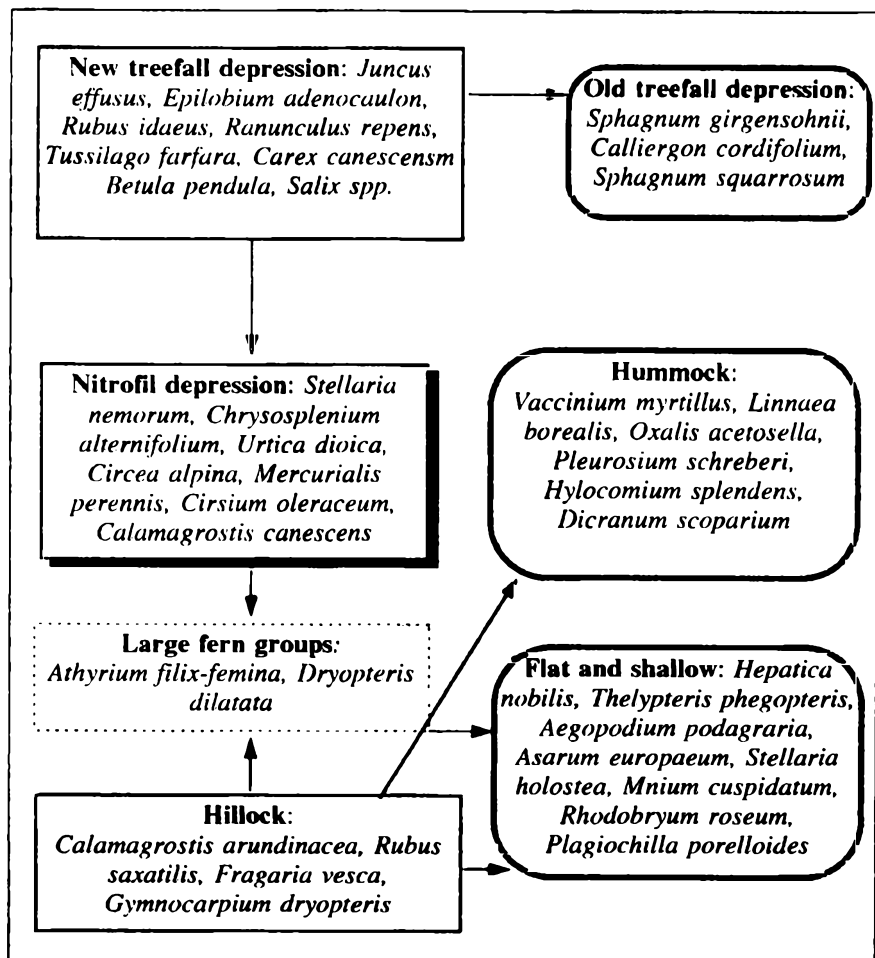


Fig. 11. Species composition of herb layer in the habitat elements connected with windfalls (CFBR).

The islands are hardly accessible areas within a large bog system (unpublished data of A.Yu.Yaroshenko). Here, unlike the CFBR, dominants of mixed forests are oak, lime, Norway maple as well as spruce, and aspen. All broad-leaved species are characterized by stable regeneration. In some places, even ash regrowth happens to be found.

Earlier, on the territories surrounding the bog, mixed forests predominated which had been almost eliminated in the XVIII-XIX centuries. However, as late as the beginning of the XX th century, forests with oak and ash dominance were present here (Yur'ev, 1912; Dyrenkov, Avdeev, 1989). A large proportion of broad-leaved trees in the northern forests may be seen the evidence that the extent pure spruce forests of the CFBR are result of human impact in the past. The most northern variants of mixed forests (lime-spruce forests with maple and elm) are described in Southern Karelia (Tsinzerling, 1932; Yakovlev, Voronova, 1959; Yakovlev, 1983).

The fifth geographical variant -- broad-leaved-fir-spruce forests (*Tilio-Piceetum* association) is described in several points. In these mixed forests, fir again becomes to occur, but here it is another species of the genus namely *Abies sibirica* Ledeb. instead *Abies alba* Mill. on the West. The spruce populations have a complex genetic structure, as *Picea obovata* Ledeb. grows side by side with *Picea abies* (L.) Karst., and these species can hybridize. In the southern part of the Volga left bank, mixed forests are described in the Volga-Kama Reserve and in forests of the lower reaches of the Vyatka river (the Tatar Republic). The regeneration of fir and spruces is successful only in slightly disturbed communities at the lower parts of slopes and in ravine valleys. Oak, lime, elm, and Norway maple are dominants in such communities, but spruces and fir are codominants here. Nemoral species predominate in the flora of such communities (Table 2). Regrowth of broad-leaved species is found almost at all habitat elements, while spruce regrowth is strictly related to decaying trunks. Fir seedlings are present both on soil and on trunks. So among conifers, fir regeneration occurs in more diverse conditions (Zhilkin, 1928; Porfir'ev, 1947, 1961, 1964, 1970).

In the central part of mixed forests of the Volga left bank (the Kilemary Protected Area of the Nizhnii-Novgorod Region), oak is absent even in slightly disturbed communities. Dominance of conifers and lime is characteristic feature of the Reserve. Other deciduous tree species do not have numerous populations, but *Acer platanoides* L. and *Sorbus aucuparia* L. are mainly represented by young generation. There are two striking representatives of species of ruderal strategy namely

aspen and birch, only one of them (*Populus tremula L.*) playing the significant role in uneven aged forests (Fig. 12).

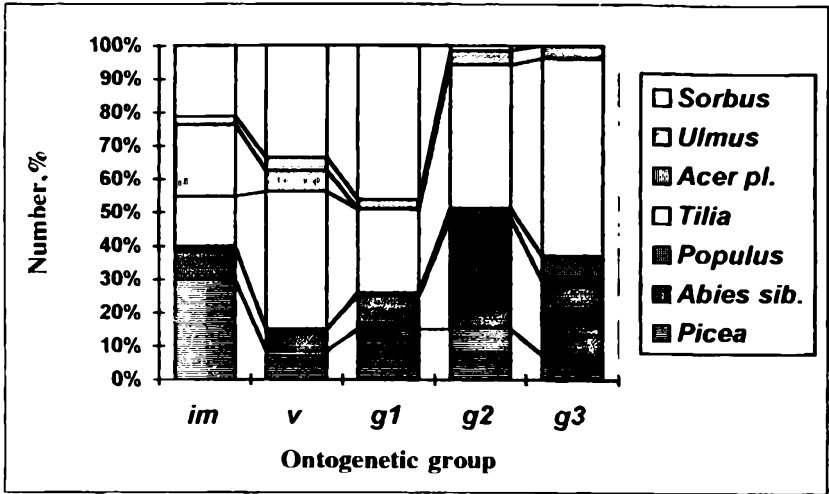


Fig. 12. Ontogenetic structure of oldgrowth in the Kilemary Protected Area.

Distribution of immature regrowth in broad-leaved-spruce-fir forests of the Middle Volga basin has been studied on decaying trunks. Here, *Picea spp.* are the dominant species (161 individuals); *Abies sibirica Ledeb.* (26), *Betula pubescens Ehrh.* (5), *Sorbus aucuparia L.* (5) are less abundant. *Ulmus scabra Huds.*, *Tilia cordata Mill.*, *Acer platanoides L.*, and *Populus tremula L.* are represented by single individuals (data of inventory on 21 trunks within the sample plot).

Northern variant of relatively undisturbed broad-leaved-fir-spruce forests is described in the "Kologrivskii Forest" Reserve of the Kostroma Region (Orlov et al., 1980; The Kologrivskii Forest, 1986). Here, communities with noticeable presence of lime in tree layer and with nemoral species in herb layer are distributed on habitat elements in the same way as in the CFBR.

The sixth geographical variant is lime-fir-spruce forests of the Western Ural. This association was investigated in two points namely in the Sabar Protected Area and Visim Reserve. In the Sabar (southern variant of mixed forests), tree layer is formed virtually by three species only: *Picea obovata* Ledeb., *Abies sibirica* Ledeb., and *Tilia cordata* Mill. Other species -- *Ulmus glabra* Huds., *Acer platanoides* L., *Sorbus aucuparia* L., and *Padus avium* Mill. -- fail to reach the size of trees of the first or second layer during the whole life span. Adult trees of *Acer platanoides* L. are periodically destroyed by winter frosts.

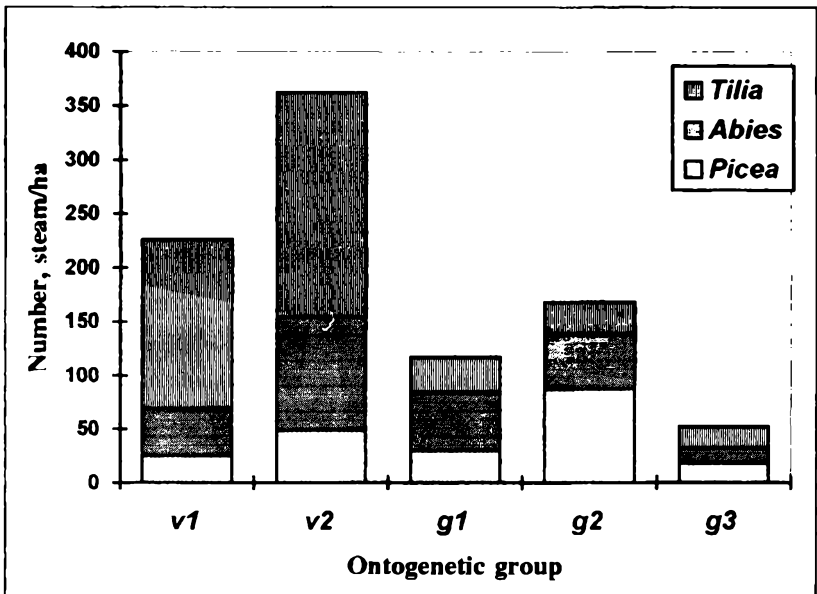


Fig. 13. Ontogenetic structure of tree population of oldgrowth in Sabar Protected Area

Only some individuals reach mature or old reproductive ontogenetic stage. Ontogenetic structure of dominants of the upper layer is complete (Fig. 13), but a specific situation is observed in populations of *Betula pubescens* Ehrh. Adult birch individuals are of big

size, but their populations exist only in very low density. An inventory of trees numbers makes possibility to build ontogenetic spectra should be made on vast territories. For this reason, ontogenetic completeness is not revealed on inventory plots of 1 ha, though trees develop normally and are commensurable in their size with adult individuals of *Picea obovata* Ledeb. Contrary to the more western variants of mixed forests, *Populus tremula* L. is completely absent in uneven aged communities of the Sabar Protected Area. This species is represented by solitary individuals in stream valleys and starts to predominate on afforested hay glades.

The uneven aged forests of the Sabar are similar to the communities of the northern part of coniferous-broad-leaved forests. There and here in old-growth, the area free from trees is greater than in communities in the western and southern parts of the mixed forest zone. Figure 14 presents a map of tree crown projections on 1 ha permanent plot and a vertical section across it's. Note, the lower part of the Figure shows crown sections of trees located on the same line. Crowns of different trees (i.e., trees of different species and age) are present at every height levels. Nevertheless, almost 40% of community map area is not covered by crown projections (ontogenetic stages of trees marked on the map vary from virginile to old reproductive).

Such sparse tree canopy gives light mosaic, where the number of highly shaded sites over herb layer is lesser than in the western uneven aged community (the "Bryansky Les" Reserve, Fig. 6). In such forests, light supplement of large (more than 2-2.5 m high) and small regrowth differs greatly. The model estimations of light fields are shown for two height levels of the permanent plot (Fig. 15). On the level of the broadest parts of crowns of adult spruce and fir trees, sites with lighting over 25% have largest area and form a background (light field on Fig. 15, A). Sites with lighting less than 6% (that is inappropriate for light-demanding species reproduction) form isolated spots of rather small size. At the height less than 2 m (Fig. 15, B), the area of sites with high lighting decreases noticeably, and sites with intermediate level of lighting (from 6 to 25%) already happen to prevail. This is caused by

shading due to tall grasses and abundant vegetative lime offsprings of immature ontogenetic stage.

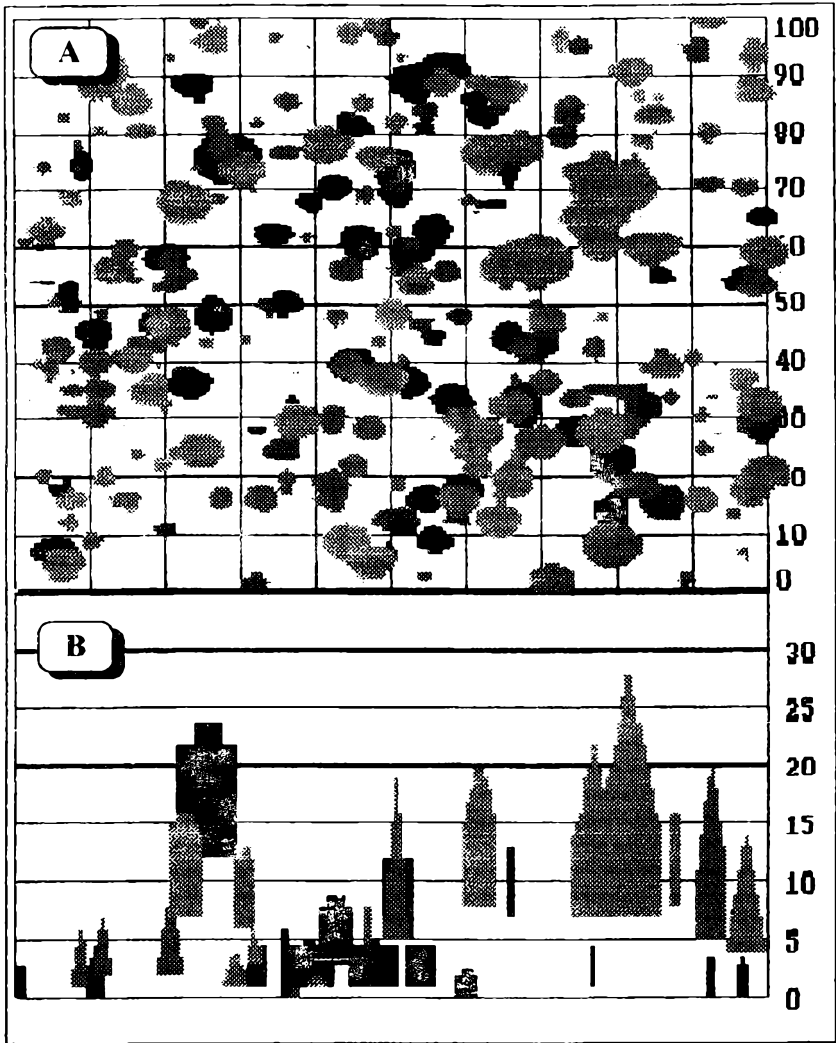


Fig. 14. Crown projection (A) and vertical section of tree layer (B) in fir-spruce oldgrowth in the SabarProtected Area.

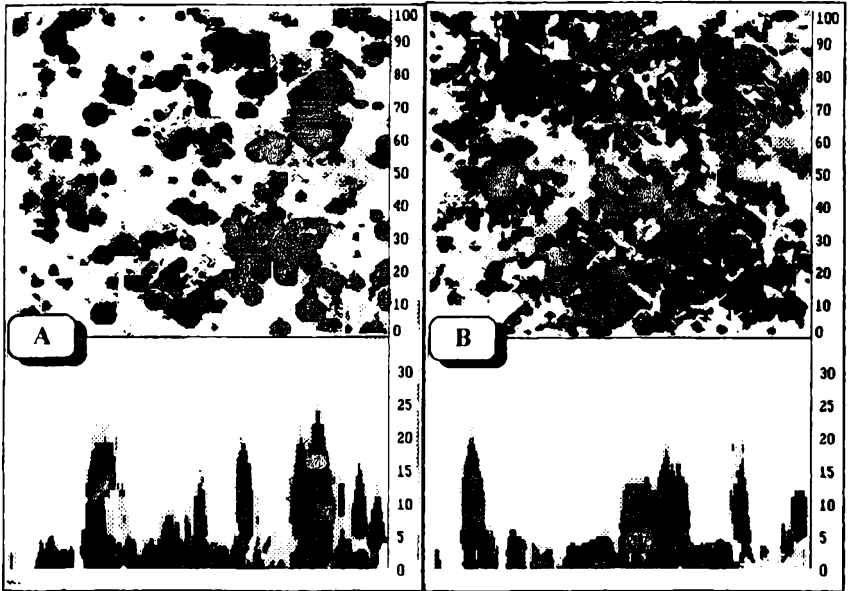


Fig. 15. Light mosaic under tall herb layer (A) and into it (B) *Computer simulation carried out by the data from the map of the permanent plot in the Sabar Protected Area.*

The lower parts of the Figure 15 present vertical sections of lighting fields, which indicate that light mosaic with considerable gradient exists not only at the level of regrowth, but on greater heights as well. Inside adult tree's crowns, there are highly shaded inner areas, where needle-bearing shoots die off, while new shoots do not appear from dormant buds.

Only insignificant number of microhabitats in the lower layer of the Sabar communities proves to be favorable for regrowth development. The situation is similar to that in communities of the northern variant of coniferous-broad-leaved forests. However, contrary to the CFBR forests, habitat elements limiting regrowth development by means of stagnant over-moisture are absent here. Aggregations of big herbs (*Urtica dioica* L., *Rubus idaeus* L., *Aconitum excelsum*

Reichenb. Stachys sylvatica L., Cicerbita uralensis Beauv., Aegopodium podagraria L., Matteuccia struthiopteris Torado) act as a limiting factor. They make 100% coverage and predominate in young gaps forming here a canopy practically impenetrable for light. In such microcommunities of tall herbs, juvenile and immature trees happen to stay for a long time in conditions of light deficiency. It seems that the group of tall herb species plays a role analogous to that of understory (shrub sinusium) in broad-leaved forests. Under shading influence of herbs, tree development and growth may undergo a considerable modification at the initial ontogenetic stages, responding to rhythm of development and degradation of population loci of tall herbs.

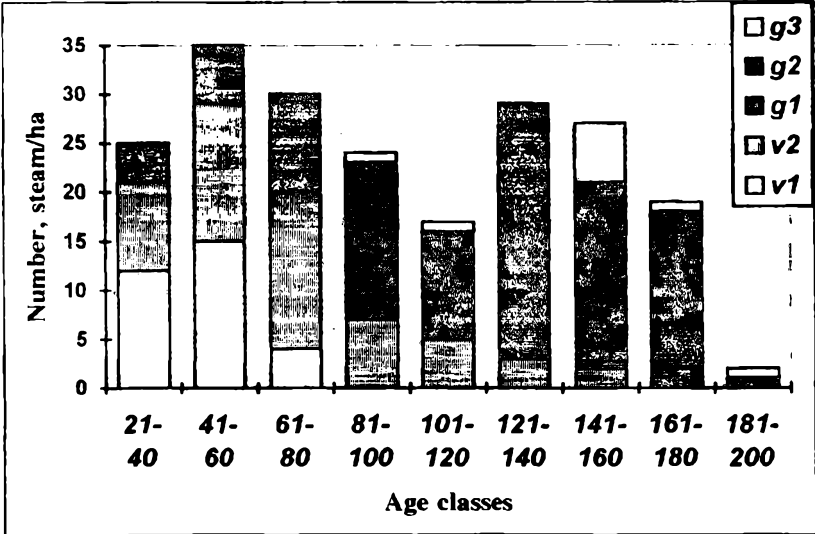


Fig. 16. Age differentiation of ontogenetic groups of *Picea obovata* Ledeb. population in the Sabar old-growth

Detailed analysis of calendar age of fir and spruce in the Sabar old-growth shows that every age group consists of individuals whose age differs for more than half a century (Fig. 16). Only in rare cases,

young trees of *Picea obovata* Ledeb. grow rapidly and reach virginile state in 20 years; much more often it takes 30-60 years. It sometimes happens that, even 80-years-old individuals, there is still much time to pass before they come to fruiting, as they have only recently formed crowns of adult shape.

A considerable developmental delay at the initial stages of ontogeny causes high mortality in the youngest age groups (number of virginile trees is just a little higher than that of reproductive ones). Later, the delay depends on the rate of growth and development of adult trees. Among mature reproductive trees, individuals of 60 to 200 years can be observed. Such a wide age range does not mean that adult trees are able to fruit abundantly for all the 140 years or that the trees, which start fruiting later than others, will live longer than others. Multiple substitution of the main axis and of lateral axes of the second order is leading to the delay of their development, disturbs the normal (for spruce and fir) monopodial type of growth. All these processes are usually accompanied by injuries, the latter increasing the probability of xylophagous insect invasions and fungal diseases (unpublished data by E.A.Prudnikov).

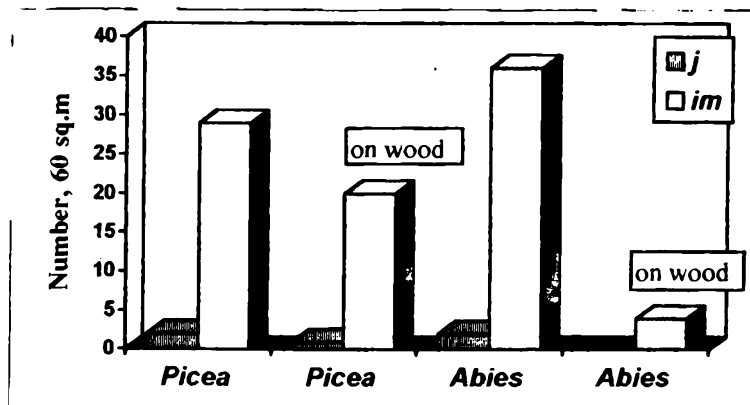


Fig. 17. Number of spruce and fir regrowth on decaying trunks and mineral substratum in the old-growth (the Sabar Protected Area).

Using the data had been collected in the uneven aged mixed stands of the Sabar Protected Area it is possible to show the importance of substratum-dependent mosaic. How the mosaic of habitat elements determines self-maintenance of tree populations one can see on the sites with sufficient light level for growth and development of young generation. Spruce and fir seedlings are observed in small numbers in various habitat elements. More long-lived outogenetic groups of juvenile and immature regrowth not only occur everywhere, but also happen to be more numerous than seedlings (apparently due to gradual replenishment with annually appearing seedlings) (Fig. 17).

Pairs of columns for each species given on the diagram, demonstrate an interesting regularity in distribution of young generation of conifers. In similar light conditions, immature spruce regrowth is considerably more numerous on decaying trunks (more than half of all the individuals) than on mineral substratum. For the case of fir regrowth, the ratio is inverse; the overwhelming majority of fir regrowth appears on soil surface. This means that the self-maintenance one of *Picea obovata* Ledeb. becomes highly impeded by substratum (i.e., the presence vs. absence of decaying wood). The *Abies sibirica* Ledeb. is characterized by successful germination of seeds on the ground, and its regrowth gradually become to dominance in secondary forests without decay woods.

The regeneration of mountain elm on old logs is as successful as that of spruce, while mountain-ash and birch regrowth are less numerous in such conditions. Seeded regeneration of lime and bird cherry is almost completely absent. Thus, such stress-tolerant species as fir, lime, and bird cherry, are dissimilar to spruce and species of ruderal strategy in that they do not need decaying logs for self-maintenance. These features of stress-tolerant species allow their populations permanently to exist in forests where decaying trunks are absent, i.e. in forests undergoing regular improvement (thinning) cuttings.

The dynamics of herb layer in gaps can be described as process with several stages. The sites where gaps of 20 m diameter are formed as a result of tree falls, the first to appear are aggregations with

dominance of *Urtica dioica* L. (abundance up to 4 grades) and *Rubus idaeus* L. (up to 4 grades). Projective coverage often reaches 100%. Besides that, other tall herbaceous species are sufficiently well represented: *Aconitum* (up to 3 grades, usually flowers), *Stachys* (up to 2 grades, flowers), *Cicerbita* (flowers, abundance rather low), *Aegopodium* (flowers, abundance rather low), *Calamagrostis* (not flowering as a rule); often *Matteuccia struthiopteris* Torado. is abundant. Three layers can be in herb synusium: the upper one consists of very tall shoots of *Urtica* and *Rubus*, the second -- include plants of middle size (*Aconitum*, *Aegopodium*, *Cicerbita*, *Calamagrostis*), and the lower one -- comprise small plants. If gap diameter is more than 30 m, *Matteuccia struthiopteris* Torado. dominate in herb aggregations, while *Urtica dioica* L. and *Rubus idaeus* L. act as codominants. In other respects, these aggregations are rather similar. Both aggregations indicate the first stage of tree fall gap afforestation.

At the second stage, the dominants are *Rubus idaeus* L. (2-3 grade's abundance) and *Calamagrostis arundinacea* Roth. (2-4 grades). Both dominants are characterized by abundant flowering and fruiting; the coverage is about 100%. Other tall herbaceous species are also sufficiently abundant: among them, *Aconitum* (usually flowers), *Equisetum sylvaticum* L., *Stachys sylvatica* L. (flowers), *Dryopteris austriaca* Woy. (abundance sometimes reaches 3 grades). Floriferous shoots of *Aegopodium podagraria* L. are met rather often. Herb synusium is usually three-layered. Small herbs locate in the lower layer, vegetative rosettes of *Aegopodium* and *Cicerbita* are in the middle layer, and annual and biennial shoots of *Rubus* and floriferous shoots of *Calamagrostis* grow to the upper layer. In these accumulations, regrowth is almost completely absent.

At the third stage, when lime regrowth is abundant, vegetative shoots of *Aegopodium podagraria* L. begin to predominate. Projective coverage is about 80%. Some other vegetatively mobile species, e.g. *Cicerbita uralensis* Beauv. (vegetative rosettes usually prevailing), can be relatively abundant. Herb synusium consists usually of two distinctly expressed layers. *Galium odoratum* (L.) Scop and others small species located in the lower layer. Taller plants, namely *Cicerbita*, *Aconitum* (vegetative and flowering individuals), some ferns species (mainly

Dryopteris austriaca Woyw.) occupy the upper layer. At the same stage, but in the locations with abundant conifer regrowth, very sparse herb layer exists. The low single-layered aggregations with coverage 30-40% are formed, and they are related to sites with the lowest light level. Maximal abundance (2 grades) is achieved by *Galium odoratum* (L.) Scop. Besides that, *Chrysosplenium alternifolium* L. and *Oxalis acetosella* L. are sufficiently abundant (2 grades).

Mapping of herbaceous vegetation on 120x120 m sample plot according to distinguished aggregations showed that aggregations of the first stage occupy from 6% to 8% of the total area. Those of the second stage cover 50-60%. The aggregations of the third stage with dominance of lime regrowth and that of conifers occupy 20-25% and 10-15% correspondedly (unpublished data of E.A. Krassil'nikov).

In the Visim nature reserve (northern variant of the Ural mixed forests), as well as in the CFBR, conifers (*Picea obovata* Ledeb. and *Abies sibirica* Ledeb.) are the dominants of the first layer. There is lime being a codominant in the second and third layers together with *Sorbus aucuparia* L., *Padus avium* Mill., and other species.

In nondisturbed fir-spruce forests with lime, all tree dominants have complete populations. In such communities, spruce reaches 200-230 years, fir -- 150-180 years and lime -- 80-120 years. Lime reproduction is exclusively vegetative, as in these conditions its seeds do not germinate (Chistyakova, 1978). The main part of spruce regrowth and half of fir regrowth are related to decaying trunks (Information materials..., 1975a, b, 1976, 1977). In the case of spontaneous development of fir-spruce forests with lime, identical state of stand is repeated every 550-600 years (Turkov, 1979b). In the works of English-speaking authors, this cycle is called "turnaround time". That is "the time necessary for the majority of species in a community to reach every patch in the community" (Van der Maarel, 1993, p. 735).

As in the Sabar reserve, *Rubus idaeus* L. predominates in gaps in the Visim forests, but the role of ferns is more prominent. Here, *Matteuccia struthiopteris* Torado., *Dryopteris austriaca* Woyw., and *D. filix-mas* Schott. act as codominants (more rarely, as dominants).

Unlike the Sabar reserve, *Urtica dioica* L. usually does not predominate in herb layer.

During the full cycle of gap afforestation, the following aggregations are formed: 1) spruce and fir regrowth and boreal small herbs; 2) mountain ash regrowth, nemoral species and tall herbs; 3) lime regrowth, nemoral and boreal species. For Visim unevenaged forests were evaluated that new gaps occupy 3.1% of area. Aggregations with lime, fir, and spruce regrowth (im, v) cover 14.3%, and aggregations with dominance of adult fir, spruce, and lime trees -- 82.6% (Information materials..., 1975a).

STRUCTURE AND DYNAMICS OF ANTHROPOGENIC MIXED FORESTS

The discussed structural and floristic traits of uneven aged communities can be observed only in a small number of forest tracts. Even on strictly protected areas, a great part of forest communities looks much unlike those mentioned above. The general features of anthropogenic successions in mixed forests are similar to those in broad-leaved forests. They are as follows: disturbance of ontogenetic structure of key species populations, disappearance of large mosaic, increase of stand density. However, concrete ways of changes in the composition and physiognomy of communities depend strongly on biomorphological features of trees, structure of herb layer, history of land-use, and the surrounding of forest tracts at present. American forest scientists in their last years' works have come to similar approach concerning anthropogenic dynamics (Romm, 1994).

In this work, anthropogenic transformations of forests are considered separately for two main types of disturbance. The first is

connected with using forest areas as agricultural lands (ploughing, haying, pasturing). After such disturbances, in southern part of plain mixed forests, secondary variants of communities are analogous to those in broad-leaved forests (East European broad-leaved forests, 1994) and are not discussed here.

Clear large-scale cuttings were widespread in northern part of plain mixed forests in the last 40-50 years. They may be considered as some kind of first type disturbances. Mechanized timber cutting with using caterpillar tractors and fire clearing of cuttings leads to complete transformation of forest habitats look like the ploughed fields.

Specificity of mountain forests is connected with virtually complete absence of ploughed areas within forest tracts and with hayfield and pasture formation without stump extraction. In these cases, even elimination of tree layer does not destroy the main set of forest herb species. They are retained and continue to participate in the composition of long-lived meadow communities.

Cuttings of different types in forests of different geographical variants lead to formation of quite different secondary communities. It is connected with bioecological traits of species forming tree layer and with different history of using concrete forest as a whole. Cutting area, cutting rotation time, intensity of stand exploitation, as well as location and size of forest tracts as a whole caused great difference in their present appearance. Unfortunately, it is impossible to give here a detailed analysis of all the existing variety of secondary forests. It is easier to show the main causes and the specific traits of restoration dynamics in the mixed forest zone and to trace its difference from the dynamics of floristic similar vegetation of broad-leaved forests.

Carpathian mountain forests (the first geographical variant) have been mainly transformed by cuttings. Agriculture on forest lands is not widely spread here, and non-woody communities are represented by pastures and hayfields which have never been ploughed up. On this territory, the prevailing management type was selective cuttings since the X-XII centuries till the middle of the XIX century.

All mixed and broad-leaved forests of the Carpathian are located within the area of *Fagus sylvatica* L. The presence of the latter species proves to be a determining factor of postcutting changes. Even selective

and mine cuttings have led to considerable gap decrease; they also have stimulated the formation of traumatic sprouts of beech. This tree possesses both high tolerance to light deficiency and high potential of vegetative reproduction. So it considerably increased its population numbers both by seeds and by vegetative offspring's. Fir and spruce positions have noticeably weakened. These species have also been completely lost from the composition of tree synusium of many communities, including uneven aged subclimax beech forests as well. The sequence of simplification or absence of gap mosaic in forests is lowering of species diversity of other synusia. Stands of high density change species composition of shrubs and herbs because suppress light demanding species. Thus, bioecological traits of European beech (one of the edificators of mixed conifer-broad-leaved forests) have led to appear completely new types of forest communities. Today, even on strongly protected territories, the consequences of the preceding cutting (selective management) are extreme in many cases. There is the restoration of uneven aged forest structure is not accompanied by the restoration of full species composition of tree layer dominants.

For example, let us consider the change of species composition and species proportions in beech-fir-spruce forests after selective and successive cuttings. As a result of this influence, the following tree species have disappeared from the tree layer: spruce (due to debris absence), birch, willows, and mountain elm (due to absence of large gaps). After installation beech-spruce communities with high density the shrubs are almost completely absent, and species composition of herb layer has been reduced by one third. A part of boreal species usually inhabiting debris (*Adoxa moschatellina* L., *Circaea alpina* L., etc.), as well as tall herb and nyctrophyte species have been lost.

In the last 100-150 years, clear cuttings have become widely used. On logged areas, spruce or more rarely fir were planted, and in the course of time such silvicultures were transformed into pure spruce or fir-spruce forests. Now they have different age, and dominance of boreal species in herb layer. In the modern forest cover, they occupy vast territories.

Summing up, we can state that both selective and clear cuttings have led to the replacement of the original mixed forests by different

types of pure stands. The scale of differentiation between them is so large that they are distinguished in the modern syntaxonomy as associations belonging to the two classes namely *Quercus-Fagetum* and *Vaccinio-Piceetum*.

Contrary to the Carpathian forests where the land use has retained uniformity for many centuries; in mixed forests of the Western Middle Ural foothills (the sixth geographical variant) forest exploitation has changed several times.

The aboriginal populations of the region are Tatar, Bashkir, Permyak, Meshcheryak. Russia assimilated the Ural-Siberian Region mainly due to deportees and members of conservative orthodox church. The drive of these peoples to the Ural Region in the second half of the XVII century seems to have been the first important migration of Russians to this region (Milovidov, 1979). This was the first wave of Slavic colonization of the Ural, but it did not result yet in considerable changes in vegetation structure. The forest exploitation and reclamation for meadows and fields had stood at the small scale and extend more likely just local.

The beginning of extent exploitation of ore deposits in the first half of the XVIII century was accompanied by forced migration of a great number of peasants from Central Russia. From this time on, the second wave of Russian colonization of the Ural had begun. Contrary to the first wave of colonization, vegetation transformations were as large scale forest cuttings and extent deforested areas of agrosylvopastoral lands near settlements. During 100 years numerous mines and industrial plants appeared (1631 -- Nitsinsk, 1700 -- Nev'yansk, 1761 -- Bisert, 1787 -- Arti). All these plants are working till the present time.

The Sabar Protected Area (southern fragment of mixed forests of the Middle Ural) was formerly the forest dacha (owner's unit) of the Arti state plants of the Zlatoust Mountain District. Till the initial forest inventory (1832-1837), forest use was here practically irregular (Central State Historical Archives, fund 37, list 13, file 287). Only decade later, the new rules of forest cutting were established, and they had set up alternate strip winter cuttings for avoiding regrowth elimination (Materials for statistics of the Krasnoufimsk District of the Perm'

Province, 1894). Along with clear and strip cuttings, the system of selective cuttings remained moreover became wider. By 1890, only 14% of the Arti's forest dacha had not yet suffered selective cuttings (Terinov, 1970).

Forest use on this territory led at first to the considerable increase of areas occupied by deciduous tree species (birch and aspen). Ageing of these forests transformed them into coniferous-birch-aspen ones on the areas where conifer seeding occurred. Since the second half of the XIX century when sparing regimes of timber logging had been introduced and fire clearing of logged areas was restricted; lime (mainly of sprout origin) began to play the main role in the afforestation. The regeneration of birch populations occurred only in places with local strong soil burning-down where brushwood was fired. Large portion of aspen offsprings was observed on deep well moistened soils (Terinov, 1970).

In the last decades, timber logging occurred in easy accessing areas, i.e., in even aged forests which have grown on the place of clear cuttings of the XVIII-XIX centuries. Forests which have been damaged by selective cuttings at the end of the XIX century (uneven aged coniferous-broad-leaved stands) by the present time have not undergone serious changes. Part of them was the subject of selective cuttings, while others have remained undisturbed.

Concerning the Sabar Protected Area, an estimate of recovery dynamics of the Ural foothill forests was made. Dynamic was studied for two types of forest use: 1) clear cuttings with elimination of ground cover and regrowth; 2) selective and clear cuttings preserving of ground cover or only regrowth. Forest restoration on cuttings of the first type begins with total invasion of tree species of ruderal strategy (birch, aspen) though these species live as assectators in uneven aged forests. In herb layer, ruderal and megatrophic tall herbs (*Urtica dioica* L., *Chamerion angustifolium* (L.) Holub, *Rubus idaeus* L., some *Compositae* species and forest-edge tall herbs) predominate. Sometimes, in the first 10-15 years, woody vegetation may be absent on considerable areas. Cuttings are covered all over with very tall and dense sward consisting of species of ruderal strategy. In rare cases tree population's

regeneration occupy the whole cutting area simultaneously. Mosaic of tree vegetation's expansion is caused by:

- 1) distribution of vegetative offsprings (lime, aspen)
- 2) location of safe sates for juvenile and immature individuals of tree species with easily flying seeds (goat willow, birch, aspen, spruce, fir)
- 3) soil disturbances.

Cuttings of the second type stimulate the appearance of abundant sprout offsprings and lead to the increase of tree canopy density. In these cases, sprouting species and those tolerant to light deficiency (lime and fir) get advantage in regeneration process. Spruce seems to be the most vulnerable species of edicator of coniferous-broad-leaved forests. The vulnerability increases as decaying wood disappears in the course of repeated cuttings. In herb layer of closed fir stands with lime, the role of boreal small herbs increases, though the forests are still not dense enough there (unlike forest plantations that are very rare in this region). As result, fir forests keep also highly diverse herb layer like mixed ones. State of shrub layer is quite different, as it is very sparse in secondary fir forests.

In the Middle Ural mixed forests where selective cuttings were used and hayfields were rather small, species composition of herbs is changed but slightly. Here, the key group of tall herb and nemoral species is characterized by high constancy in all secondary forest; whether they are fir, spruce, aspen or birch ones. The constants of such communities are: *Aegopodium podagraria* L., *Aconitum septentrionale* Koelle, *Asarum europaeum* L., *Pulmonaria obscura* Dumort., *Stellaria holostea* L., *Urtica dioica* L., *Viola mirabilis* L., *Calamagrostis arundinacea* (L.) Roth, *Myosotis sylvatica* Ehrh. ex Hoffm., *Cicerbita uralensis* Bauv., *Stellaria nemorum* L. Many of the listed species can be also met on small hayfields within closed forests, though a significant role there is also played by meadow grasses.

Shrub synusium in secondary forests happens to be much more disturbed. Only *Padus avium* Mill. has a relatively high frequency, i.e., it occurs in every third sample plot. The cause of this is species capacity for vegetative reproduction. Other species (*Sorbus aucuparia* L., *Rosa canina* L., *Sambucus racemosa* L.) may be observed very seldom.

Hay-glades in forests were made without tree stubbing, and they retain nemoral forest species and forest-edge tall herbs (*Bupleurum aureum* Fisch., *Crepis sibirica* L., *Veratrum lobelianum* Bernh., *Knautia tatarica* (L.) Szabo., *Heracleum sibiricum* L., etc.) in their composition. When afforestation by aspen occurs, these tall herbs find themselves under its canopy; such aspen forests are rather widespread in the Sabar. Spruce and fir may early invade into aspen forests. Then, at the late phases of mixed forest restoration, there appears also lime. It spreads from adjacent areas as the vegetative reproduction, but this process is very slow.

The Visim Reserve (northern variant of the Middle Ural mixed forests) is situated 200 km to the north of the Sabar Protected Area. There are archaeological data indicate the copper smelting as far as 3500 years ago, and the beginning of iron smelting and slash-and-burn agriculture as far as 2500 years ago (Raushenbakh, 1956; Bader, Oborin, 1958; Bader, 1964; Information data..., 1976).

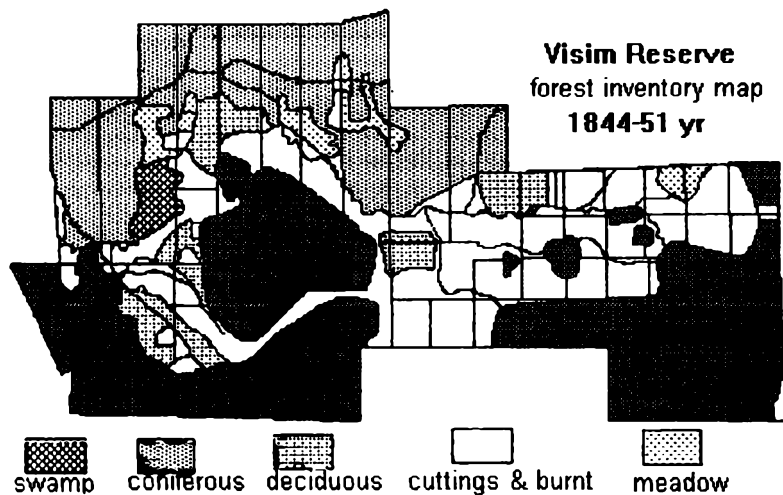


Fig. 18a. Ancient forest inventory map of the present protected areas; data from V.G.Turkov (1979a).

As in case of the Sabar Protected Area, the most significant transformations of forests of the Reserve are connected with the second wave of Russian colonization, when metallurgical plants were built. One of them was the Visim-Shaitan plant (1741) located on the territory of the modern Reserve office (Turkov, 1979a). Till the middle of the XIX century, charcoal procurement on the territory of the modern Reserve took place on large areas while separate locations. The extent logging and burned areas appeared and fragmented continuous uneven aged forests (Fig. 18a)

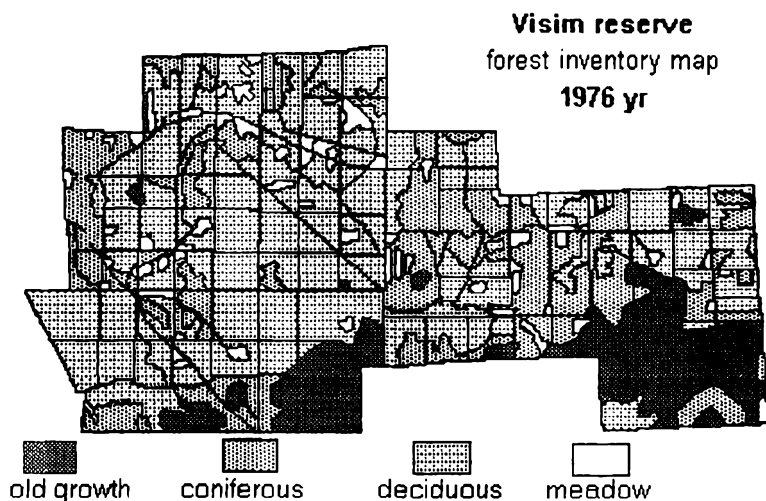


Fig. 18b. Present forest inventory map the Visim Reserve; data from V.G.Turkov (1979a).

During 200-300 years, dark coniferous or pine-spruce forests had grown on the former fire and cutting areas where conifer seedling occurred; during the last 100-150 years pine forests with spruce and fir regrowth. On extremely large fire and cutting areas, conifer seedling did not occur even after 100-150 year's period, and here old sparse birch-

aspen forests of park type exist. The present-day distribution of old growth and disturbed forests is shown in Fig. 18b (Turkov, 1979a).

In the forests of the Central Russia (the fourth geographical variant), consequences of anthropogenic transformation of woodland landscapes are shown with reference to the "Bryansk Forest" Reserve (southern part of mixed forests). These landscapes are mainly formed by fluvio-glacial and alluvial sandy deposits underlain by moraine loams. In some places, moraine loams are exposed to daylight forming the richest habitats.

Everywhere the Eastern Europe, sandy soils of woodlands have been cultivated since the Early Neolithic. Quick depletion of this soils caused broad extension of pine forests on abandoned fields. Further dynamic of pine forests was closely connected with fires and cuttings. By the end of the XVIII century, one third area of the modern Reserve was occupied by pine forests. The rest of the territory was covered by mixed and birch-aspen forests. Though the last two centuries, there have been no large-scale ploughing forest use included tar extraction, charcoal burning, potash making, and cuttings of different types (unpublished archive data obtained from T.V. Belyaeva).

Selective cuttings on these wood lands result strongly in spruce populations. Its populations have been reduced in numbers and are rather sparse. The reproduction occurs exclusively on decaying trunks, but dead logs are few in modern stands. So this species is almost lost from the composition of tree layer.

In secondary forests on light sandy soils, populations of ash, elm, aspen, lime, and maple disappear from stands according to decreasing of their demand for soil fertility. Here, light regime under forest canopy does not limit reproduction of species because one can see a plenty regrowth of the highly light-demanding edicator of mixed forests -- *Quercus robur* L. In herb synusia only species of boreal group tolerant to poor soils remain in the forests.

In communities on moraine loams, only the most nitrophilous species namely ash and elm are lost from tree synusium at the first stages of anthropogenic digression. In herb synusium, the number of nemoral and nitrophyte species decreases, while the percentage of boreal species is one and a half times higher. Besides substratal

differences, clearing of gap mosaic get advantages for species with low light demanding and capable to reproduce vegetatively. Under dense canopy, the Norway maple and lime regrowth is most abundant (Table 3). despite oak dominate in the upper layer. As in forests of the Sabar Protected Area, spruce disappears along with disappearance of large decaying trunks in secondary forests. For example, ontogenetic spectra of woody species in lime-maple community of the "Bryansky Les" Reserve (compartment 39, unit 4) are presented.

Table 3.

Ontogenetic spectra of tree populations after clear cutting.

| Species | Ontogenetic groups, indiv. per ha. | | | | | | Total number |
|---------------------------|------------------------------------|------|------|----------------|----------------|----------------|--------------|
| | j | im | v | g ₁ | g ₂ | g ₃ | |
| <i>Quercus robur</i> | 22 | - | - | - | 156 | - | 178 |
| <i>Acer platanoides</i> | 5956 | 911 | 89 | 40 | - | - | 6996 |
| <i>Tilia cordata</i> | 178 | 1800 | 1511 | 133 | - | - | 3622 |
| <i>Betula pendula</i> | - | - | - | 90 | 45 | - | 135 |
| <i>Populus tremula</i> | 134 | - | - | - | - | - | 134 |
| <i>Sorbus aucuparia</i> | - | 22 | - | - | - | - | 22 |
| <i>Corylus avellana</i> | 20 | 202 | 25 | 42 | - | 21 | 310 |
| <i>Euonymus verrucosa</i> | 911 | 1356 | 44 | - | - | - | 2311 |

The extreme variant of mixed forest degradation on sandy and sandy-loam substrata is monodominant pine forests with dominance of boreal species in herb layer. Most these pine forests appeared as a result of forest planting at different time. Their spreading is connected with planting practice which had begun in the middle of the last century recommended by the circular letters of the Forest Department (Tsvetkov, 1958). Now pine populations consist only reproductive

trees; and under the pine canopy populations of deciduous trees (especially of oak) are numerous. This indicates that the modern pine forests will be with time replaced by deciduous stands.

In the northern part of the Central Russia, the modern forest management is the large-scale cuttings. Such cuttings were used last fifty years and led to elimination of original vegetation almost everywhere. Afforestation is mainly determined by the possibilities of dominant tree species to invade on woodless areas.

The general schemes of forest restoration on large cuttings include the following phases (Ibragimov, Poluyakhtov, 1982): (1) dead cover, (2) herb-meadow, (3) tree-shrub open stand, (4) pioneer tree's closed stand, (5) mature stand of climax tree species.

Community dynamic is determined by a complex of factors (Melekhov, 1954):

- by type of cutting and its rotation,
- by forest type (environmental conditions of natural forest),
- by presence or absence of seed bearing trees,
- by conservation of the safe sites for seedlings,
- by degree of soil disturbance, etc.

The highest diversity of plant communities during secondary successions is observed at the initial phases of afforestation corresponding to mixed-spotted thickets moreover to herb-meadow and shrub vegetation. If use the types of logging area which is the traditional for Russian scientists (Melekhov, 1954; Nilov, 1967; Tikhonov, 1979) one can distinguish several community variants. They differ by dominants in herb layer and environmental conditions.

In the Northern Central Russia the following types of logging area are most frequent: wood-reed, fire-weed, fire-weed-wood-reed, haircap-moss, raspberry, dropwort, rush, nemoral, and clumpy-pine communities. The parameters of herb layer (sodding degree, rate of herb litter destruction and mineralization, photo-optical characters of canopy, etc.) determine seedling survival and, consequently, structure of tree canopy in the future (Fig. 19).

Secondary birch and aspen forests on the logging areas represent rather wide spectrum of associations: *Rhodobryo-Piceetum*, *Quercopiceetum*, and *Vaccinio-Piceetum*. In nemoral birch and aspen forests,

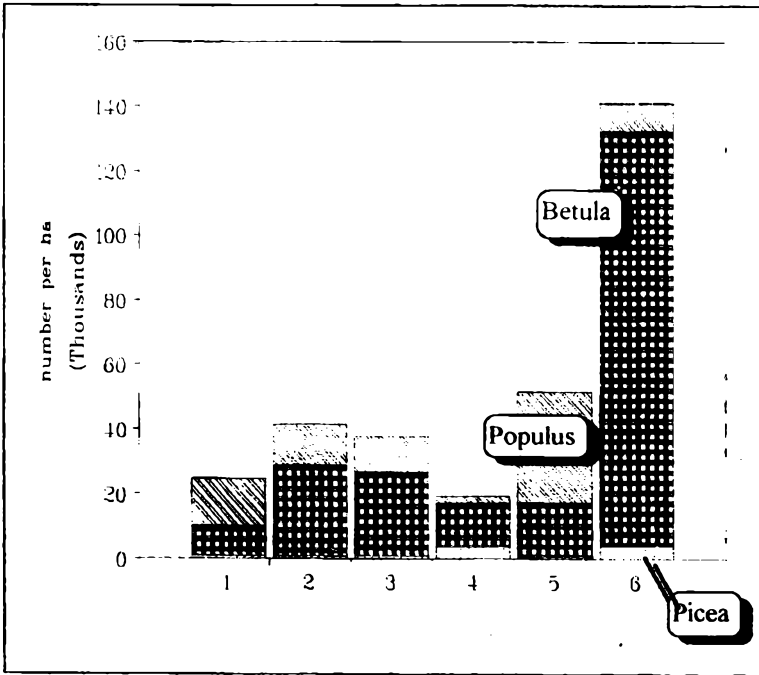


Fig. 19. Numerosity of trees regeneration in different types of clearcuttings, according (Nilov, 1967); types of cutting: (1) *Calamagrostis* type, (2) *Chamerio-calamagrostis* type, (3) *Nemoral* type, (4) *Rubus* type, (5) *Lichen* type, (6) *Chamerion* type.

considerable abundance of broad-leaved tree species is observed in regrowth and tree layer. Another group of secondary forests is formed by associations of *Alno-Padion* union, *Quercus-Fagetea* class.

In most cases, invasion of populations of species predominating in original (precutting) communities does not happen at once. During the first 15-40 years after cutting, there occur changes in stand structure connected with change of the role of species with ruderal strategy. After that, the proportion of spruce and broad-leaved species in secondary communities becomes noticeable. The most widespread directions of transformation of spruce-broad-leaved forests in the

Central Russia into secondary stands are generalized in the (Fig. 20; according to Kurniaev, 1968; Rechan et al., 1993, with changes).

Changes occurring in the structure of secondary forests throughout more than 150 years can be illustrated by a concrete example. According to archive data, it has been established that a fragment of meadow with shrubs of about 900 ha existed on the CFBR lands in the forties of the previous century (Karimov, 1994). It is most likely that one of the initial phase of afforestation of abandoned ploughed fields and logging area (non closed young stands) had been recorded on the archive map. The materials of the 1939 forest inventory for this territory show that, 100 years earlier, communities reached the phase of mixed forests. Instead of adult birch and aspen trees that had died off, 50-80-year old trees of spruce and broad-leaved species appeared in tree layer. Up to this moment, isolated big pine trees (their age being 200-250 yr) still happened to exist in the composition of mixed communities, these trees seem to have been growing sporadically on the former meadow with shrubs as well. At present these forests have reached the phase of mixed, relatively age-heterogeneous spruce communities in the most fertile habitats, and the restoration of mosaics typical of mixed forests is observed here. In poorer wood-sorrel and fern spruce forests one can observe in most cases classical (described by G.F.Morozov) process of replacement of birch-aspen stands by pure spruce stands without any admixture of broad-leaved species. Thus, 150 years after the beginning of regeneration process, spruce dominance in the first layer is established. Simultaneously, there begins the formation of heterogeneous structure of stand with tree synusium represented by fewer species than in initial uneven aged spruce-broad-leaved forests. According to A.V.Pugachevskii's (1992) data, a restoration of age-heterogeneous climax structure of stands lasts 600 years. The evaluations of this process duration (i.e. the process of formation of uneven aged spruce forests in fire areas or in the place of even aged birch-aspen forests) close to that mentioned above were obtained by P.V.Voropanov (1950); they are 550 years in case of spruce forests of the north of European Russia.

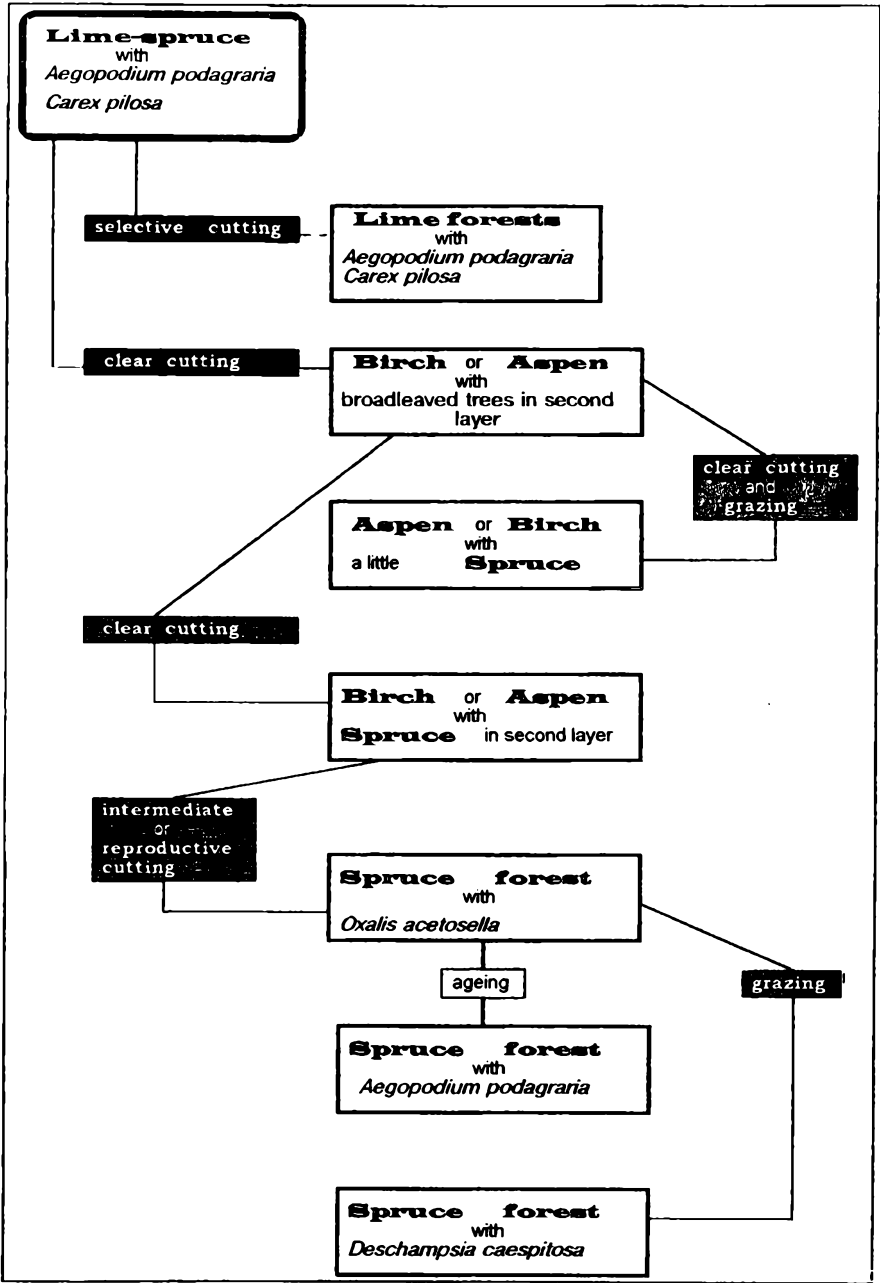


Fig.19. Scheme of succession of the mixed forest in Central Russia

In the forests of the Volga left bank (the fifth geographical variant), some differences can be traced in dynamics of secondary communities in southern and northern parts of the mixed forest zone. In its south part (the Volga-Kama Reserve and the lower reaches of the Vyatka river), selective cuttings have led to fir and spruce disappearance from community composition (Porfir'ev, 1947). The same phenomena have been noted for Chuvashia forests (Pletneva-Sokolova, 1952). In the place of mixed forests, there appeared broad-leaved communities usually with lime dominance. The role of spruces and fir decreased already 100-150 years ago due to general decrease in forested area on this territory (Porfir'ev, 1947, 1961). In case of all other cutting types, changes of forests in southern part of the zone occurred in the same way as in broad-leaved forests.

In central and northern parts, selective and clear cuttings with elimination of regrowth and herb layer led to the decrease spruce proportion and to the increase one of fir and lime. The cuttings of the same type combined with pasturing and lime barking led to absolute dominance of fir. As a rule, these are forests around settlements (Zhilkin, 1928; Vasil'ev, 1935).

CONCLUSIONS

Historical analysis of coniferous-broad-leaved forests allows to conclude that their recent subdivision is largely the consequence of traditional land use management. Development of industry influence structure and dynamics of both slightly disturbed (in the past) and strongly disturbed forests. Forest's usage transforms their state in different ways in the northern and southern parts of their area.

In the southern part of coniferous-broad-leaved forests the overall had been decreased the wooded areas. This process together with different kinds of cuttings leads first to the disappearing of dark coniferous species (spruce and fir) connected with the lacking of decaying trunks necessary for seeded reproduction and with the

decrease of air moisture. All these phenomena lead to the shift of southern borderlines of *Picea abies* (L.) Karst., *P. obovata* Ledeb. and *Abies sibirica* Ledeb. areas to the north moreover to the formation of pure broad-leaved forests instead of coniferous-broad-leaved ones.

In the northern part of coniferous-broad-leaved forests' cuttings and burning have led to the increase of bogging and to the decrease of nemoral species diversity. At the same time the decrease of broad-leaved species density in these forests was caused by the development of traditional land use as well as by wide distribution of spruce plantings. As a result, forests similar to southern tajga appeared instead of communities with equal proportions of coniferous and broad-leaved species.

Descriptions made in several fragments of slightly disturbed forests allow to reveal the main features of coniferous-broad-leaved forests of preagricultural type:

- 1) completeness of ontogenetic spectra of the main edificators;
- 2) clearly expressed mosaics in tree layer;
- 3) connection of general herb layer mosaic with the main elements of windfall-hillock complexes.

The floristic specificity of coniferous-broad-leaved forests finds its expression in relatively equal participation of nemoral, boreal and tall herb species in its composition. Structural specificity of tree layer depends on narrow-conical crown shapes which cannot be observed in mature broad-leaved trees. This peculiarity leads to the better lighting in the gaps of smaller size in comparison with those in broad-leaved forests.

Anthropogenic disturbances (cuttings, ploughings, burnings etc.) lead both to the changes in taxonomic composition of all synusia and to the simplification of ontogenetic structure in the populations within tree synusium. Turning of the coniferous-broad-leaved forests into broad-leaved ones as a result of clear or selective cuttings diminishes the contribution of boreal and nemoral species in herbaceous layer. The dominants of broad-leaved forests get the absolute prevalence. The appearance of communities with coniferous dominants leads to the

predominance of boreal species in herb layer. In both cases the tall herb species appear to be the most vulnerable. They are usually the most light-demanding and sensitive to the soil fertility.

The bringing out of preservation regime may lead to the decrease of species diversity in the cases of strongly transformed communities with the areas many times exceeding those necessary for effective propagation of species inherent to the flora of coniferous-broad-leaved forests.

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