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ONTOGENY OF A TREE

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The concept of the discrete ontogenesis of plants, by the first, was made by T. A. Работнов (1950). Detailed ontogenetic researches of tree plants had begun since 1970th. At present, the most tree species ontogeny have been described in the East-European forests. Development of all plants has the universal periods that we divide into the structural-functional stages. The last ones were named «ontogenetic stages». The ontogenetic stages mark biological age of plants. Individuals of different species show quite similar enlistment of ontogenetic stages. Each stage in marked by specific growth and morphological characteristics. The plants of the each ontogenetic stage can be distinguished by vitality level. Each vitality level is characterized by specific signs. The vitality of plants may be changed many times during ontogeny. The plants of different life forms and type of propagation have specific traits of ontogeny. The species show high individuality of ontogenetic behavior; it is clear especially in the heterogeneous natural forest community. These results we take into account as a basis for forecast of behavior of species and their groups in permanent changing mosaic environment of natural community.

Key words: ontogeny, biological age, ontogenetic stages, vitality level, life forms.

Ontogeny is a process of both structural and functional development of an organism' from its birth to death. The genetic program of this process is expressed in unstable environment, in natural community created by species coexisting together. So we can consider the development of such community from the ontogenetic point of view, i. e., as a set of complementary processes of both individuals and populations development. The comparative study of ontogeny of all species making up the community could be considered as a basic tool for the study of community functioning and development. In order to carry out this approach a concept adequate for comparison of ontogenetic features of various species have to be introduced. Ontogeny is a continuous process. Its duration may be characterized not only by physical time (years, months, etc.) but also by biological time inherent to organism's life (Harper, 1977; Passeker, 1977; Grubb, 1979). Division of the continuous ontogenetic proces into functional stages allows to obtain the coherent scales of biological time for different species with different life span. This approach is developed in the works of Russian botanists under the name of the «concept of discrete ontogeny» (Работнов, 1950; Уранов, 1975; Ценопопуляции..., 1976, 1988; Rabotnov, 1978; Gatzuk et al., 1980; The population structure..., 1985).

A detailed study of ontogeny of a lot of species in different communities gives us possibility to state the main principles of this concept.

1. Continuos process of individual plant development may be subdivided into several stages on the ground of structural indicators which reflect functional importance. There are: the presence vs. absence of embryonic, juvenile or mature morphological features; the ability of an individual to reproduce or to propagate vegetatively; the ratio between alive and dead as well as growing and non-growing plant parts.

2. Ontogenetic stages are universal and adequate for plants of various life forms. Ontogeny of plant organism is subdivided into 4 periods and 9 stages (I. Latent period (seed); II. Pre-reproductive period (seedling, juvenile, immature, virginal); III. Reproductive period (young, mature, and old reproductive); IV. Post-reproductive period (senile)).

3. Individual development may be expressed by different ways (polyvariant ontogeny). The polyvariant ontogeny means both temporal and structural diversity of ontogenetic pathways. Temporal variations are expressed in: a) developmental delays, i. e. longer duration of certain ontogenetic stages occurring in unfavorable conditions comparing with the same stages duration in optimal habitats; b) omission of some ontogenetic stages; c) recurrence to earlier ontogenetic stages. Structural variations are expressed in: a) different vitality; b) different life forms; c) different types of propagation.

4. There are no direct correlation between ontogenetic stages and calendar age.

The aim of our study is the analysis of tree synusium in the East European forests from the ontogenetic point of view.

Materials and methods

Field data were collected in 45 areas in Ukraine, Belarus and Russia during 20 years. The field work consisted of two stages. At the first stage model trees of each species were selected (22 tree species were studied). The following parameters were measured for each model tree.

I group. Size parameters: tree height (m); length of primary and secondary crowns (m); crown radii along cardinal directions (N, O, S, E) (m); annual elongation of frame branch (cm); length and width of a leaf or a needle (mm); diameter of trunk at the soil level (cm); diameter of trunk at breast height (cm); length of the trunk part covered by periderm or bark (crust) (m); diameter of root system (m); depth of root system (m); biomass of trunk and branches, i. e., woody biomass (kg); biomass of leaves or needles (kg); leaf surface area (m^2).

II group. Numerical parameters: calendar age (year — yr); order of branching; number of leaves (needles) per annual shoot; number of dead branches; number of seeds; number of anchor roots; number of replacements (substitutions) of leader axis.

III group. Qualitative parameters: shape of primary or secondary crown; leaf (needle) shape inherent to different ontogenetic stages; type of crust (bark) and the extent of its cracking; type of root system; type of diaspore giving rise to the tree.

These statistically verified quantitative and qualitative data were used for compiling the list of diagnostic indicators used for determination of ontogenetic stages, vitality level and other ontogenetic parameters for each tree species (Заугольнова, 1968; Чистякова, 1979; Буланая, 1985; Полтинкина, 1985; Диагнозы и ключи..., 1989; Смирнова и др., 1989; Махатков, 1991; Недосеко, 1993).

At the second stage of our study we set up sample plots (from 1 to 4 ha). Then we determined the ontogenetic stage, vitality and type of propagation for each tree in these plots using diagnostic parameters listed above. Statistical processing and analysis of these data gave us the opportunity to reveal both general and specific ontogenetical peculiarities for tree species under consideration.

Results and discussion

The general description of the ontogeny of tree species

On fig. 1 the sequence of ontogenetic stages of tree plant with different vitality levels is shown. The ontogenetic stages of tree plant have following features.

Seed is characterized by size and biomass, degree of embryo development, duration and type of dormancy, nutrient storage.

Seedling (p) usually possesses partially heterotrophic nutrition type, i. e. it uses both the substances of the maternal plant stored in seed and its own assimilates. It usually consists of cotyledons (which may be either aerial or subterranean), primary shoot, and primary root.

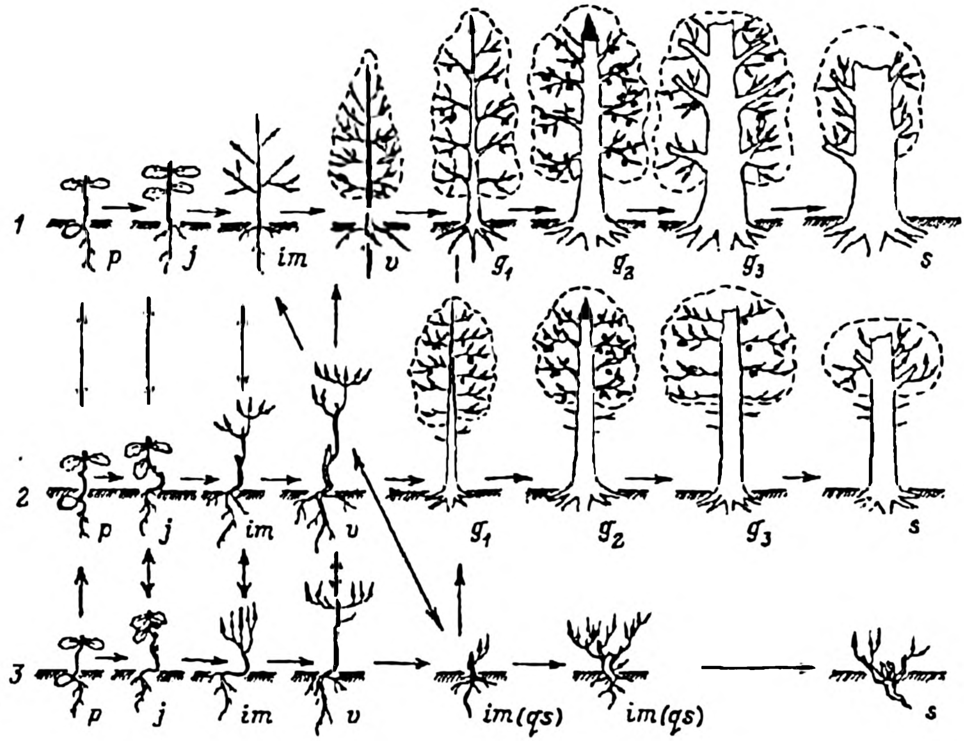

Fig. 1. Scheme of ontogeny of deciduous tree of different vitality.

Vitality: 1 — normal, 2 — subnormal, 3 — low. Arrows mark the transition between vitality levels. Ontogenetic stages: *p* — seedling, *j* — juvenile, *im* — immature, *v* — virginile, g_1 — young reproductive, g_2 — mature reproductive, g_3 — old reproductive, *qs* — quasisenile, *s* — senile plant.

Juvenile plant (*j*) usually demonstrates structural simplicity. It already loses the cotyledons, however it possesses some other embryonic structures. Juvenile tree has a small unbranched primary shoot bearing juvenile leaves or needles. Its root system consists of primary root and few lateral ones. Plant in this stage shows maximal shade tolerance.

Immature plant (*im*) demonstrates structural peculiarities which are transitional between juvenile and mature ones. A plant begins to ramify at this stage so its shoot system consists of branches of low order, though a definite crown shape is not formed yet. The leaves or needles display mature form and structure; the exceptions are the species with compound leaves. The root system includes either entire primary root or its residuals, lateral roots of second and higher orders and for some species adventitious roots.

Virginal plant (*v*) has mature features mainly. It is a young tree with distinct trunk and crown. The trunk is covered only with periderm, and branch order increases. Root system includes a taproot (or residuals of primary root), lateral roots of several orders, and adventitious roots. This plant does not produce seeds, but it has maximal annual increment of a leader shoot. Both monopodial and sympodial trees have a crown of elongated shape with distinct leader axis. This stage is a cardinal point of ontogeny, because the light demand increases sharply.

Young reproductive plant (g_1). It is similar to the adult tree. The reproductive structures apprear, the seeds are located within an upper part of crown, however the number of seeds is rather small. The tree growth in height is fast, but the branching order increases relative to trees of pre-reproductive period. The upper part of the trunk is covered with periderm while the lower one bears thin and smooth bark. Trees from *j* to g_1 ontogenetic stages show general strengthening of growth processes.

Mature reproductive plant (g_2) demonstrates the decrease of a rate of the vertical growth while the radial increment becomes maximal. The crown and root system also reach their maximal size and maximal branching order. The bark becomes more rough so it is clearly visible on the trunk. The seeds develop in both upper and middle parts of the crown; the number of seeds is maximal. Trees of g_2 stage show stabilization of all the parameters. The plant at this stage is the strongest one, but it shows some traits of aging. They are as follows: reducing of annual increment of lateral branches; ceasing of apical growth of few frame (skeletal) branches; opening of dormant buds and thus appearing of secondary crown; some anchor roots dying off.

Old reproductive plant (g_3) ceases the height growth, radial increment is very small. The size of both crown and root system decreases because many frame branches and anchor roots had died off. The secondary crown may in some cases replace the primary one. Tree biomass is still large due to the continuous increase of trunk diameter. The bark is rough and deeply fissured on both the trunk and frame branches. Seeds appear irregularly and their number varies.

Senile plant (s) has alive shoots in secondary crown only, and the leaves may be of the juvenile type. The upper parts of the crown and trunk are lost; the root system is destroyed. Seeds do not appear at all. Trees of g_3- and s-stages show suppressed growth.

Description of vitality levels

We have assumed that the vitality level could be changed at each ontogenetic stage if the conditions become unfavorable. Our own investigations and work of other authors (Ценопопуляции..., 1976, 1988; Смирнова и др., 1989; Махатков, 1991) confirm this assumption. Trees of all vitality levels were found in many natural forests. We distinguish three levels of vitality in most cases (fig. 1).

1st level. Normal vitality. It usually occurs in optimal conditions. Plant has maximal size, biomass, and life longevity relative to other trees at the same ontogenetic stage growing in other habitats. The tree of normal vitality grows and develops without delays, omissions and recurrences of ontogenetic stages. Size and biomass increments strongly correlate with calendar age till senile ontogenetic stage. Quantitative traits of vitality depend on geographical region.

2nd level. Subnormal vitality. A plant has smaller size and biomass compared with the normal one. Pre-reproductive period (p, j, im, v) is longer, reproductive (g_1, g_2, g_3) and post-reproductive (s) periods are shorter relative to a plant with normal vitality. The tree top may occasionally die off, so monopodial species become similar to sympodial ones. Residuals of dying tops are visible on the trunk.

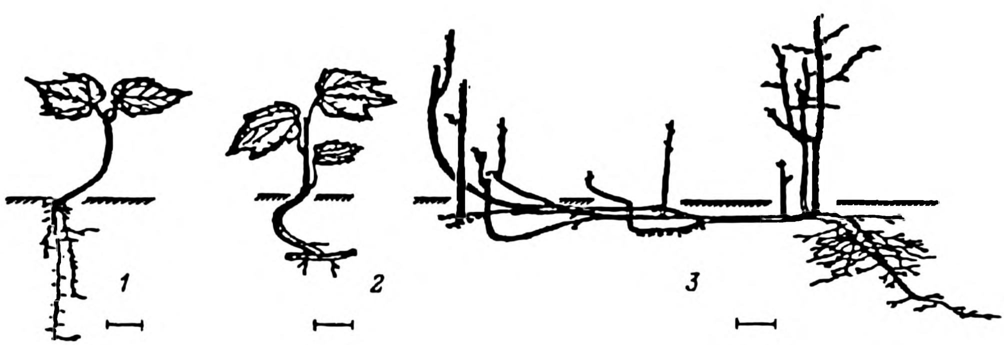

Fig. 2. Young trees of *Tilia cordata*.

1 — seed generation, *2* — vegetative generation, *3* — development of epigeogenic xylorhizomes. Bars: *1*, *2* — 1 cm; *3* — 20 cm.

3d level. Low vitality. A plant has minimal size and biomass, and it grows very slowly. Tree top frequently dies off, and a crown has many dead branches. Ontogeny of a tree may be incomplete because some ontogenetic stages are omitted or the latest stages are absent. The omission and recurrence of ontogenetic stages are connected with dying of aerial part of a tree. Restoration of trunk and crown takes place due to the shoots produced by dormant buds on the trunk bottom. Such a way of restoration is inherent to deciduous trees (fig. 2). Conifers cannot restore trunk and crown completely by means of dormant buds activation but they survive by elfin forms as well as deciduous trees. Size and biomass increments are not correlated with calendar age, this trait being specific for 2 and 3 levels of vitality. Moreover, trees may change their level of vitality several times during ontogeny.

Life forms and types of propagation

All ontogenetic peculiarities mentioned above also depend on propagation unit (seed or vegetative diaspore) giving rise to the tree, on type of propagation, presence vs. absence of vegetative offspring's and life forms. The new trees may arise either from vegetative diaspores or from seeds, but in both cases their development always starts from juvenile stage. Ontogeny of trees, arisen from different propagation units, differs only quantitatively, i. e. the limits of quantitative parameters may be different. Strength and life span of vegetative offspring's is determined by the type of diaspores; the latter may be dormant buds situated either on the trunk bottom or on xylorhizomes, and adventitious buds on roots. Type and diversity of diaspores depend on the life form of a plant. Special ontogenetic studies (Чистякова, 1979; 1988; Полтинкина, 1985; Буланая, 1985; Недосеко, 1993) show great diversity of life forms as well as pathways of their development for deciduous and coniferous trees (table 1).

«Monotrunk» (monocaulous) life form possesses only one trunk, its ontogeny starts from a seed. Occupation of a new place occurs also by seeds only. Compact «polytrunk» (polycaulous) life form has few trunks, but a parent tree arises from seed. The subsequent generations of trunks appear from dormant buds situated on the basal part of the parent trunk. The vegetative offspring's are of two types: first, possessing adventitious roots, and second, lacking them. The second type usually has shorter life span than the first one. Diffuse «polytrunk» life form develops just in the same way as compact «polytrunk» one but new trunks are distant from the parent tree. Vegetative offspring's appear either on hypogeogenic and epigeogenic xylorhizomes (stems) or on roots. Vegetative offspring's always have adventitious roots and are distant from the parent tree. Elfin form is very similar to the diffuse «polytrunk» one (xylorhizome variant), but consists of juvenile and immature ramets only.

Some peculiarities of ontogenesis on the example of the model species

Picea obovata Ledeb. It is the monopodial monotrunk tree, architectural model Massart (Halle et al., 1978), which propagates only by seeds. The modification of its habitus in the course of life history is shown on fig. 3. All ontogenetic stages for trees with normal vitality are shown except seedling stage, for trees with the low vitality only three ontogenetic stages are presented. The main feature of *Picea obovata* habitus (shared by *P. abies* and *Abies sibirica*) is the prevalence of the leader axis in the crown during all life history. The trees of the normal vitality have always a monopodial leader axis. As a rule, the decrease of vitality level leads to the tree top dying off, so the leader axis becomes sympodial.

The trees with subnormal and especially with low vitality are often devoid of the tree tops, so their annual terminal elongation is considerably reduced. These trees have a small height and they may probably die because of light deficiency. The crown shape changes from one ontogenetic stage to another, and these transformations seem to be similar for the individuals of all vitality levels. Initial shape of crown (immature plant) is widely

TABLE 1

Life forms and type of vegetative propagation of various tree species

N group	Species	Mono trunk	Polytrunk				Elfin
			Compact		Diffuse		
			aeroxylic	geoxylic	geoxylic		
			butt sprouting without adventitious roots	butt sprouting with adventitious roots	xylorhizome sprouting;	root sprouting;	xylorhizome sprouting;
1	*Pinus sylvestris* L.	+					
	Picea abies (L.) Karst	+					
	P. obovata Ledeb.	+					
	Betula pubescens Ehrh.	+					
	B. pendula Roth	+					
	Fagus sylvatica L.	+					
	Ouercus robur L.	+					
2	*Populus tremula* L.	+				+	
	Abies sibirica Ledeb.	+					+
	Acer pseudoplatanus L.	+	+	+			
	A. platanoides L.	+	+	+			
	Salix caprea L.	+	+	+			
3	*Sorbus aucuparia* L.	+	+	+	+		
	Fraxinus excelsior L.	+	+	+	+		
	Carpinus betulus L.	+	+	+	+		
	Alnus incana (L.) Moench	+	+	+	+		
	A. glutinosa (L.) Gaertn.	+	+	+	+	+	
4	*Ulmus laevis* Pall.	+	+	+	+	+	
	U. glabra Huds.	+	+	+	+	+	
5	*Acer campestre* L.	+	+	+	+		+
	Tilia cordata Mill.	+	+	+	+		+
	Padus avium Mill.	+	+	+	+		+

pyramidal or umbrella-like. The crown of mature tree is narrow pyramidal in the virginal stage, then it becomes cylindrical with very obtuse cone on the top when the tree reaches old reproductive stage. Crowns of mature trees are heterogeneous lengthwise and therefore may be subdivided into four parts. The first one is the top region which bear needles both on the leader axis and on all lateral branches. Branching order is up to 2—4. The second part of crown has only one kind of lateral shoots namely those appearing from buds lacking period of dormancy (buds of regular renewal). Needles occur on all branches except the trunk; branching order is 4—5. The third part of a crown is distinguished by the awaking of dormant buds on the frame branches. This process begins from basal part of branch and results in formation of secondary shoot system. As a result, frame branches have two types of shoots namely ones appearing from buds of regular renewal (primary shoots) and those produced by dormant buds (secondary shoots). Branching order of the first type shoots is 5—8. The secondary crown produces assimilatory surface significantly larger than the primary crown does (Gruber, 1988). The fourth part of the crown contains the frame branches with a few living shoots. The shoots are either primary or secondary. The ability to create the secondary crown allows the tree to grow and produce seeds for longer period of time. All parts of the crown may be clearly distinguished on the adult

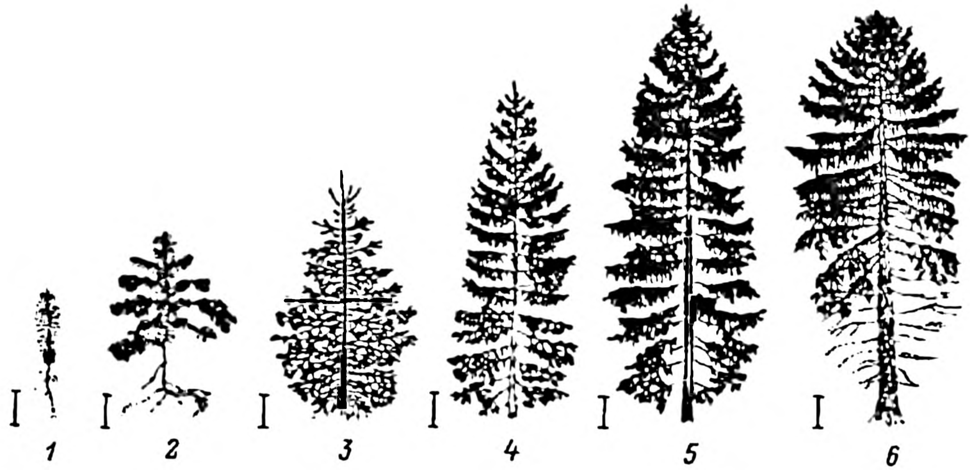

Fig. 3. Ontogeny of *Picea obovata* with normal vitality.

Ontogenetic stages: *1* — *j*, 2 — *im*, *3* — *v*, *4* — g_1, *5* — g_2, *6* — g_3 (see fig. 1). Bars: *1* — 2 cm, 2 — 5 cm, *3* — 50 cm, *4*—*6* — 2.5 m.

individuals (g_1, g_2). The younger trees have only the top and second parts of the crown. The elder trees have crown with very small top part and large extended third and fourth parts. The ratio between the overall tree height and the length of alive part of a crown is constant during the whole reproductive period due the appearance of secondary crown.

Due to that, the tree can effectively utilize the light, because the crown always possesses large lateral surface. Such construction of a crown allows *Picea obovata* to compete with deciduous trees which have more productive photosynthesis.

Tilia cordata Mill. is the sympodial tree, architectural model Troll (Halle et al., 1978), which propagates by seeds as well as by vegetative offspring's. This species differs from other trees by its great diversity of life forms, i. e., from the monotrunk tree to the elfin one. The ontogeny of monotrunk life form agrees with the general scheme of ontogeny as a rule, but this life form is rather rare variant in linden populations inhabiting natural forests. More frequently *T. cordata* shows compact or diffuse polytrunk life form in the favorable sites of community and elfin one in the highly shaded sites.

Polytrunk life form consists of numerous ramets (2 to 10 trunks) with different calendar age, ontogenetic stage and vitality. The life duration and developmental rates of these ramets mostly depend on the position of dormant buds producing them. First type of ramets arises from dormant bud situated on the basal part of a trunk, while the second

TABLE 2

Some ontogenetic parameters of *Tilia cordata*

Ontogenetic stage	Age, yr			Height, m			Annual growth increment, cm/yr		
	1	2	3	1	2	3	1	2	3
j	15	6	2	0.3	0.3	0.8	1.8	10.8	35.7
im	40	20	8	2.5	2.5	2.5	12.8	14.5	24.9
v	60	40	20	8.0	4.5	4.5	45.1	44.7	58.7
g_1	80	50	30	17.0	17.0	10.0	33.5	33.5	33.5
g_2	100	100	50	25.0	25.0	17.0	20.8	20.0	13.0
g_3	300	300	90	30.0	30.0	18.0	5.1	5.1	6.3

Note. 1 — seed generation; 2—3 — vegetative generation: 2 — diffuse geoxylic ramet, 3 — compact geoxylic ramet.

type originates from buds situated on the epigeogenic xylorhizome, and the third one appears on the hypogeogenic xylorhizome. The daughter trees are dispersed depending on xylorhizomes length, the latter varying from dozen centimeters to a few meters.

The epigeogenic xylorhizomes arise initially as aerial shoots on the youngest trees (ontogenetic stages *j* and *im*), these shoots later lying down and producing the adventitious roots. The hypogeogenic xylorhizomes are initially subterranean. These xylorhizomes are mainly shorter than the epigeogenic ones (fig. 2). Ontogenetic variations of trees of different origin are illustrated by the table 2. The ramets close to parental tree grow faster during pre-reproductive period than the ramets of other types, and they have also shorter life span and smaller size. The ramets remote from parental tree are very similar to the individuals originated from seeds, and their roles in community are identical. The diffuse polytrunk life form degrades to elfin one due to environmental stress (shading, over mastering, soil depletion), but it may be reversed to the original form when stress disappears.

All ontogenetic peculiarities mentioned above make *Tilia cordata* to be the permanent component of different forests, and give the species high resistance to various environmental changes.

Polyvariancy of ontogeny of the tree species

In this paper we consider polyvariancy of ontogeny using only a part of the studied parameters.

Diversity of the life forms. Some of the species investigated demonstrate only one life form while the other ones have few. The diversity of the life forms arises spontaneously without human impacts, fungal diseases, and animal damages. We studied 22 tree species within zones of the broad-leaved and mixed forests. Each species has its own set of the life forms. Table 2 shows the maximal life form diversity of species in all the areas investigated. However, some species may be presented by several life forms in the same community. The full list of species is subdivided in five groups.

The first group is the most uniform. It contains 7 species possessing only a form of monotrunk tree. The second group includes 5 species that have 2—3 life forms. Three species of this group demonstrate monotrunk form and two variants of compact polytrunk form. Two species demonstrate two life forms: *Populus tremula* may grow either as monotrunk or as diffuse polytrunk tree with root sprout, and *Abies sibirica* has either monotrunk or elfin form. Three other groups (3rd to 5th) are rather similar. They include species each possessing 4—5 variants of life forms. Species of the third group have all variants of the compact forms and only one variant of the diffuse form with xylorhizome sprouts. Species of the fourth group are similar to the these of the third group, but they represent full set of the compact and diffuse forms. Fifth group differs from the third one in the presence of elfin forms. An example is the diversity of the life forms in Tilieto-Nemoretum in the Central Russia, Penza Region (Чистякова, 1982) (fig. 4). It must be noted that the table 1 does not include life forms inherent in the borders of area.

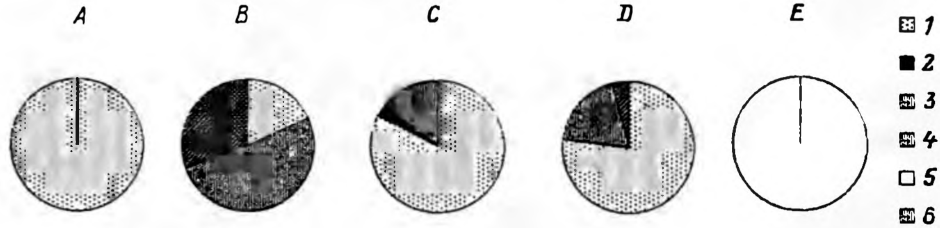

Fig. 4. Spectra of life forms of some tree species in Tileto-Nemoretum association (Penza region of the Central Russia).

Trees: *A* — *Quercus robur*, *B* — *Tilia cordata*, *C* — *Acer platanoides*, *D* — *Ulmus glabra*, *E* — *Populus tremula*. *1*—*6* — life forms: *1* — monotrunk, *2* — polytrunk compact aeroxylic butt sprouting without adventitious roots, *3* — polytrunk compact geoxylic butt sprouting with adventitious roots, *4* — polytrunk diffuse geoxylic xylorhizome sprouting, *5* — polytrunk diffuse geoxylic root sprouting, *6* — elfin xylorhizome sprouting.

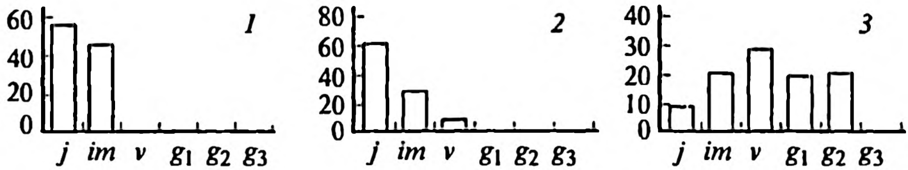

Fig. 5 Ontogenetic structure of genet of *Prunus avium* in Carpineto-Nemoretum (L'vov region of Ukraine). *1*, *2* — in shade: *1* — without virginal plant; *2* — with virginal plant; *3* — in light. Axis: *x* — ontogenetic stages. *j*—g_3; *y* — number of ramet, %.

Diversity of life forms increases the ability of surviving in unfavorable conditions and provide the continuos flow of generations in community.

Diversity of the propagation types. Species belonging to each group of the life forms are similar in relation to the type (types) of propagation. Species of the first group (table 1) maintain their population by seeds only. The main characteristics of these trees are seed number and dispersal ability, because the population of the species may be stable if every generation could occupy new free sites in the community. In the second group, *Populus tremula* can occupy new sites both by the vegetative offspring's (root sprouts) and by seeds, but seeds germinate very rarely in natural forests. Species of all groups which possess compact life forms are quite similar to species of the first group by their selfmaintenance ability. However, these species may prolong the life span in the cases when vegetative offspring (basal sprouts) replace the parental trunk. The life span of ramet is longer if it has adventitious roots. Species with diffuse life forms have indefinitely long life span of a genet. The offspring's which appear both on xylorhizomes and on roots begin their ontogeny at *j* ontogenetic stage, and the life span of each daughter individual (ramet) is just the same as the trees arising from seeds. Unlike the compact forms, vegetative offspring's may be dispersed so far as they grow independently from parental tree.

In this way, temporal continuity and space dispersion of the genet allow these species to occupy favorable conditions or survive in unfavorable ones. We illustrate the development of the diffuse polytrunk form in light and shade habitats by the structure of *Padus avium* genet (fig. 5). Permanent appearance of juvenile and immature ramets allow the species to hold place in the community because these ramets are analogous to the

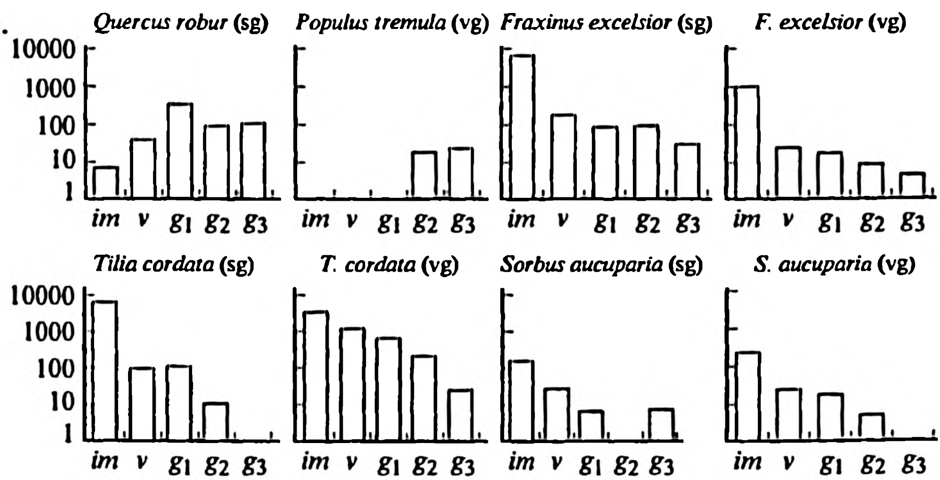

Fig. 6. Ontogenetic structure of tree species populations in Tilieto-Nemoretum association («Kaluzskiye zaseki» reserve of Central Russia).

sg — seed generation, *vg* — vegetative generation. Axis: *x* — ontogenetic stages, *j*—g_3; *y* — number of individuals.

seed bank. Species of the fifth group differ from the species of all other groups in their ability to make the elfin forms. Such forms appear only in stress conditions, i. e., in highly shaded sites of community. The daughter rooted trunks never reach reproductive stages if the light intensity is constantly low. If environmental conditions are changed locally some ramets raise up their vitality and thus have the opportunity to become reproductive and to produce seeds. When a genet gains reproductive ramets the elfin forms transform into diffuse xylorhizome forms. We can observe the different types of propagation in the same community (fig. 6).

Longevity and rate of development. Longevity of ontogenetic stage (or period) may be calculated as difference between maximal calendar age of two successive ontogenetic stages (or periods). The developmental rate is estimated by the longevity of every ontogenetic stage (period). According to these parameters all species studied were subdivided into four groups.

I group includes *Fagus sylvatica*, *Fraxinus excelsior*, and *Quercus robur*. This group is characterized by the maximal longevity of the reproductive stages as well as all life history (table 3). Maximal longevity of the life span of each generation provides these species the ability to hold the occupied area in the community for a long time. Large longevity of reproductive period often permits to occupy new sites, thus giving them the ability to maintain their populations in the community.

II group consists of *Acer platanoides*, *A. pseudoplatanus*, *Tilia cordata*, *Picea abies*, *P. obovata*. Total life span and reproductive period of these species are two times shorter if compared with the previous group. Consequently, the chances to give new generations and to maintain current positions in the community are decreased.

The III group includes *Abies sibirica*, *Acer campestre*, *Betula pendula*, *B. pubescens*, *Padus avium*, *Populus tremula*, *Carpinus betulus*, *Ulmus glabra*, *U. laevis*. The life span of these species is three times shorter than that of the first group. The reproductive period begins in 10—20 years. Such short pre-reproductive period gives these species the advantages in occupying the new site.

The IV group includes *Alnus incana*, *A. glutinosa*, *Salix caprea*. Life longevity of the species is very short (60—80 years). Fructification begins at 5—10 yr., and even young trees can produce large amount of seeds. This ontogenetic feature allows these species to explore any free places in community earlier than the species of other groups can.

The above-mentioned quantitative traits connected with the life longevity and developmental rates were observed for trees of the normal vitality. Trees of the subnormal

TABLE 3

Duration of ontogeny in some tree species

Species	Longevity, years					
	prereproductive periods		reproductive periods		all ontogeny	
	1	2	1	2	1	2
Quercus robur	60	100	390	270	500	390
Fagus sylvatica	50	80	250	170	350	260
Tilia cordata	35	75	245	90	300	180
Pinus sylvestris	20	40	200	60	240	110
Picea obovata	40	60	200	90	240	150
Acer platanoides	30	40	170	90	220	170
Abies sibirica	30	60	90	40	130	90
Betula pendula	20	40	90	50	120	85
Padus avium	10	20	60	40	80	65
Alnus incana	10	15	50	30	65	50

Note. 1 — normal vitality, 2 — subnormal vitality.

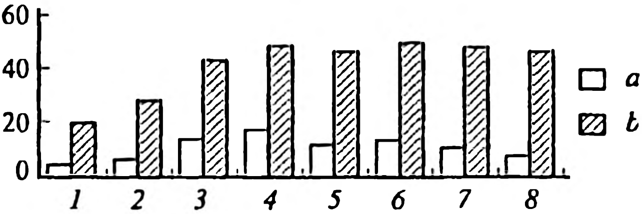

Fig. 7. Minimal (*a*) and maximal (*b*) longevity of immature stage for trees with low vitality in Carpineto-Nemoretum association («Kanev» reserve, Ukraine).

1 — *Betula pendula*; *2* — *Quercus robur*; *3* — *Acer platanoides*; *4* — *Tilia cordata*; *5* — *Ulmus glabra*, *6* — *Acer campestre*; *7* — *Fraxinus excelsior*; *8* — *Carpinus betulus*. Axis: *x* — species, *y* — years.

vitality have shorter life span and reproductive period (table 3). Therefore their overall seed productivity is lower as compared with the trees of normal vitality. However, the developmental rate of pre-reproductive subnormal individuals is two times slower than that of normal ones. So the young subnormal individuals may have favorable conditions for rather long time. It is possible because *j*, *im*, *v* individuals need only small portions of resources for survival. So they make up a kind of population buffer for withstanding unfavorable environmental and community conditions.

The trees with low vitality can survive under stressed conditions because of their minimal resource demand. The examples of immature stage duration for the individuals of low vitality growing in highly shaded habitats are shown in fig. 7. New site favorable light conditions allow these young trees of the low vitality to change their vitality level. Later they may turn into adult individuals. All samplings early had low vitality, now light supplement is reached and some individuals change up vitality even to normal level (Евстигнеев, 1991). The diversity of longevity and rate of development within multispecies community define the time heterogeneity of population mosaics. Each species in different ontogenetic stages exploit different portion of resources in different time; and together they use maximum of habitat resources. The variation of development rate allows the species to use existing condition diversity in unstable mosaic habitat.

Conclusion

The ontogenetic concept proposed by T. A. Работнов (1950), has been verified by the investigations of species of different life forms. Our study of tree species confirms the assumption that this concept is appropriate for the analysis of woody plant populations. The ontogenetic analysis of trees shows polyvariations of ontogenetic pathways if trees grow under diverse community and environmental conditions. Individuals within the same species can show different ontogenetic patterns even within the same community, due to their belonging to the different population mosaic elements occurring in the natural forests. The species show high individuality of ontogenetic behavior; it is clear especially in the heterogeneous natural forest community. Studying peculiarities of species ontogeny through its area allows to reveal spectrum of ontogenetic polyvariancy of every species. It determines potential of species. In concrete community only the part of these species abilities are realized. These results we take into account as a basis for forecast of behavior of species and their groups in permanent changing mosaic environment of natural community.

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РЕЗЮМЕ

С позиций концепции дискретного описания онтогенеза, предложенной Т А. Работновым, проанализированы структура и развитие древесных растений. Обобщены многолетние исследования авторов и литературные данные по описанию онтогенеза 22 видов деревьев восточноевропейских лесов. Выявлены общие для всех видов индикаторные признаки онтогенетических состояний и охарактеризованы особенности развития деревьев на разных уровнях жизненности. Описана поливариантность онтогенеза: морфологическая (разнообразие жизненных форм и способов размножения) и по темпам развития. Выделены группы видов, различающихся по темпам развития, разнообразию жизненных форм и способов размножения.