

STATE OF COENOPOPULATIONS OF *QUERCUS ROBUR* L. GROWING IN RAVINES LOCATED IN THE DNIEPER RIVER'S RAPIDS SECTION (RECREATION ZONE OF THE CITY OF ZAPORIZHZHYA), UKRAINE

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Abstract

The research was conducted in three typical ravine forests of the southern variant of the Ukrainian Steppe. The age and vitality structure were studied, demographic characteristics of *Quercus robur* L. coenopopulations in 1999 and 2019 were calculated and changes that occurred over a 20-year period were analyzed. These forests are subject to a high anthropogenic pressure, being a part of the recreational area of residents of the large industrial city of Zaporizhzhya as well as tourists visiting the island of Khortytsia. There is a gradual change of the structure of the elementary demographic unit of the coenopopulation of *Q. robur* with an increase in anthropogenic impact starting from spotted and then through diffuse to eventually becoming pointlike. Coenopopulations of this edicator species sampled from the ravines under study are many-component and have a bimodal real spectrum. During the study period, significant changes occurred in the left, pregenerative parts of the spectrum and are associated with the changes in the quantitative ratios of juvenile, adult and virginile individuals. As a result of recreational exposure, the range of variants of ontogenetic development of *Q. robur* decreases, and the variants themselves include a smaller number of age states. Estimation of the state of *Q. robur* coenopopulations using eight demographic indices showed some decrease in the regenerative potential and increase in the share of generative and postgenerative individuals in the coenopopulations of Heneralka and Khortyts'ka gullies. Due to the decrease of the anthropogenic impact, the changes in Shyroka gully are less apparent. All coenopopulations of *Q. robur* are young and have significant adaptive potential. Therefore, they are capable of sustainable generational turnover even in case of low amount of specimens.

Key words: adaptive potential, age and vitality structure, edicator, polyvariance of ontogenesis.

Introduction

Common oak (*Quercus robur* L.) is one of the main forest-forming and most valuable deciduous trees of Ukraine from an

economical standpoint (Slyepkyh and Korshykov 2016, Kopyi et al. 2017). During the process of its growth and development, it is capable to form mixed in composition and complex in structure

relatively high-yielding and biologically relatively stable tree groups under favourable conditions (Dyatlov 2007). *Q. robur* is highly valued for its high-quality wood, which is strong, flexible, durable and with a beautiful structure. On the one hand, *Q. robur* is a source of natural raw material, the stands of which perform various environmental functions, and on the other hand, it is a tree species that is constantly negatively affected, which results in a significant reduction of oak stands (Puryaev et al. 2019). Weakening of the resilience of natural oak forests is caused by different reasons, including the impact of two powerful environmental factors – anthropogenic pressure and global climate change, leading to their degradation and en masse desiccation (Kharchenko and Kharchenko 2012). The decline of oaks in Europe is a matter of serious concern. The causes of the challenging natural regeneration of *Q. robur* and phytopathological aspects of its growth have attracted the attention of many researchers (Marçais and Desprez-Loustau 2014, Jensen and Löff 2017, Bobiec et al. 2018).

Q. robur is the main species of ravine forests in the southern part of the Ukrainian Steppe, which display an intrazonal character under the aforementioned conditions. Ravine forests play a role in the protection of soil, nature, erosion control, regulating water regime as wells as a recreational resource. They alone contain a valuable gene pool consisting of forest (Yakovlieva-Nosar et al. 2005, Yakovlieva-Nosar 2007, Bessonova and Zaitseva 2016, Yakovlieva-Nosar and Bessonova 2018), steppe (Bessonova et al. 2014), meadow, swamp, psammophytic and petrophytic vegetation with a number of rare and endemic species.

The ravines of the Zaporizhzhya region belong to a special geographic va-

riant – the ravines of the Dnieper Rapids area (Bel'gard 1950). Coenoses of ravine forests in the vicinity of such industrial giant as the city of Zaporizhzhya are not only affected by industrial emissions, but also suffer from large-scale recreational activities of city residents. To substantiate comprehensive measures for their conservation, it is necessary to monitor the state of natural populations of *Q. robur*.

In this regard, the aim of this study was to monitor changes in age and vitality structure of populations of *Quercus robur* L. in three typical ravine forests of southeastern Ukraine, differing in the level of anthropogenic load, over the 20 year period.

Material and Method

The analysis of the state of *Q. robur* populations was carried out in the ravine forests on the island of Khortytsya (Heneralka and Shyroka gullies) and on the right bank of the Dnieper River (Khortyts'ka gully) (Fig.1). The island of Khortytsia is located in the subzone of grass-fescue-feathergrass steppe and is part of the recreational zone of Zaporizhzhya. Khortyts'ka gully is located opposite the Heneralka gully across the Dnieper River and is an object of mass recreation for citizens. The Shyroka gully is also subject to a strong anthropogenic pressure, as the sanatorium-dispensary of the Zaporizhzhya Titanium and Magnesium Plant adjoins its north-western side. Its territory is connected to the ravine by the stairway. In addition to the transit type of recreational activities, ravine plantings are exposed to bivouac and mining forms of recreation.

According to the forest site typology characteristics determined by Bel'gard

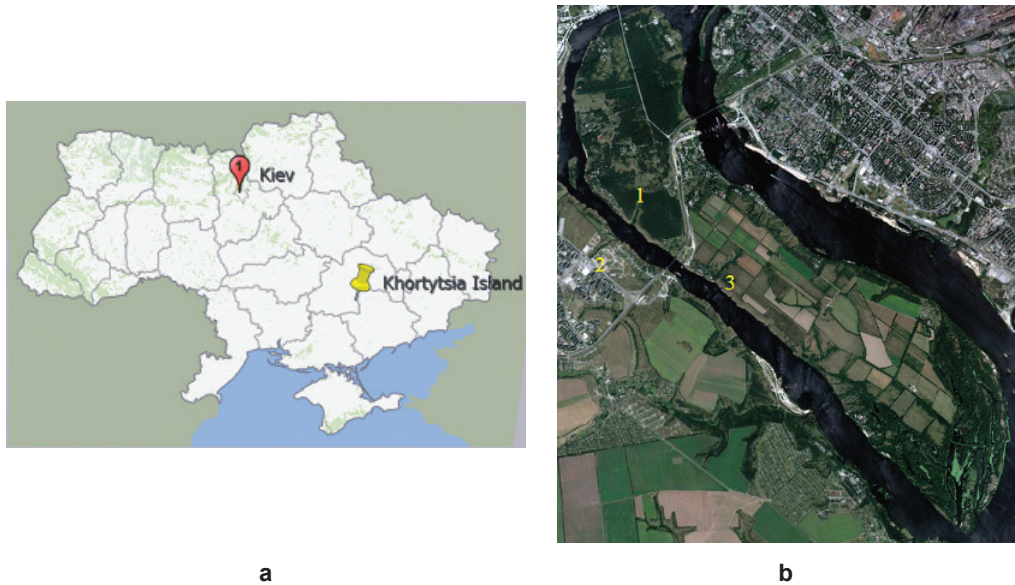


Fig. 1. Location of the island of Khortytsia on the map of Ukraine (a) and map of the island of Khortytsia (b) (SAS.Planet 2020).

Note: Coordinates of the extreme points (tops and mouths) of the gullies under study: 1 – Heneralka (47°83′06.1″ N 35°06′73.5″ E; 47°82′67.9″ N 35°06′57.8″ E); 2 – Khortyts’ka (47°49′15.99″ N 35°03′18.66″ E; 47°49′27.69″ N 35°03′44.35″ E); 3 – Shyroka (47°49′23.1″ N 35°05′29.2″ E; 47°49′04.16″ N 35°05′00.24″ E).

(1971), the ravine forest of the Heneralka gully can be considered to be of type E_1 (birch/black maple oak forest), Shyroka gully to type Dn_{1-2} (derived from birch-hazel type of forest with no *Fraxinus excelsior* L. and *Acer campestre* L.); Khortyts’ka gully is a degraded specimen of E trophotope with a simplified structure (mainly curtains of *Acer campestre* L. and *A. tataricum* L. with a slight admixture of other species). According to EUNIS forest type T1-99 Steppe *Quercus* forests (G1.7A1Euro-Siberian steppe *Quercus* woods) (Didukh 2020, EEA 2020) (Fig. 2).

While studying the coenopopulations of *Quercus robur* L., the elementary demographic unit (EDU) was taken to be a set of individuals of the species, which

grew in each of the gullies under study and was able to self-sustain due to the cycle of generations. Ontogenetic spectra and the spatial type of EDU were established by Smirnova et al. (1993).

The localization of individuals of the generative fraction and undergrowth clusters were mapped for each of the coenopopulations under study.

The age states of *Q. robur* were determined based on the recommendations of Chistyakova (1989) and Rabotnov (1964). The generally accepted classification ($p \rightarrow s$) was used for their description (Zlobin 1989, Evstigneev and Korotkov 2016). Characteristics of periods of ontogenesis and age (ontogenetic) states are given in Table 1.



Fig. 2. Phytocenosis of ravine forests (a – Heneralka, b – Shyroka).

Table 1. Ontogenetic periods and ontogenetic stages of trees.

Ontogenetic period	Ontogenetic stage	Symbol	Duration (Chistyakova 1994)	Description (Chistyakova 1994, Sklyar 2014)
1. Latent	(1) Seed	se		
	(2) Seedling	p		the youngest plants that have a primary root and scaly leaves
	(3) Juvenile	j		young individuals with a trunk without branching and 3–5 green leaves of the juvenile type, which differ in size and shape from adults
2. Pregenerative	(4) Immature	im	20	side shoots of the II–V order appear, and the diameter of a trunk no more than 2 times exceeds diameter of lateral branches
	(5) Virginile	v	40	have a characteristic morphological structure for adult plants, but such individuals have not yet entered the phase of flowering and fruiting
3. Generative	(6) Young	g1	60	crown pointed, fruiting capable of sparse and irregular
	(7) Mature	g2	120	generative crown obtuse, fruiting reproduction abundant
	(8) Old	g3	140	crown broadly rounded
4. Postgenerative	(9) Subsenile	ss	20	lose the ability to generative reproduction, begin to collapse
	(10) Senile	s	20	have a secondary crown with juvenile leaves, no fruiting

The recovery index ($I_{\text{recov.}} = \sum j \rightarrow v / \sum g_1 \rightarrow g_3$) was determined by the formula recommended by Zhukova (1987), which characterizes the ratio of all individuals of the pregenerative period to these of the generative period of development. We calculated the indices developed by Kovalenko, which characterize the participation of individual ontogenetic groups of individuals in the population: renewal index ($I_{\text{renew.}} = \sum p \rightarrow v / \sum p \rightarrow s$, characterizes the participation of all specimens of the pregenerative period), generative index ($I_{\text{gener.}} = \sum g_1 \rightarrow g_3 / \sum p \rightarrow s$, characterizes the participation of all specimens of the generative period of development), the aging index ($I_{\text{aging}} = \sum g_3 \rightarrow s / \sum p \rightarrow s$, characterizes the participation of the plants from old generative to senile), the general age index (I_{age} , represents the ratio of $I_{\text{aging}} / I_{\text{renew.}}$) (Zlobin et al. 2013).

To characterize the ontogenetic structure of coenopopulations, the index δ (Zhukova 1967), the age coefficient (Δ) (Uranov 1975, Zlobin 1989) and the average energy efficiency (ω) were calculated (Zhivotovskiy 2001).

Index δ is the ratio of the difference between the number of old (P) and young (p) specimens to the total number of specimens in the population calculated by formula (1).

$$\delta = \frac{P - p}{P + p}, \quad (1)$$

The age coefficient of the coenopopulation was determined by the formula (2).

$$\Delta = \frac{\sum k_i m_i}{\sum k_i}, \quad (2)$$

where: k_i – number of the i -th age state, m_i – age of individuals.

The energy efficiency index was calculated using the formula (3).

$$\omega = \frac{\sum n_i e_i}{\sum n_i}, \quad (3)$$

where: n_i – number of plants that belong to an i -th age state, e_i – energy efficiency of plants.

The type of coenopopulation was determined by Rabotnov (1964) taking into account the coefficient Δ and the ‘delta-omega’ classification by Zhivotovskiy (2001) (Fig. 3).

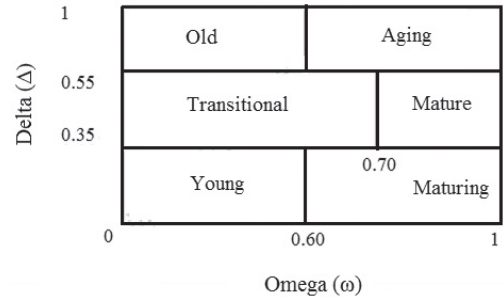


Fig. 3. Types of normal plant populations according to the ‘delta-omega’ classification.

The vitality of specimens and coenopopulations was determined using classical methods (Vorontsova 1967, Zlobin 1989). The following parameters were calculated:

1) the average score of vitality of specimens as per a given period;

2) the average score of vitality of specimens in the coenopopulation calculated by formula (4):

$$F = \sum \frac{p}{Ns}, \quad (4)$$

where: p – points, Ns – number of specimens.

3) vitality criterion of the coenopopulation calculated by formula (5):

$$P = P_{\text{PrG}} + P_{\text{G}} + P_{\text{PsG}}, \quad (5)$$

where: P_{PrG} – vitality criterion of specimens of the pregenerative period; P_{G} – indicator of vitality of specimens of the generative period; P_{PsG} – vitality criterion of specimens of the postgenerative period.

4) criterion of relative vitality of coenopopulations calculated by formula (6):

$$P_{rel.} = \frac{P}{P_{max}}, \quad (6)$$

where: P_{max} – the largest possible vitality estimate (the sum of the products of the maximum points of vitality of individuals of each period divided by the average number of individuals of a given period).

Models of ontogenetic development were determined using the methods developed by Chistyakova (1989) and Sklyar (2014).

Results

Q. robur is an edicator of the ravine forests under study with its specimens forming the first layer. In the past, this species was dominant in the ravine forests, as in the first half of the XIX century oak groves used to cover the territory of the island of Khortytsia, but uncontrolled logging led to their significant decline in the second half of the same century (Novyts'kyi 2005).

The population size of *Q. robur* in the Heneralka gully is small – only 74 individuals were found in 1999; however, this number is sufficient for self-sustaining of the population under study. 37 individuals of *Q. robur* were registered in the ravine forest of the Khortyts'ka gully, subjected to the highest recreational pressure. The population of *Q. robur* in Shyroka gully reached 318 individuals, of which 260 were full-fledged plants, and 58 became the so-called 'sticks'. This can be explained by the lack of sunlight for the young specimens to develop properly under the shadow of maternal trees. This feature of the development of the younger generation of *Q. robur* is pointed out by other authors (Kharchenko and

Kharchenko 2012, Annighöfer et al. 2015). In 2019, the number of *Q. robur* individuals was 71, 28 and 286, respectively. The total number of individuals in 1999 in the Heneralka gully was 14.0 % compared to the tree stand of the ravine forest, in the Shyroka gully – 31.3 %, in the Khortyts'ka gully – 10.8 %. Over the 20 year period of controlled observation, their share in the stands did not change substantially and in the year of 2019 it reached 12.2 %, 30.5 % and 8.1 %, respectively.

Q. robur, as a strong edicator, is characterized by a continuous spotted type of EDU, which is realized under optimal and suboptimal conditions (Smirnova et al. 1993). The signs of the spotted structure still remained in the area of the ravine forest of the Heneralka gully in 1999, but there was a tendency of gradual transition to EDU of the diffuse type. In the coenopopulations of *Q. robur* of Khortyts'ka and Shyroka gullies the type of EDU approached the pointlike stage, which may indicate a long-term significant impact of anthropogenic load. Only in some undisturbed areas of these gullies with the highest concentration of individuals, *Q. robur* retained its edificatory effect. No changes in the type of EDU were registered for *Q. robur* in the ravine forests under study in 2019 in comparison with 1999. Generally, there is an adaptive response of the population to prevent it from reaching a critical stage: the ability to form small-sized EDU and ensure the turnover of generations at low population size. The existence of these mechanisms is reported by Zaugol'nova et al. (1992), but also Chadayeva and Shkhagapsoyev (2016).

The age spectra of *Q. robur* coenopopulations in the studied ravine forests are presented in Figure 4. These spectra are bimodal, which is typical for species with

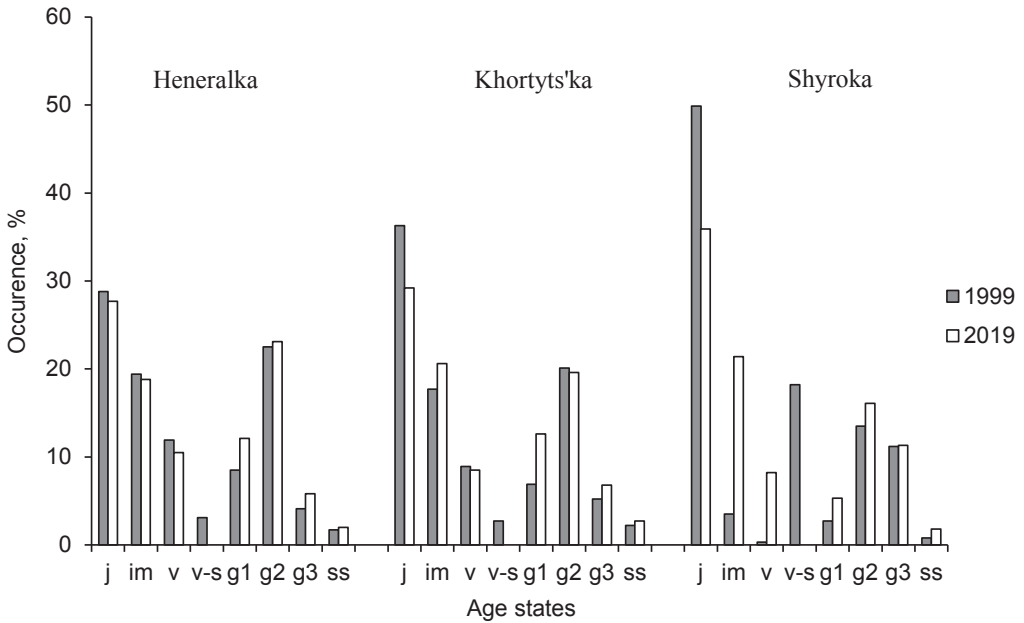


Fig. 4. Age spectra of *Q. robur* coenopopulations in ravine forests.

significant lifespan, with a well-defined period of aging and periodicity of natural regeneration, with maximum juvenile (*j*) and in most cases – middle-aged generative (g_2) individuals. The participation of virginile (*v*) individuals was insignificant.

In 1999, the juvenile and middle-aged generative ontogenetic fractions accounted for the majority of population of the Heneralka gully. A similar pattern was observed in the ravine forest of the Khortyts'ka gully. In the Shyroka gully, the first maximum value corresponds to the specimens that belong to the juvenile age state, and the second one – to quasi-senile individuals (Fig. 2). Smirnova et al. (1984) characterizes the aforementioned 'sticks' as being compact individuals of a quasi-senile ontogenetic state.

Quasi-senility, as a phenomenon of morphological imitation of senility under adverse conditions, is viewed from the standpoint of phytocoenotic tolerance.

The share of this group among immature and virginial *Q. robur* plants, in particular in deciduous oak/hornbeam forests, can reach 20–25 %. The relative participation of quasi-senile specimens in the coenopopulations of *Q. robur* increases from south to north within its natural range. They constitute a reserve for the formation of adult plants under the low-light conditions (Smirnova et al. 1984).

Studies conducted in 2019 also showed the presence of a bimodal ontogenetic spectrum for all studied coenopopulations of *Q. robur*, with peaks observed in the areas of juvenile and middle-aged generative age states. At the end of the 20 year study period, senile individuals of *Q. robur* were absent in all of the populations under study.

It is believed that in the steppe forests the coenopopulation of *Q. robur* is characterized by an ontogenetic spectrum with the absence or suppression of imma-

ture/virginal and adolescent generative groups (Smirnova et al. 1990). Because *Q. robur* is a strong edicator, adult plants prevent the emergence and development of the younger generation in the understory space when forming a solid tree canopy. Its natural regeneration occurs in canopy breaks, so-called 'regeneration windows' (Smirnova et al. 1993). In small forests, and in particular, ravine forests, some areas of the phytocoenosis are affected by the 'marginal effect'. That is, edificatory species have the opportunity to regenerate in the marginal zone of the forest, where seedlings are not hindered by the canopy of generative trees. In such situations, the ontogenetic spectrum of the coenopopulation becomes bimodal or even left-handed (Travlyeyev et al. 1996).

According to the 'Gap mosaic concept' (Korotkov 1991, Remmert 1991, Yamamoto 2000, Burke 2006, Smirnova and Toropova 2016), forests are formed by a large number of elements of the mosaic-tier structure, which develop asynchronously and are the so-called 'regeneration windows' at different stages of development. As we have already mentioned, clusters of young trees are tied to breakouts in the forest canopy. In the gullies under study there are areas with marginal deviation, as the ravine forests of the Dnieper rapids are near the ecological limit of their distribution and are characterized by curtain-meadow complexes.

Young plants of the population – juvenile and immature – are located mainly on the periphery of the projections of the crowns of maternal trees, as well as in micro-depressions with a small layer of plant litter (up to 4 cm thick) and are confined to canopy breaks. It should be noted that undergrowth in the ravine forest of the Shyroka gully is in the least fa-

vourable light conditions. Up to 80 % of *Q. robur* plants that belong to the pregenerative age states are affected by powdery mildew in all of the ravine forests under study.

Age structure is one of the most important features of the population. It reflects such important processes as the intensity of reproduction, mortality, the rate of the cycle of generations. The ability of the population system to self-sustain and its stability depend on this aspect of the structural organization. The age structure of the population depends on the genetic characteristics of the species, which can be realized in different ways depending on the specific conditions of existence of individual populations (Krychfalushiy and Mezev-Krychfalushiy 1994).

To characterize the age of *Q. robur* populations, we first used the index δ (Zhukova 1967), which can differentiate the age level only of those populations with the presence of both young and old individuals, which is observed in the ravine forests under study. As noted by Uranov (1975), in the absence of one of these categories, δ is equal to +1 or -1, regardless of the differences in the age of the population. In 1999, the highest value of this index was in the coenopopulation of *Q. robur* growing in the Heneralka gully (-0.89) (Table 2), while a slightly lower value was registered in the Khortyts'ka gully (-0.84) with the lowest attributed to the ones growing in the Shyroka gully (-0.78), which is explained by the small share of mature and virginal plants in the coenopopulation of this ravine forest. Minus when calculating the index δ shows that the young specimens prevail over the old in the coenopopulation (formula 1). The numerical expression (in modulo) is used for a general idea of the age of the coenopopulation.

Table 2. Dynamics of demographic indicators of *Q. robur* coenopopulations.

Gully	Years	Indices							Type of coenopopulations	
		$I_{\text{renew., \%}}$	$I_{\text{gener., \%}}$	$I_{\text{aging, \%}}$	$I_{\text{recov., \%}}$	I_{age}	Δ	ω		δ
Heneralka	1999	62.2	36.5	5.4	1.63	0.09	0.23	0.46	-0.89	Young
	2019	52.1	45.1	8.5	1.16	0.16	0.26	0.52	-0.83	Young
Khortyts'ka	1999	62.2	35.1	8.1	1.69	0.13	0.22	0.43	-0.84	Young
	2019	53.6	42.9	14.3	1.25	0.27	0.26	0.47	-0.71	Young
Shyroka	1999	71.1	28.3	11.0	1.87	0.15	0.34	0.39	-0.78	Young
	2019	66.4	32.5	12.2	2.04	0.18	0.31	0.40	-0.76	Young

Shyroka gully was a place of active recreation at the time not only for citizens and tourists, but also for the guests to the sanatorium, which is located on its north-western side. Active recreational activities led to the fact that the natural renewal of *Q. robur* was recorded in the ravines situated the furthest from the main thalweg. Clusters of quasi-senile individuals were seen growing in the soil loosened previously by human hands, under a forest canopy in the main thalweg.

After 20 years, in the areas of ravine forests of the Heneralka and Shyroka gullies, the index δ did not change, and in the Khortyts'ka gully it decreased by 15.5 %, indicating a reduction in the total number of young individuals at the expense of juveniles.

As it turned out, the age estimate according to the previous index appears to be very rough. According to Uranov (1975), each age state of an individual tree has its own corresponding numerical value and the greater the value is, the closer the specimen is to the completion of its ontogenesis. In this regard, we calculated the Δ index, which showed the highest age values of the coenopopulation of *Q. robur* in the Shyroka gully in the year of 1999, which is consistent with the previous statement about the difficulty of recovery under the conditions of active recreation (Table 1). Analyzing the chan-

ges that have taken place over the 20-year period, we have concluded that the current trend of aging of *Q. robur* coenopopulations in Heneralka and Khortyts'ka gullies is weak, which can become stable and significant provided that the existing level of recreational load is maintained. At the same time, a relative increase in the value of the index Δ by 13.0 % and 18.2 %, respectively, was registered. In the Shyroka gully against the background of a decrease in recreational pressure and the associated increase in the number of individuals on the left side of the spectrum, no such negative changes were observed.

Uranov (1975), while calculating the age of coenopopulation Δ , introduced the concept of the share of the energy available to the plant, utilized the moment of registering its age state. This aspect was extended by Zhivotovskiy (2001) in the form of the efficiency index (ω) – the value of the 'load' on the energy resources of the environment, which is expressed in shares of their use by individuals of the middle-aged generative state of the population. The values of the index ω calculated by us indicate an increase in the magnitude of the load for the time span from 1999 to 2019, being most apparent in the coenopopulation of *Q. robur* growing in the Heneralka gully (by 13.0 %), and slightly less – in the Khortyts'ka gully (by

9.4 %). This indicator practically did not change in the case of the Shyroka gully.

Relying on the combined use of both indices (Δ and ω) by Zhivotovskiy (2001) we identified the types of investigated populations of *Q. robur* as 'young' both at the beginning of observations – in 1999; as well as 20 years later – in the year of 2019. The calculated values of the index Δ , which varied from 0.22 to 0.34, and the index ω , the values of which ranged from 0.39 to 0.52, were used to determine the position of each coenopopulation in the 'delta-omega' space.

The next block of indices that has been used by us characterizes the contribution of each ontogenetic cohort relative to the total number of specimens in the population.

Thus, the recovery index ($I_{\text{recov.}}$) in young normal populations should exceed the value of 1. In 1999, the value of this index varied from 1.63 to 1.87, and in 2019 – from 1.16 to 2.04. This determines the state of the coenopopulation as stable and the ability of the pregenerative fraction to completely replace its generative fraction. It should be noted that for the past 20 years the value of this index in the ravine forests of the Heneralka and Khorityts'ka gullies decreased by 28.8 % and 26.0 %, respectively, while there was no change in the case of Shyroka gully.

Analysis of the set of indices proposed by Kovalenko shows the presence of a fairly high regenerative potential of the coenopopulation of *Q. robur* in all of the gullies studied both in the year of 1999 as well as in 2019. Although over a 20 year period there is some decrease in the value of $I_{\text{renew.}}$, especially in the Heneralka and Khorityts'ka gullies (by 16.2 % and 13.8 %, respectively). At the same time, in the coenopopulations of these gullies, the values of the indices of generative-

ness ($I_{\text{gener.}}$) and aging (I_{aging}) actually increased. The values of the age index (I_{age}) were quite low both at the beginning of the study (1999) (in a 0.09 to 0.15 range) and in 2019 (from 0.16 to 0.27), which also adds to the evidence of relative youthfulness of the populations under study.

Such changes in the values of age indices over the period of 20 years in ravine forests are due not so much to endogenous causes (individuality of environmental and coenotic conditions, peculiarities of formation etc.), as to the influence of such a powerful exogenous factor as anthropogenic load (in this case recreation). Active recreational activities also affect the implementation of models of ontogenetic development of woody plants (Table 3) through the creation of difficult conditions for the existence of seedlings and juvenile specimens (trampling, soil compaction, mechanical damage) and the deterioration of sanitary conditions of generative part of coenopopulation due to mechanical damage, which significantly compromises their immune system.

Increasing anthropogenic pressure leads to a decrease in the variety of variants of *Q. robur* ontogenesis in ravine forests, and the variants of ontogenetic development themselves include a smaller number of age states (Table 2).

According to Sklyar (2014), model No 1 describes a variant of development of *Q. robur*, in which plants undergo a complete ontogenetic cycle and die in a senile state. In models No 2–7, the ontogenetic cycle is incomplete: individuals die in the generative or in any of the pregenerative states. The shortest cycle of development is according to the model No 7, when the plant dies in the seedling state. In models No 1–5, the letter 'a' indicates a variant of ontogenetic development, when a fraction of immature *Q. robur* plants is being attri-

buted to the 'sticks' category. Such plants, for the most part, stop their development at this stage and die, that is, the incomplete ontogenesis has been realized in such a case, or, even though it happens less often, pass to the next ontogenetic state.

In 1999, the 'sticks' (v-s) were registered in all of the ravine forests under study (Fig. 1). In 2019, some of them were eliminated, and the rest were able to transition to the next age state.

The distribution of individuals by levels of vitality is one of the manifestations of morphological heterogeneity of coenopopulations. Plant morphogenesis integrates the level of metabolic processes and through the morphological status of vegetative and generative organs informatively characterizes the vitality of individuals (Osmanova 2009). In this regard, we determined the vital signs of ontogenetic groups and coenopopulations with an interval of 20 years (Table 4).

Table 3. Polyvariance of ontogenetic development of *Q. robur* in ravine forests.

Name of the gully	Model of ontogenetic development								
	No 1 (p...s)	No 1a (p...t...s)	No 3 (p...v)	No 3a (p...t...v)	No 4 (p...im ₁)	No 4a (p...t...im ₂)	No 5 (p...im ₁)	No 6 (p...j)	No 7 (p...)
Heneralka	+	+	+	+	+			+	+
Khortyts'ka	+						+	+	+
Shyroka	+	+		+		+		+	+

Note: + is symbol designating the model realized in the ravine forest.

Table 4. Vitality structure of *Q. robur* coenopopulations in ravine forests.

Gully	Age	Vitality indicators of ontogenetic groups clustered according to a given period			Vitality indicators of a coenopopulation		
		PrG	G	Psg	F	P	P _{rel.}
Heneralka	1999	5.7	6.5	2.0	19.2	14.2	0.74
	2019	5.4	6.4	1.5	18.8	13.3	0.71
Khortyts'ka	1999	4.6	5.9	2.0	33.7	12.5	0.63
	2019	4.2	5.7	1.0	39.0	10.9	0.62
Shyroka	1999	3.8	6.6	3.5	4.4	13.9	0.57
	2019	4.1	6.6	2.7	4.9	14.0	0.61

Note: Age periods: PrG – pregenerative, G – generative, Psg – postgenerative; the parameter F – the average score of vitality of specimens.

As is the case with all the variants of observation, the highest vital signs were attributed to generative individuals, and the lowest – to the individuals of the post-generative period (Table 3). Lower values of this indicator in young pregenerative plants of *Q. robur* compared to the generative ones are associated with the affection of powdery mildew and the transition of some of them to a quasi-senile state.

Over a 20 year period, the vitality of pregenerative and generative ontogenetic groups of *Q. robur* coenopopulations of Heneralka and Shyroka gullies practically did not change, but saw a significant decrease in the case of postgenerative ones, especially in the case of the Khortyts'ka gully (by 50.0 %). The regularity and direction of changes in the vitality of the *Q. robur* coenopopulation as a whole

is clearly demonstrated by the indicator P : in the Heneralka and Shyroka gullies it changed insignificantly, while in the Khortyts'ka gully's case it has decreased by 12.8 %.

Indicator P_{rel} shows what proportion of vitality score from the maximum possible value a coenopopulation has at the time of the study. In the case of Heneralka gully this indicator is the highest of all the coenopopulations under study during the entire period of observation (0.74 and 0.71), and it was the lowest in the case of the Shyroka gully (0.57 and 0.61), but for the past 20 years this parameter has not changed in any meaningful way in all of the gullies under study.

Thus, over the 20 year observation period, practically the same type of EDU and the bimodal nature of the ontogenetic spectra of *Q. robur* coenopopulations have been carefully preserved. Analysis of age using eight indices demonstrates the adaptive capacity of the studied coenopopulations and the ability to function given a low quantity of the population. As is the case with all of the coenopopulations that consist of young individuals, plants belonging to the pregenerative fraction are capable of replacing the generative specimens in the future. With the decrease in anthropogenic pressure in the Shyroka gully, the condition of the left side of the ontogenetic spectrum has improved.

Conclusions

In the ravine forest of the Heneralka gully there are signs of a spotted structure of EDU. There is a tendency to transform the spatial structure of EDU: a gradual change to the diffuse type in the case of Heneralka gully, and to the pointlike type

in the case of Khortyts'ka and Shyroka gullies, which indicates a chronic, significantly pronounced anthropogenic stress.

Coenopopulations of *Q. robur* in the gullies under study are many-component with a bimodal real spectrum. During the 20 year observation period, the share of mature and virginal plants decreased slightly in the case of Heneralka gully and increased in the case of Khortyts'ka and Shyroka gullies. The number of juveniles decreased in all the gullies.

As a result of recreational exposure, the range of variants of ontogenetic development of *Q. robur* decreases, and the variants themselves include a smaller number of age states.

Comprehensive analysis using eight demographic indices shows a slight decrease in the intensity of natural regeneration in the Heneralka and Khortyts'ka gullies, increase in the share of generative and postgenerative individuals (increase in the load on energy resources of the environment), but the changes did not lead to a critical stage of coenopopulations of *Q. robur* in these gullies. The Shyroka gully shows some improvement concerning the demographic situation due to the decrease in anthropogenic pressure.

All coenopopulations of *Q. robur* in the 'delta-omega' space are defined as young, which due to their adaptive potential are able to self-sustain the cycle of generations.

The studied ravine forests are located on the territory of the Khortytsia National Reserve. Regulation of recreational activities is taking place to reduce the anthropogenic impact on the phytocenoses of the ravine forest. To maintain the *Q. robur* population, it is recommended to plant acorns collected from mother trees within each small ravine in blanks.

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