Analysis of the spatial distribution of the ecological niche of the land snail *Brephulopsis cylindrica* (Stylommatophora, Enidae) in technosols

O. V. Zhukov*, D. V. Kovalenko**, S. S. Kramarenko***, A. S. Kramarenko**

*Oles Honchar Dnipro National University, Dnipro, Ukraine  
**Bohdan Khmelnytsky Melitopol State Pedagogical University, Melitopol, Ukraine  
***Mykolayiv National Agrarian University, Mykolayiv, Ukraine

The aim of our work is to describe the ecological niche of the land snail *Brephulopsis cylindrica* (Menke, 1828) in terms of the edaphic properties and properties of the vegetation cover and to show the spatial features of the variation of the habitat preference index within the artificial soil body – technosols (soddy-lithogenic soils on loess-like clays) using the ecological niche factor analysis (ENFA). The research was carried out at the Research Centre of the Dnipro Agrarian and Economic University in Pokrov. Sampling was carried out on a variant of artificial soil (technosols) formed on loess-like clays. The test site where the sampling was conducted consists of 7 transects of 15 samples each. Test points form a regular grid with a mesh size of 3 m. Soil mechanical impedance, aggregate-size distribution, soil electrical conductivity, vegetation physiognomic characteristics, and Didukh phytotaxonomic indices were used as ecogeographic predictors of the mollusc’s ecological niche properties. Phytoindication assessment indicates that the technosol ecological regimes are favourable for sub-mesohyphens, hemi-hydrocontrastrophilophytes, neutrophilous, semi-eutrophs. The test for statistical significance showed that an axis of marginality of the ecological niche of *B. cylindrica* and axes of specialization are significantly different from the random distribution. We found that the ecological niche of the mollusc is determined by both edaphic factors and ecological features of vegetation. The marginality of *B. cylindrica* ecological niche over the entire period of study is determined mainly by preferences for physiognomic vegetation types, higher values of the continentality and thermality regimes. Often greater content in the soil of aggregates 1–3 mm in size coincides with greater numbers of *B. cylindrica* individuals. Individuals of this species avoid physiognomic type III and areas with higher soil alkalinity and mineralization detected both by means of the phytotaxonomic approach and soil electrical conductivity data. Ecological niche optima may be presented by integral variables such as marginality and specialization axes and plotted in geographic space. The spatial distribution of the *B. cylindrica* habitat suitability index (HSI) within the technosols is shown, which makes it possible to predict the optimal conditions for the existence of the species.

**Keywords**: molluscs; marginality; biodiversity; ecological niche; spatial distribution; ecological niche factor analysis.

Introduction

The small scale spatial distribution of land-snail species and individuals has been extensively researched (Myšák et al., 2013; Faly et al., 2018). Much of the research on the habitat selection by land molluscs is based on comparison of mollusc communities from geographically different sampling points that differ in plant cover, soil type, and moisture level (Millar & Waite, 1999; Martin & Sommer, 2004; Müller et al., 2005; Weaver et al., 2006). Mollusc populations may be relatively evenly distributed or highly aggregated (Knálka, 1986; Locasciulli & Boag, 1987). These patterns may be associated with the distribution of microhabitats (Walden, 1981; Knálka, 1986; Hylander et al., 2005). The effect of microhabitat conditions was detected (Hylander et al., 2005; Juríčková et al., 2008).

Studies at a large scale level have made it possible to determine the role of edaphic factors in the spatial distribution, abundance, and diversity of mollusc communities (Nekola & Smith, 1999; Juřičková et al., 2008; Szybiak et al., 2009). The response of species to mineral richness (Horsák, 2006), humidity gradient (Čejka & Hamerlík, 2009), or calcium content gradient (Juřičková et al., 2008) was studied. Particular attention is drawn to the problem of spatial scale and hierarchy of factors affecting molluscs (Nekola & Smith, 1999; Bohan et al., 2000; McClain & Nekola, 2008; Myšák et al., 2013). Habitat is characterized by the presence of resources and conditions for a given species in a particular territory, as a result of which the colonization of this territory becomes possible, including the species’ survival and reproduction (Hall et al., 1997). The purpose of studying the choice of habitats for species is to identify the characteristics of the environment that make the place suitable for the existence of the species (Calenge, 2005).

Ecological niche models are useful for describing the choice of habitat by species. Hutchinson (1957) proposed a formal, quantitative concept of the ecological niche as a hyper volume in a multidimensional space, defined by ecological variables delimiting where stable populations can be maintained (Kearney et al., 2010). Methodologically, an ecological niche can be described by means of a General Niche-Environment System Factor Analysis (GNEFA) (Calenge & Basille, 2008). The ecological niche model for a species is measured in terms of marginality (the difference between the mean of the distribution of the cells representing species observations and the global cells) and specialization (the difference between the variance of the species in the global cells) (Skov et al., 2008). The performance of six presence-only models that have been selected to represent an increasing level of model complexity (BIOCLIM, HABITAT, Mahalanobis distance, DOMAIN, ENFA, and GARP) was compared using data on the distribution of 42 species of land snails, nesting birds, and insectivorous bats. These
models showed relatively small (though statistically significant) differ-
ences in predictive accuracy (Tsour et al., 2007).

Brephulopsis cylindrica (Menke, 1828) (Stylommatophora, Enidae) is a land snail native to the Crimean Peninsula (Ukraine). Now it is wi-
dely distributed in the grasslands of the Black Sea Lowlands and some
adjacent regions in Ukraine (Sverlova et al., 2006; Vychalkovskaya,
2008; Balashov & Gural-Sverlova, 2012; Balashov et al., 2013; Bal-
ashov et al., 2018). The intra-population variation of conchimetry traits
in the land snail B. cylindrica were estimated (Kramarenko, 2009). In
the Crimean Peninsula this terrestrial snail inhabits open dry habitats
such as steppe and rocky grasslands (Sverlova et al., 2006). The
dispersal of the different populations of this species was measured in
different experimental conditions (Vychalkovskaya & Kramarenko,
2006). Analysis of the genetic structure of continuous and ephemeral
populations of the land snail B. cylindrica led to the conclusion that
small, isolated animal populations (including, urban) tend to experience
reduced levels of genetic diversity, which arises due to the manifesta-
tion of genetic and stochastic processes (Kramarenko & Snegir, 2015). The
formation of spatial variability patterns with distinct fractal nature was
explained as result of the self-similar elements in spatial distribution of
B. cylindrica. The relative roles both of the random and the regular
components were detected for separate characters according to the
degrees of proximity (Kramarenko & Dovygal, 2014). Live and dead
lichens and plants are the favourable B. cylindrica feeding habitat
(Balashov & Baidashnikov, 2013). Outside the native area, B.
cylindrica is often spread by people transporting plants, building
materials etc., thus extending its range (Sverlova et al., 2006). It is most
likely that its expansion outside the Crimea to mainland Eastern Europe
took place in the Holocene (Balashov et al., 2018). The aim of our work is
to describe the ecological niche of the land snail B. cylindrica in terms
of the edaphic properties and properties of the vegetation cover and to
show the spatial features of the variation of the habitat preference index
within the artificial soil body – technosols (soddy-lithogenic soils on
loess-like clays) using the ecological niche factor analysis (ENFA).

Material and methods

The research was carried out at the Research Centre of the Dniprop
Agrarian and Economic University in Pokrov (Fig. 1). This experiment-
mental site for the study of optimal regimes of agricultural recultivation was
established in 1968–1970. The territory has a temperate-continental
climate with an annual mean maximum decade temperature of 26.4 ºC,
and a minimum of –8.2 ºC, and with a mean annual precipitation of
approximately 511 mm (20-year average according to data of the Niko-
pol meteorological station).

Sampling was carried out on a variant of artificial soil (technozems)
formed on loess-like clays (the geographic coordinates of the south-
western corner of the test site are 47°38′55.24″ N.L., 34°08′33.30″ E.L.).
According to WRB 2007 (USSW Working group WRB, 2007), the exa-
mined soil can be classified among the RSG Technosols. The examined
profile, also, satisfies the criterion for the prefix qualifier Spolic having
mined soil can be classified among the RSG Technosols. The examined

Determination of the aggregate-size distribution was carried out by
methods of dry sieving. To measure the electrical conductivity of soil in
situ, an HI 76305 sensor (Hanna Instruments, Woodsocket, R. I.), wor-
king in conjunction with the portable instrument HI 993310, was used.
The tester estimates the total electrical conductivity of the soil, i.e.
combined conductivity of soil air, water and particles. The results of
measurements of the device are presented in units of saturation of the
soil solution with salts (g/l). Comparison of the measurement results
obtained with the instrument HI 76305 with laboratory data allowed us
to estimate the conversion factor of units as 1 DS/M = 155 mg/l.

The vegetation cover was described within squares with a lateral side
of 3 m. The physiognomic characteristics of the vegetation cover were
established by the results of decoding the digital photographs of the
surface of the experimental plot made from a height of 1.5 m. The main
physiognomic types of vegetative cover were singled out visually:
type I – cereals (indicator Bromus squarrosum); type II – Seseli
torvissum; type III – Lactuca tatarica (L.) C. A. Mey.; type IV –
legumes (Medicago sativa L.); type V – dead plant residue; type VI –
open soil cover. The most typical fragments for the corresponding
species were chosen for the images, according to which their colour
characteristics in RGB format were set. They were used as a testing
sample for discriminant analysis. After that, all pictures were decoded,
which allowed us to estimate the share that each of the physiognomic
types in the cover occupied (Yorkina et al., 2018).

Geobotanical prospecting became the basis for phytodiversity
indication of environmental regimes (Zhuskov et al., 2016). Daidak (2011) distin-
guishes edaphic and climatic phytodiversity scales. Soil water regime
(Hd), variability of dumping (Hl), soil aeration (Ae), soil acidity (Re),
total salt regime (Si), carbon content in soil (Ca), nitrogen content in
soil (Nt) comprise the edaphic scales. The scales for the next four factors
comprise the climatic scales. These are radiation balance (Tm),
aridity or humidity (Om), cryoclimatic (Cr) and continentality (Kn).
In addition, the scale of light regime (Lo) is allocated as the microclima-

Biosyst. Divers., 2019, 27(1)
te scale. We can assume that edaphic scales and the scale of light regime will be light-sensitive properties of soil variability at a single point, which can be the basis for the application of phytoindication scales for large-scale mapping. Thermal properties of soils are indicated by the radiation balance scale; hydrothermal properties of soils are indicated by aridity scale (Didukh, 2012). Phytoindication scales are presented by Didukh (2011). Phytoindication assessment of gradations in environmental factors is presented by Buzuk (2017).

Statistical calculations were performed using the Statistica 12.0 (StatSoft Inc., 2014, version 12, www.statsoft.com) Program and the project for statistical computations R (www.r-project.org) using adehabitat libraries (Calenge, 2006) and vegan (Oksanen, 2011), two-dimensional mapping, estimation of geostatistics and creation of ascii files with data of spatial variability of the environment indicators – using the program and ArcGis 10.0 (ESRI, 2011, ArcGis Desktop: Release 10, Redlands, CA, Environmental Systems Research Institute).

Results

The mollusc *B. cylindrica* population decreased during the study period (Fig. 2). The greatest abundance was detected in 2012. This index was 56.4 ± 1.8 ind./m². The smallest abundance was found in 2014 – 32.1 ± 1.5 ind./m². The electrical conductivity of the technosol is in the range of 0.51 to 0.52 dSm/m (Table 1). In aggregate fraction, dominant sizes were 1–5 mm. The soil penetration resistance of the soil top layer was between 2.48–3.66 MPa and increased with depth. The sharpest increase in soil penetration resistance was observed at a depth of 10–15 cm, and then the growth of this index is rather moderate. Vegetation-free soil surface was between 38.2–41.4%. The physiognomic types II, III and V had the highest degree of projective cover.

Phytoindication assessment indicates that the technosol water regime is favourable for sub-mesophytes. According to Didukh (2011), sub-mesophytes are the plants adapted to rather dry forest-meadow habitats with moderate rain and melted water drenching of the soil layer where plant roots penetrate. The regime of the water damping variability was favourable for hemi-hydrocontrastophiles. Technosol acidity was favourable for neutrophiles, plants which grow on acidulous and neutral (pH = 6.5–7.1) soils. The total salt regime was favourable for semi-eutrophs. This ecological group indicates soils enriched with salt (150–200 mg/l) with a content of HCO−_4–16 mg/100 g of soil, and trace of SO_4^{2−} and Cl−. The content of carbonates creates conditions that were favourable for carbonatophiles. These plants grow best on carbonate soils where CaO, MgO = 5–10%. The regime of the nitrogen content was favourable for hemi-nitrophiles. Hemi-nitrophiles indicate soils...
moderately rich in mineral nitrogen (0.2–0.3%). The sub-aerophiles formed the dominant ecological group that indicates highly aerated habitats with inclusions of broken stones. The lighting regime was indicated to be characteristic of open spaces.

Table 1

<table>
<thead>
<tr>
<th>Properties</th>
<th>2012</th>
<th>2013</th>
<th>2014</th>
</tr>
</thead>
<tbody>
<tr>
<td>Conductivity, dSm/m (EC)</td>
<td>0.51 ± 0.01</td>
<td>0.52 ± 0.01</td>
<td>0.52 ± 0.01</td>
</tr>
<tr>
<td>Aggregate structure, size of fractions, mm</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>&gt;10</td>
<td>7.49 ± 0.30</td>
<td>5.95 ± 0.21</td>
<td>5.90 ± 0.22</td>
</tr>
<tr>
<td>7–10</td>
<td>5.95 ± 0.17</td>
<td>4.21 ± 0.09</td>
<td>4.44 ± 0.08</td>
</tr>
<tr>
<td>5–7</td>
<td>7.83 ± 0.18</td>
<td>9.64 ± 0.15</td>
<td>9.61 ± 0.15</td>
</tr>
<tr>
<td>3–5</td>
<td>18.93 ± 0.47</td>
<td>20.58 ± 0.20</td>
<td>20.55 ± 0.21</td>
</tr>
<tr>
<td>2–3</td>
<td>16.97 ± 0.19</td>
<td>23.36 ± 0.24</td>
<td>23.48 ± 0.24</td>
</tr>
<tr>
<td>1–2</td>
<td>25.45 ± 0.29</td>
<td>15.57 ± 0.16</td>
<td>15.65 ± 0.16</td>
</tr>
<tr>
<td>0.5–1.0</td>
<td>5.17 ± 0.23</td>
<td>6.19 ± 0.13</td>
<td>6.18 ± 0.12</td>
</tr>
<tr>
<td>0.25–0.50</td>
<td>6.00 ± 0.30</td>
<td>7.73 ± 0.17</td>
<td>7.69 ± 0.15</td>
</tr>
<tr>
<td>&lt;0.25</td>
<td>5.62 ± 0.21</td>
<td>6.77 ± 0.12</td>
<td>6.75 ± 0.12</td>
</tr>
</tbody>
</table>

Table 2

<table>
<thead>
<tr>
<th>Properties</th>
<th>2012</th>
<th>2013</th>
<th>2014</th>
</tr>
</thead>
<tbody>
<tr>
<td>Conductivity, dSm/m</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>&gt;10</td>
<td>-0.08</td>
<td>-0.20</td>
<td>-0.12</td>
</tr>
<tr>
<td>7–10</td>
<td>0.12</td>
<td>0.12</td>
<td>0.29</td>
</tr>
<tr>
<td>5–7</td>
<td>0.14</td>
<td>-0.15</td>
<td>-</td>
</tr>
<tr>
<td>3–5</td>
<td>-0.12</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>2–3</td>
<td>0.10</td>
<td>0.19</td>
<td>-</td>
</tr>
<tr>
<td>1–2</td>
<td>0.10</td>
<td>0.19</td>
<td>-</td>
</tr>
<tr>
<td>0.5–1.0</td>
<td>0.10</td>
<td>0.19</td>
<td>-</td>
</tr>
<tr>
<td>0.25–0.50</td>
<td>0.08</td>
<td>-0.22</td>
<td>0.14</td>
</tr>
<tr>
<td>&lt;0.25</td>
<td>0.15</td>
<td>0.21</td>
<td>-0.13</td>
</tr>
</tbody>
</table>

The test for statistical significance showed that an axis of marginality of the ecological niche of B. cylindrica (γmarg = 0.11–0.17, P < 0.001) and axes of specialization (γsp = 1.53–1.68, P < 0.001) are significantly different from the random distribution. Marginality of the ecological niche of the mollusc is determined mainly by the following ecological-geographical predictors: contents of some aggregate fraction in the soil, phystosynomical types of plant cover and such soil regimes as humidity, carbonate and nitrogen content (Table 2). In 2012 the effect of soil electrical conductivity on the ecological niche was not found. According to the results of the ENFA-approach, it can be argued that the molluscs prefer sites with a high content of the aggregate fraction with size of <0.25 to 0.5–1.0 mm and 5–10 mm and avoid areas with high contents of aggregate fraction with size 1–5 and >10 mm. The role of soil penetration resistance as a marker of the ecological niche of B. cylindrica is not significant. In 2012, B. cylindrica preferred phystosynomical types III and VI and avoided areas with a predominance of types II, IV, and V. In 2013, the mollusc preferred types I and V, and avoided types II and III. In 2014, they preferred types IV and V, and avoided types I and III. The main aspects of the B. cylindrica ecological niche specialization are content of the aggregate fraction with size 0.25–
0.50 and 0.5–1.0 mm, the soil penetration resistance at a depth of 20–25 cm, and cover of the physiognomic types II, IV and V.

Ecological niche optima may be presented by integral variables such as marginality and specialization axes and may be plotted in geographic space by means of Habitat Preference Index (HSI) reproduction (Yorkina et al., 2018) (Fig. 2). The results indicate the repeatability of the spatial patterns of molluscs in time. The repeatability of the spatial patterns may be explained by the time invariants of the ecological niche. The marginality of *B. cylindrica* ecological niche over the entire period of study is determined mainly due to the preferences of physiognomic vegetation types II and IV, higher rates of the continentality and thermality regimes (Fig. 3). Often, higher content in soil of aggregates 1–3 mm in size and greater number of *B. cylindrica* individuals coincide. Individuals of this species avoid physiognomic type III and areas with higher soil alkalinity and mineralization detected both by means of the phytointerpretation approach and soil electrical conductivity data. The small-sized aggregates (0.25–0.50 mm) indicate areas with relatively unfavourable conditions for *B. cylindrica*.

**Fig. 2.** Spatial distribution of the habitat suitability index (HSI) for *Brephulopsis cylindrica* within the experimental site on loess-like clays based on ENFA: a − 2012, b − 2013, c − 2014, on the abscissa ordinate axis – local polygon coordinates (m), scale – habitat suitability index (%)

**Fig. 3.** Parameters of the *B. cylindrica* ecological niche marginality for the whole period of investigation (the largest and smallest marginality markers are presented): marginality percentiles of the relevant characteristics; Cr – cryoclimate, Rc – soil acidity, Nt – nitrogen content in soil, Hd – soil humidity, EC – electrical conductivity, T 1 – cereals (indicator *Bromus squarrosus* L.), A 0.25 – aggregate fraction with size < 0.25 mm, A 7 – aggregate fraction with size 5–7 mm, Agr 7 – aggregate fraction with size 7–10 mm, A 10 – aggregate fraction with size > 10 mm, Im 05 – soil penetration resistance at depth 0–5 cm, Im 10 – soil penetration resistance at depth 5–10 cm

**Discussion**

The remediation of disturbed territories simulates the initial stages of ecosystems’ succession (Wali, 1999). The young artificial technosol is still very far from the quasi-steady state which is characteristic of the soil which had been in this place before the surface mining (Klimkina et al., 2018). The moisture content of soils plays an important role (Nekola, 2003). However, the limited data on the role of soil moisture at a given time in view of the significant variability of this parameter was noted (Ondina et al., 2004). To solve this problem, it is appropriate to use phytointerpretation data to assess the autecological features of molluscs and the structure of their communities (Horsák et al., 2007; Dvorská & Horská, 2012). For describing habitat preferences of the mollusc *Vertigo geyeri* Lindholm, 1925, the Ellenberg phytointerpretation scales were successfully used in Poland and Slovakia (Schenková et al., 2012).

The dynamism of the soil conditions creates the prerequisites for a high degree of heterogeneity in the soil conditions and the diversity of vegetation. The site age was the most important factor influencing plant species richness and abundance (Wali, 1999). A total of 96 plant species were detected in the study polygon (Maslikova et al., 2016; Zhakov & Maslikova, 2018). Such species diversity is enough to evaluate the spatial variation of environmental conditions by means of phytointerpretation methods. Local trends, as well as the mosaic nature of the organization of the soil body determine the structure of the vegetation cover, which explains the role of indicators in the structure of ecological niches of molluscs (Yorkina et al., 2018).

Outside the native area, *B. cylindrica* mostly lives in anthropogenic habitats such as roadsides and tracks, lawns and wastelands (Guralská & Gural, 2012). The abundance of *B. cylindrica* and the distribution of age groups in the adventitious populations vary during the season. Near Belgorod, the highest population densities are observed in late spring – early summer (149–205 ind./m²) (Adamova et al., 2018). Our data revealed that technosols create favourable conditions for this species. The population density of *B. cylindrica* reached a considerable value within the study period. Snails can reach high levels of species abundance even within single quadrats (1 m² areas or less) (Coles & Nekola, 2007; Cernohorsky et al., 2010; Kunakh et al., 2018). But ecological conditions for *B. cylindrica* within the study polygon are not uniform. This result is in agreement with data obtained for another invasive population near the Belgorod (Adamova et al., 2018).
Within the natural range the climatic conditions in the hot season are the most important factor determining the demographic population structure in the late season (Kramarenko & Popov, 1993.) The B. cylindrica population abundance in the Crimea was found to decrease in value in September to 40 ind./m² (Kramarenko, 1997). With a significant geographical extension of the study area, the indicators that determine the level of the mollusc population acquire importance – the moisture gradients, the calcium content and the acidity of the soil, as well as their phytointeraction estimates (Millar & Waite, 1999; Marti & Sommer, 2004; Müller et al., 2005; Weaver et al., 2006; Schenkova et al., 2012). On a large scale, chemical indicators, such as availability of food elements or the characteristics of leaf litter, also usually attract attention. The indexes of the physical state of the soil – aggregate structure, shrinkage, temperature, play an important role for the Vallonia pulchella geobiont micro-molluscs (Yorkina et al., 2018). The selection of favours microhabitats is the one of the key mechanisms for avoiding excess loss or gain of water (Luchtel & Deyrup-Olsen, 2001), which are rable microhabitats is the one of the key mechanisms for avoiding excess loss or gain of water (Luchtel & Deyrup-Olsen, 2001), which are

B. cylindrica remains have the most invariant impact on mollusc abundance. Thus the nature of the impact varies greatly over time. Dead plant individuals avoid sites with a high projective cover of dead plant remains.

The most significant edaphic factors that affect molluscs are the content of calcium in the soil, pH and soil texture (Ondina et al., 2004), as well as the content of exchangeable cations and aluminum (Ondina et al., 1998). For B. cylindrica, one feature of adaptive behaviour is known: these snails burrow in the soil (Kramarenko, 1993). Mostly B. cylindrica juveniles burrow in the soil in the hottest summer months (Kramarenko, 1997). This ecological property of B. cylindrica explains the effect of the soil condition on the spatial distribution of the mollusc population. Electrical conductivity may be used as a proxy measure of mineral richness. A unimodal response of local mollusc species diversity to mineral richness (expressed as conductivity) was found (Horská, 2005). In our study, B. cylindrica individuals avoided areas with higher soil alkalinity and mineralization detected both by means of the phytointeraction approach and soil electrical conductivity data.

Conclusion

Our data revealed that technosols create favourable conditions for this species. The population density of B. cylindrica reaches a considerable value within study period. The results indicate the repeatability of the spatial patterns of molluscs in time. The repeatability of the spatial patterns may be explained by the time invariants of the ecological niche. The marginality of B. cylindrica’s ecological niche over the entire period of study is determined mainly due to its preferences for phytoindication estimates. Periphyton communities and their environmental gradients in New Zealand rivers. New Zealand Journal of Marine and Freshwater Research, 24, 367–386.


Kramarenko, S. S., & Popov, V. N. (1993). Izmenchivost' morfologicheskikh priznakov nazemnykh moll'yuskov roda Brephulusis Lindholm, 1925 (Gastropoda; Pulmonata; Buliminidae) v zone intrategmennyh gibrizdatyi [Variation of morphological traits in land snails, Brephulusis cylindrica (Gastropoda; Pulmonata; Buliminidae) in the intratrophic hybridization zone]. Zhurnal Obshchi Biologii, 56(6), 682–690 (in Russian).


