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Article

Formation of a life strategy in plant species from technogenic ecotopes by the example of short-rhizomatous Orchids

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Abstract. The paper presents the results of the analysis of a life strategy formation in plant species under conditions of anthropogenically transformed ecosystems by the example of short-rhizomatous orchids: *Epipactis atrorubens*, *Epipactis helleborine*, *Neottia ovata*, and *Cypripedium calceolus*. In 2020–2022, 16 cenopopulations of the studied species from a non-reclaimed limestone quarry overgrown with trees were examined. These species grow in forest communities and forest-meadow ecotone biotopes in the technogenic environment. Vascular plants of the studied phytocenoses, meadow and meadow-edge species dominate. Representatives of the family Orchidaceae have two types of ontogenetic strategies distinguished by the alternation of protective and stress components. Morphobiological parameters almost in all taxa exhibit mixed types of tactics: divergent-convergent and convergent-divergent.

Keywords: plant adaptation, life form, variability of traits, coefficient of determination, disturbed ecosystems, ontogenetic tactics, fam. Orchidaceae Juss., ecocline, ecological-cenotic groups

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Научная статья

Формирование жизненных стратегий растений техногенных экотопов на примере коротко-корневищных орхидей

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Аннотация. На примере коротко-корневищных орхидей *Epipactis atrorubens, E. helleborine, Neottia ovata* и *Cypripedium calceolus* показаны результаты анализа жизненной стратегии видов растений в измененных биотопах. В 2020–2022 гг. проанализировано 16 ценопопуляций орхидей на зарастающем деревьями не восстановленном карбонатном карьере. Показано, что рассматриваемые виды растут в лесных и лесо-луговых сообществах. Среди сосудистых растений изученных фитоценозов преобладают луговые и лугово-опушечные виды. У рассматриваемых орхидей наблюдаются две стратегии развития, которые отличаются последовательностью защитных и стрессовых элементов. Морфометрические параметры почти всех изученных видов проявляют дивергентно-конвергентные или конвергентно-дивергентные тактики.

Ключевые слова: адаптации растений, жизненная форма, изменчивость признаков, коэффициент детерминации, нарушенные экосистемы, онтогенетические тактики, сем. Orchidaceae Juss., экоклин, эколого-ценотические группы

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Introduction

The anthropogenic pressure on natural ecosystems is increasing from year to year. As the scale, intensity and diversity of anthropogenic impacts on nature grow, the study of mechanisms of species stability in post-technological territories becomes more relevant.

It is known that stability of a species is achieved through its life strategy that is a set of adaptations arising from the natural selection and characterizing the most common adaptations of species to factors of the biotic and abiotic environment. At the same time, each type of a strategy is characterized by its own complex of adaptive reactions, a detailed study of which at the organismal and population-ontogenetic levels allows to identify the mechanisms of species stability in the community aimed at its survival, preservation of its place in the cenosis, restoration of the structure and functions after stressful effects (Ishbirdin et al., 2005; Mirkin and Naumova, 2005; Rabotnov, 1992). When analyzing strategies, it should also be borne in mind that strategies are species characteristics, and they can be learned only through studying a species position in different communities and habitats (Vasilevich, 1987). As noted by A.R. Ishbirdin and M.M. Ishmuratova (2004), the assessment of plant survival strategies remains one of the key tasks of population botany. The important characteristics, determining the state of an individual and a population, is the degree of wholeness (integration) of the organism at the anatomical and morphological level that is provided by the adaptive development of various structures in ontogenesis.

Along with natural habitats, the representatives of the Orchid family are often found in anthropogenic landscapes (Filimonova et al., 2014; Suyundukov, 2011; Teleganova, 2019), where they form quite numerous populations. Currently, investigations of the adaptive potential of rare and protected plants in the secondary biotopes are among topical directions in studying both the processes of anthropogenic transformation of the flora and the ability of native species to develop in various disturbed habitats (Berezutsky et al., 2012; Teleganova, 2019). The orchids *Epipactis atrorubens* (Hoffm. ex Bernh.) Bess., *Epipactis helleborine* (L.) Crantz., *Neottia ovata* (L.) Bluff & Fingerh., *Cypripedium calceolus* L. are the objects of our study. These species have an international protection status. They are included in Annex II of the CITES Convention on International Trade (Bilz at al., 2011; Convention..., 2013)[1] and protected in many regions of the Russian Federation (Plantarium, 2022)[2].

The purpose of this work is to identify the type of life strategy of short–rhizomatous species of the family Orchidaceae Juss in conditions of anthropogenically transformed ecosystems by the example of a non-reclaimed limestone quarry overgrown with tree species.

Material and methods

The research was carried out at the territory of a spent limestone quarry (Pervomaisky village, Slobodskoy district, Kirov Oblast) in 2020–2022. The quarry is located in the upper part of the steep slope of the indigenous bank of the Vyatka River (a subzone of the southern taiga). For more than 30 years, biological reclamation via passive and active settling protozoa, plants and animals from surrounding forests, meadow phytocenoses and agrocenoses was implemented on this quarry and 16 cenopopulations (CPs) of the studied species were examined (Table 1).

The description of the studied plant communities was made in accordance with the generally accepted geobotanical methods and approaches (Andreeva et al., 2002). The names of the species are given according to the Plants of the World Online Database (http://www.plantsoftheworldonline.org)[3]. The species affiliation to the ecological-cenotic group (ECG) was determined from a reference database (Smirnov et al., 2006; Smirnova et al., 2004).

Methodological developments of Yu.A. Zlobin (1989, 2009), A.R. Ishbirdin and M.M. Ishmuratova (2004) were used in assessing the types of ontogenetic tactics and strategies. A total of 10 morphological features were analyzed in *Neottia ovata*, 18 in *Cypripedium calceolus* and 11 each for *Epipactis atrorubens*

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[1] Convention on International Trade in Endangered Species of Wild Fauna and Flora. Web page. URL: https://cites.org/eng/disc/text.php (accessed: 26.12.2022).

[2] Plantarium. Plants and lichens of Russia and neighboring countries: open online galleries and plant identification guide, 2007–2024. Web page. URL: https://www.plantarium.ru/lang/en.html (accessed: 26.12.2022).

[3] Plants of the World Online Database. Web page. URL: http://www.plantsoftheworldonline.org/ (accessed: 12.02.2024).

Table 1. Characteristics of cenopopulations of the studied species. CP – cenopopulation; IVC – index of vitality of cenopopulations.

Species	CP	Type of phytocenosis	IVC
Neottia ovata	1	Wintergreen pine forest	0.991
	2	Edge of spruce forest with an admixture of aspen and pine	0.988
	3	Wintergreen willow forest	1.042
	4	Green moss wintergreen pine forest	0.980
Epipactis atrorubens	1	Edge of mixed-grass and legume pine forest	0.94
	2	Edge of grass and legume pine forest	0.97
	3	Wintergreen mixed grass pine forest with an admixture of aspen and spruce	1.03
	4	Wintergreen willow forest	1.01
Epipactis helleborine	1	Wintergreen willow forest	1.11
	2	Green moss and grass spruce forest	0.84
	3	Mixed grass willow pine forest	1.06
Cypripedium calceolus	1	Mixed grass spruce forest	1.00
	2	Grass spruce forest	1.01
	3	Grass pine forest	1.02
	4	Grass spruce forest with an admixture of fir and pine	1.14
	5	Mixed grass willow pine forest	0.83

and *E. helleborine*. From the complex of morphometric parameters, we included in the analysis the most variable features: height of vegetative-generative shoots, number of leaves of the median formation, length of inflorescence, number of flowers, length of a leaf blade of the 2nd leaf, width of a leaf blade of the 2nd leaf, number of veins of a leaf blade[4].

The ontogenetic tactics of the species reflects trends in feature variations depending on a cenopopulation position on the ecocline (Zlobin, 1989, 2009). The level of such variations is estimated by the coefficient of variation (CV, %). To establish the ecocline (gradient of deterioration of growing conditions), the index of vitality of cenopopulations (IVC) was applied, i.e. the vitality coefficient calculated from the formula (Ishbirdin and Ishmuratova, 2004; Ishmuratova and Ishbirdin, 2002):

$$IVC = \frac{\sum_{i=1}^{N} X_i / \overline{X}_i}{N}$$

where X_i – is the average of i- feature in the cenopopulation, $\overline{X}_i$ – is the average of i-feature for all cenopopulations, *N* – is the total number of features.

The ontogenetic strategy of the species was determined in accordance with the dynamics of morphological integration (plant wholeness) on the ecocline (Ishbirdin and Ishmuratova, 2004). Morphological integrity was estimated as the average of the determination coefficients (the square of the feature correlation coefficient), the coefficients of determination (R^2m), or the squares of feature correlation coefficients of all pairs.

Statistical data analysis was performed using Microsoft Office Excel 2010 and Statistica 10.

[4] The materials of the article were presented at the international scientific conference “Biomorphology of plants: traditions and modernity”.

Research results

In the man-disturbed environment, the studied species grow in forest communities (wintergreen pine forest, grass pine forest, green moss wintergreen pine forest, mixed grass willow pine forest, wintergreen mixed grass pine forest with an admixture of aspen and spruce, wintergreen willow forest, green moss and grass spruce forest, grass spruce forest, mixed grass spruce forest, grass spruce forest with an admixture of fir and pine, mixed grass willow pine forest) and forest-meadow ecotone biotopes (edge of mixed-grass legume pine forest, edge of spruce forest with an admixture of aspen and pine) (Egorova and Suleimanova, 2021, 2022a, b; Egorova et al., 2022) (Table 1).

Forest-meadow ecotone biotopes. The total projective coverage of the grass-shrub layer here ranges from 30 to 50%. Herbage height varies from 20 to 35 cm. In the grass tier, among described (46–53) species, *Pyrola rotundifolia* L., *Fragaria vesca* L., *Prunella vulgaris* L., *Hieracium umbellatum* L., *Plantago lanceolata* L., *Origanum vulgare* L., *Trifolium pratense* L., *T. hybridum* L., *T. repens* (L.) Nevski, *Alchemilla xanthochlora* Rothm., *Melica nutans* L., *Tussilago farfara* L., *Veronica chamaedrys* L., *Pimpinella saxifraga* L., *Centaurea jacea* L., *Festuca pratensis* Huds., *Chamaenerion angustifolium* (L.) Scop., *Lathyrus pratensis* L., *Veronica longifolia* L., *Medicago sativa* L., *Solidago virgaurea* L., *Rubus saxatilis* L., *Taraxacum officinale* F.H. Wigg. etc. are present with the greatest constancy.

Secondary forest communities. The studied forest phytocenoses include such tree species as *Pinus sylvestris* L., *Picea abies* (L.) Karst and *Salix caprea* L. The understory is of medium closeness and mainly formed by *Sorbus aucuparia* L., *Frangula alnus* Mill., *Salix caprea* L., *Chamaecytisus ruthenicus* (Fisch. ex Woloszcz.) Klásk., *Hippophae rhamnoides* L., *Viburnum opulus* L., *Lonicera xylosteum* L., and less often – by *Padus avium* Mill., *Rosa majalis* Herrm. The average height of the undergrowth is 1.5–2.0 m. In total, 9 species of shrubs are noted there. The total projective coverage of the grass-shrub layer varies from 25 to 40%, whereas herbage height - from 15 to 25 cm. The number of vascular plant species in the grass-shrub layer of the studied forest phytocenoses ranges within 22–41. With the greatest constancy, species (*Pyrola rotundifolia* L., *Pyrola minor* L., *Prunella vulgaris* L., *Hieracium umbellatum*, *Plantago lanceolata* L., *Origanum vulgare* L., *Alchemilla xanthochlora* Rothm., *Trifolium hybridum* L., *Melica nutans* L., *Fragaria vesca* L., *Tussilago farfara* L., *Veronica chamaedrys* L., *Pimpinella saxifraga* L., etc.) form the grass tier. The moss cover is formed by 2 species of leaf-stemmed mosses: *Pleurozium schreberi* (Brid.) Mitt. and *Hylocomium splendens* (Hedw.) Bruch et al. makes up 3–5% (fragmentary, spots) in pine and willow forests and up to 40–50% in spruce ones.

The habitats of the studied species, confined to anthropogenically transformed biotopes, are an example of the coexistence of species of various ecological cenotic groups (ECGs), including vascular plants from 6 ECGs (Fig. 1). Meadow and meadow-edge species are best represented (42.11–58.82%). These are *Centaurea phrygia* L., *Trifolium hybridum*, *Trifolium repens* L., *Lathyrus pratensis* L., *Medicago falcata* L., *M. sativa, Taraxacum officinale*, *Galium mollugo* L., etc. Wide distribution of species from this ECG is associated with current succession changes occurred in the studied territories in the form of alternation of the meadow community by the forest one. In this regard, in the cenotic structure of the considered biotopes there are many boreal species (13.04–15.79%): *Sorbus aucuparia* L.*, Rosa acicularis* Lindl., *Rubus idaeus* L., *Orthilia secunda* (L.) House, etc. and slightly fewer small grasses (5.88–13.04%): *Rubus saxatilis*, *Pyrola rotundifolia*, *Solidago virgaurea*, *Equisetum pratense* Ehrh., *Equisetum sylvaticum* L., *Luzula pilosa* (L.) Willd., etc . The proportion of nemoral species varies from 4.35 to 15.79%. These are, for example, *Epipactis atrorubens*, *E. helleborine*, *Platanthera bifolia* (L.) Rich., *Convallaria majalis* L., *Neottia ovata*, *Viola mirabilis* L., etc. Wetland species account for 8.57% (*Veronica longifolia*, *Gymnadenia conopsea* (L.) R. Br.) and boreal species (*Hieracium umbellatum*, *Chamaecytisus ruthenicus* and others) – 7.54% of the total number of species. Tallgrass (*Chamaenerion angustifolium*) and nitrophilic (*Ribes nigrum* L.) species are found in small numbers – 4.46 and 2.22%, respectively.

Cenopopulations of *N. ovata*, *E. atrorubens*, *E. helleborine* from wintergreen mixed grass pine and willow forest demonstrate the highest vitality (IVC: 0.991–1.110). Here, more favorable conditions for the development are formed (low projective coverage of grass-shrub layer species, moss cover is absent or fragmentary) that resulted in bigger size of plants (Table 1). A noted decrease in species vitality in CPs confined to the edge biotopes (IVC: 0.94–0.98) is explained by acting simultaneously biotic and anthropogenic factors, i.e. aggravation of interspecific competition (increase in species diversity and general projective coverage) and increased trampling (adjacent training tracks of motorcycle racers). A low vital-

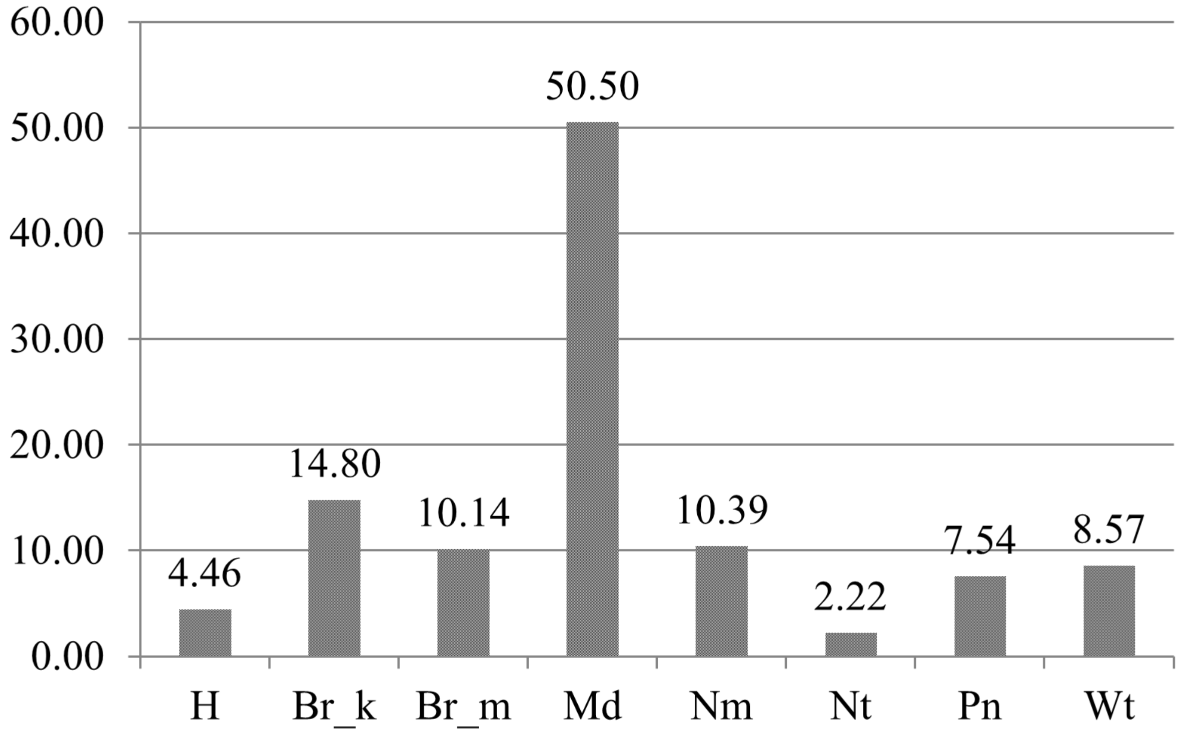

Fig. 1. The share of species participation of different ecological-cenotic groups (%) in the studied phytocenoses. H – tallgrass, Br_k – boreal (shrubs and evergreen grasses), Br_m – boreal (small grasses), Md – meadow and meadow-edge, Nm – immoral, Nt – nitrophilic, Pn – boreal, Wt – wetland (hygrophilic).

ity index is noted in CPs of these species growing in spruce and pine forests with a pronounced moss cover and high closeness of the stand (IVC: 0.84–0.98). In these communities, shorter plants with lower resource demands and energy consumption for shoot formation develop that is important for preserving the species place in the phytocenosis.

Slightly different results were obtained when assessing the viability of *C. calceolus* CP in the studied plant communities. Cenopopulations in coniferous medium-full plantations (closeness of the stand crowns: 0.3–0.4) are in the most favorable conditions. These plantings represent the preserved small fragments of forest vegetation not affected by limestone mining. The least favorable conditions are formed for CP of *C. calceolus* in mixed grass pine with willow forest (IVC = 0.83), which is a secondary biotope appeared due to succession changes in the spent quarry.

Discussion

Plant population adaptations to habitat conditions are implemented through various tactics of morphological structures development (Zlobin, 1989). The level of variability of individuals serves as a tactics manifestation. In cenopopulations of the studied species, variability of morphological features ranges widely: from low to very high (10.35–66.71%). The most variable are the features of the generative sphere (inflorescence length, number of flowers). In *C. calceolus* and *N. ovata*, a level of variability is from medium to high (CV = 21.9–40.89%), in species of the genus *Epipactis* – from medium to very high (CV = 14.64–66.71%). The vegetative parameters are less variable (Table 2).

Table 3 presents the ontogenetic tactics of the organismal features of the studied short-rhizomatous orchids from different-type habitats of the spent quarry. Such features as height of vegetative-generative shoots, width of a leaf blade of the 2nd leaf, number of flowers in all studied taxa exhibit divergent-convergent tactics, except for *N. ovata* in terms of first two features and *E. atrorubens* – number of flowers with the revealed convergent-divergent tactics. At the same time, the coefficient of variability of a trait with deterioration of living conditions in the case of divergent-convergent tactics first increases and then decreases, while at convergent-divergent tactics, on the contrary, it first decreases and then increases.

Table 2. Coefficients of variation and determination of morphological features of the studied species. In the numerator – CV (coefficient of variation of morphological features), in the denominator – R^2ch (coefficient of determination of morphological features)..

Feature	Species															
	Neottia ovata				*Epipactis atrorubens*				*Epipactis helleborine*			*Cypripedium calceolus*				
	CP 1	CP 2	CP 3	CP 4	CP 1	CP 2	CP 3	CP 4	CP 1	CP 2	CP 3	CP 1	CP 2	CP 3	CP 4	CP 5
Height of vegetative-generative shoot	24.35/0.40	16.54/0.24	22.0/0.66	39.07/0.40	23.52/0.37	26.67/0.38	26.05/0.23	35.65/0.64	21.98/0.28	22.26/0.38	31.79/0.56	22.27/0.23	26.07/0.23	25.85/0.41	14.10/0.30	32.09/0.36
Number of leaves of the median formation	–	–	–	–	22.76/0.13	22.61/0.12	27.21/0.03	26.95/0.31	23.14/0.04	22.87/0.33	18.96/0.18	15.49/0.08	14.17/0.04	12.87/0.15	14.79/0.27	15.86/0.06
Inflorescence length	31.14/0.43	32.64/0.12	26.55/0.47	35.02/0.50	32.36/0.34	42.40/0.37	37.03/0.27	55.70/0.62	49.73/0.21	36.63/0.45	46.86/0.26	–	–	–	–	–
Number of flowers	33.33/0.28	21.90/0.14	23.22/0.49	24.64/0.54	39.14/0.33	42.17/0.28	43.98/0.23	14.64/0.55	37.32/0.22	57.0/0.44	66.71/0.50	35.85/0.13	35.54/0.03	32.49/0.15	40.89/0.04	35.59/0.06
Length of a leaf blade of the 2nd leaf	20.37/0.42	19.82/0.26	22.60/0.65	22.13/0.47	29.98/0.13	26.72/0.14	23.48/0.03	33.61/0.47	18.22/0.06	19.44/0.26	18.04/0.08	17.90/0.17	16.25/0.25	15.74/0.34	10.35/0.16	20.56/0.30
Width of a leaf blade of the 2nd leaf	21.96/0.55	21.98/0.38	26.46/0.69	27.84/0.60	20.67/0.22	24.56/0.26	27.39/0.12	44.48/0.55	17.54/0.35	15.70/0.38	28.78/0.59	18.57/0.12	23.42/0.07	21.20/0.23	12.53/0.31	20.46/0.21
Number of leaf veins	11.57/0.07	16.67/0.39	17.88/0.51	16.87/0.33	43.82/0.14	35.59/0.04	32.91/0.17	–	15.82/0.09	12.45/0.14	21.74/0.36	22.74/0.16	24.14/0.18	29.75/0.27	19.90/0.27	21.74/0.28

Table 3. Ontogenetic tactics of short-rhizomatous species of the family Orchidaceae Juss. in conditions of anthropogenically transformed ecosystems. "–" – the feature was not analyzed.

Feature	Species			
	Epipactis atrorubens	*Epipactis helleborine*	*Neottia ovata*	*Cypripedium calceolus*
Height of vegetative-generative shoot	divergent-convergent	divergent-convergent	convergent-divergent	divergent-convergent
Number of leaves of the median formation	convergent	convergent-divergent	–	divergent
Inflorescence length	divergent-convergent	convergent	divergent	–
Number of flowers	convergent-divergent	divergent-convergent	divergent-convergent	divergent-convergent
Length of the leaf blade of the 2nd leaf	divergent-convergent	convergent-divergent	convergent-divergent	divergent-convergent
Width of the leaf blade of the 2nd leaf	divergent-convergent	divergent-convergent	convergent-divergent	divergent-convergent
Number of leaf veins	divergent	divergent-convergent	convergent-divergent	divergent

In all short-rhizomatous orchids, for such morphometric parameters as inflorescence length, number of leaves, and number of veins four different ontogenetic tactics are formed: convergent, divergent, divergent-convergent, convergent-divergent.

E. atrorubens demonstrates the greatest variety of ontogenetic tactics (4 types). This may indicate increased heterogeneity of cenopopulations in the pessimal conditions and can act as a manifestation of the protective mechanism of the species' response to stress. In *C. calceolus*, only two types of tactics (divergent, divergent-convergent) are noted. It is, apparently, due to reduced morphological diversity of individuals of this species under the pronounced stress effect of a complex ecological-cenotic factor.

The group of species under consideration is characterized by a mixed type of the ontogenetic strategy. The species *Epipactis atrorubens* and *E. helleborine* correspond to a protective stress strategy (Fig. 2**A**, **B**). At the same time, the protective component, which is one of the mechanisms of population adaptation of the species, is manifested in the ontogenetic strategy only at the initial stages of conditions deterioration (the coefficient of determination increases to 0.52 for *E. atrorubens* and 0.41 for *E. helleborine*). Further stress strengthening contributes to a decrease in morphological integration of plants against the general destabilization of morphobiological vegetative-generative parameters and causes adaptive variability. Thus, in the conditions of ecological-cenotic pessimum (CP 1, CP 2), the suppression of adaptive capabilities of species in the form of disintegration of morphological structures of their individuals is observed against the background of a reduced variability of organs; it also reflects a decrease in the index of morphological integration (up to 0.24 and 0.34, respectively).

Ontogenetic strategies of such species as *N. ovata* and *C. calceolus* are characterized by a substitution of the protective element of the ontogenetic strategy to a stress one that is expressed in a corresponding decrease in the value of the coefficient of determination to 0.14 in *C. calceolus* and to 0.28 in

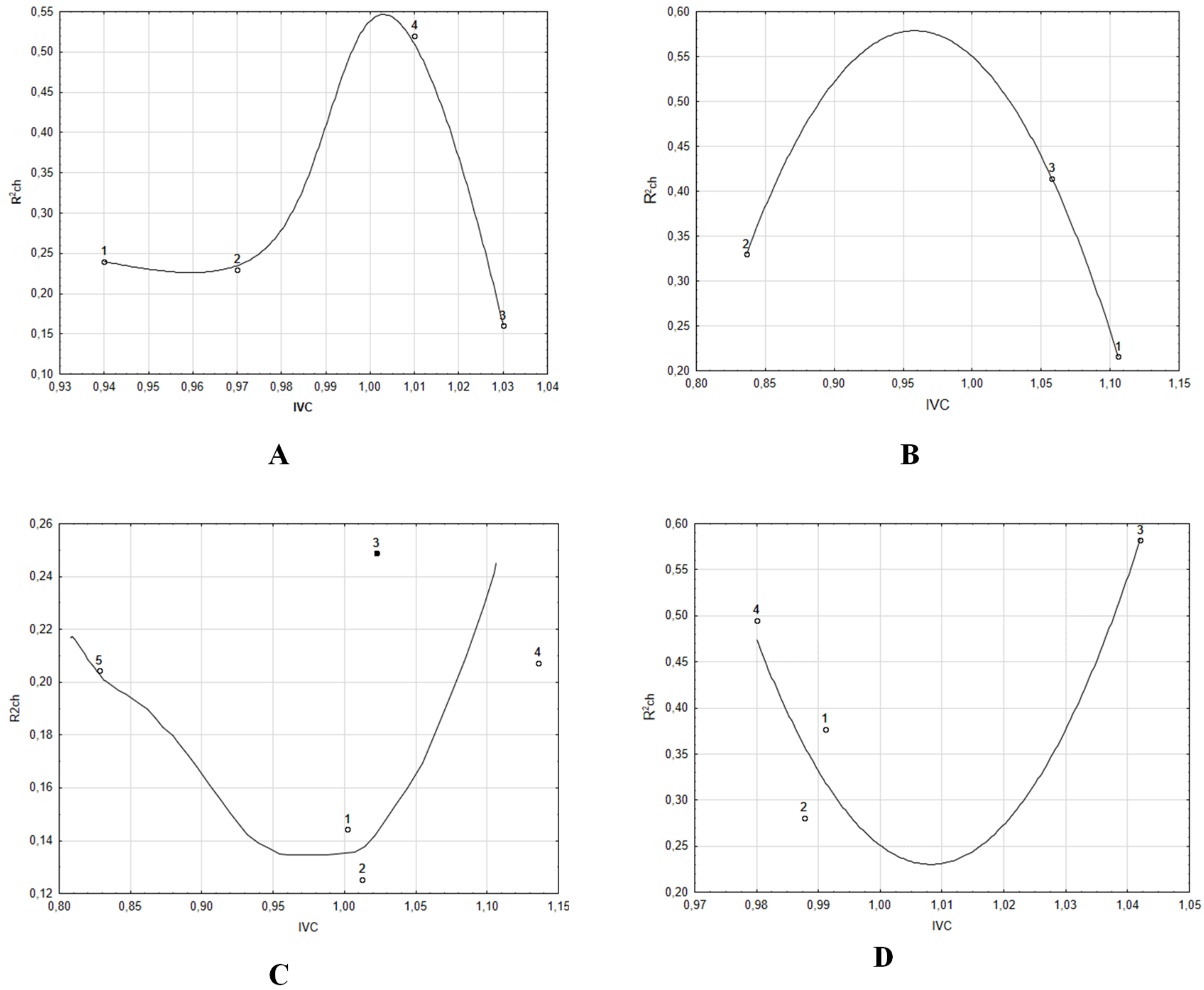

Fig. 2. Trends of ontogenetic strategies of species Orchidaceae Juss. in the conditions of anthropogenically transformed ecosystems by the example of the non–recultivated limestone quarry overgrown with tree species. **A** – *Epipactis atrorubens*; **B** – *Epipactis helleborine*; **C** – *Cypripedium calceolus*; **D** – *Neottia ovata*. Along x-coordinate: index of vitality of cenopopulations (IVC); along y-coordinate: morphological integrity (coefficient of determination of signs, R^2ch).

N. ovata, as well as its subsequent increase to 0.25 and 0.58, respectively. According to M.M. Ishmuratova et al. (2010), I.V. Blinova (2014), the stress-protective ontogenetic strategy is most characteristic for many species of the Orchid family (Fig. 2**C**, **D**). Under conditions of anthropogenic impact, the strategy is complemented by ruderal features.

Conclusion

Changes in the feature variation coefficient suggest that most morphobiological parameters in all taxa exhibit mixed types of tactics: divergent-convergent and convergent-divergent. Studying variability of the correlation structure of plants in various cenotic conditions of the spent limestone quarry made it possible to identify (in short-rhizomatous representatives of the family Orchidaceae) two types of ontogenetic strategies distinguished by a sequence of protective and stress components. The formed mechanisms of species stability under ecological and cenotic stress contribute to maintaining heterogeneity and lability of their cenopopulations, preservation of species as a part of phytocenoses and reduction of destructive processes at the organismal and population levels.

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