DIVERGENCE OF MORPHOLOGICAL FLORAL TRAITS AMONG EUROPEAN *OENOTHERA* L. POPULATIONS

VALERI K. TOKHTAR[1],
RUDIGER WITTIG[2]

[1]*Belgorod State University*
[2]*Frankfurt-on-Main University, Institute of Botany*

e-mail: oleg_minaev@mail.ru

We studied the structure of stable phenotypic markers in thirty-six populations of the s. str. Oenothera species from the Czech Republic, Germany, Poland, Slovakia, and Ukraine were analyzed. Some diagnostic quantitative traits of Oenothera biennis L. s. str. and/or s.l. phenotypes showed higher differentiation at the population level as compared to the species level. The study of six generative features in different geographic populations of the genus Oenothera allows us to make the conclusion of a considerable isolation of the species Oe. issleri and some distinctions of Oe. glazioviana and Oe. rubricaulis from the species investigated. Different geographical Oenothera biennis populations are distinctly differentiated by the discriminant analysis. Obviously, the divergence of the morphological traits can be explained by the microevolutionary processes within these populations, as well as by their adaptation to local environments.

Key words: Oenothera, morphological characters, variability.

Invasions of alien plant species may result in the formation of evolutionarily isolated phenotypes, races, and even species. The majority of alien species is recorded from ruderal habitats, such as railway areas, disturbed sites, abandoned farmland, and riparian habitats [1, 2]. The genus *Oenothera* L. (Onagraceae) is one of the most widespread genera of American origin in Europe. *Oenothera* species are successful invaders of disturbed riverbanks, sandy dunes, and seacoasts in Europe. *Oenothera's* high invasive potential is achieved due to a particular breeding mechanism (permanent translocation heterozygosity), which allows two species to hybridize and to form a third species. Furthermore, when *Oenothera* species spread into new habitats, new taxa adapted to new conditions may arise [1, 3,]. Therefore, this genus is a good subject for research of microevolutionary changes and adaptation of the correlation structure of features of the invasive species in man-made habitats.

Furthermore, many diagnostic features of *Oenothera* species have a quantitative expression. It explains the need for the studies of the variability of stable quantitative taxonomic traits under different ecological and geographical conditions. The objectives of our investigation were to study the structure of taxonomic quantitative morphological features (phenotypic markers) in *Oenothera* L. populations, to assess the patterns of morphological variation among populations of different taxa in man-made habitats, and to reveal some divergent traits within *Oenothera* populations.

Material and methods

In our study, we used data from 36 populations of 9 species of *Oenothera* (see Appendix). Floral polymorphism related to sexual differentiation has been a topic of interest for evolutionary biologists for over a century. Therefore, we used some floral characteristics in our research. For each plant individual, the following quantitative taxonomic characters (phenotypic markers) were measured: the length and width of a petal, the lengths of a sepal apex, hypanthium, stigma and anther, respectively. All the measurements were made at the main (earliest) phase of blooming, when the flowers have a normal size. All the populations investigated were isolated from the others by natural or anthropogenous limits in different localities. Thus, we consider them as independent units for our analysis.

The level of variation was expressed by the coefficient of variation.

In order to study the differences between populations and species, we arranged these populations according to morphological distances between them along any axis. The inter-populational differences were estimated by Tsarapkin's coefficients of characters' divergence

[4]. This method enabled us to assess both infraspecific (according to the standardized deviations of individual features) and interspecific (as to the values of whole divergence coefficients, which include the deviations of features) differences in populations of *Oenothera*. The method allows evaluating divergence of populations, forms, subspecies, and even species, based on the respective reference taxon. According to this method, the standardized (standard) deviation of a mean value of a character in a population from mean value of a character in the standard population is determined as:

$$(1) \quad \delta = \frac{M_i - M_{st}}{\sigma_{st}},$$

where δ is a standardized deviation of a character; M_i: arithmetical mean of a character, M_{st}: arithmetical mean of a character in a standard population , σ_{st}: geometrical mean deviation of a character in a standard population.

A morphological distance between the populations, i.e. the sum of differences between the corresponding traits, was found using the following formula:

$$(2) \quad CD = \sigma_s \sqrt{\frac{\sum \delta^2}{N-1}},$$

CD: coefficient of divergence of a population from a standard one, σ_s : standardized deviation of a character, $\sum \delta^2$: sum of quadratic deviation of characters from a standard, N: the number of characters.

We chose the standard population to arrange the studied populations along an axis for the comparison of morphological distances between them. According to the method applied, any population may be used as a standard one without bias to the results [7]. The morphological distances between the populations do not depend on that choice. However, it is more convenient to take for a standard population the most typical population selected *a priori* [7].

The herbarium specimens of *Oenothera biennis* L. population have been reported from the valley of the Siversky Donets River (the South-East of Ukraine) since 1936. It is a naturalized population within a natural ecotope. The habitat is similar to those from the native areas of the species. Because of that, this easternmost population (N15) was chosen as a standard to compare the populations and species under different geographical and ecological conditions.

To study the differences among morphological traits of the populations, the discriminant analysis was also used.

The population correlation structure is a system of links between all traits in a population, and it provides important information about complex regularities in organization of the morphological structure of a population. Each correlation coefficient can be examined as a particular taxonomic character. In the present study, a particular correlation structure was evaluated by the coefficients of divergence of correlation structures (CDC) [4]. The correlations of characters were estimated by the strength of the link and their factor structure [5]. The coefficient of determination, a square of the correlation coefficient, the averaging for the whole matrix [6], was used to assess the average level of the correlative connection.

The principal component analysis of all trait values of the 36 populations investigated was conducted in order to evaluate the differences among the population correlative structures of morphological characters. The correlative coefficients of characters were preliminarily z-transformed for each single population to approximate them to the normal statistical distribution:

$$(3) \quad z = 0,5 \ln \{(1+ r)/(1- r)\},$$

r: correlation coefficient of a feature.

Results and discussion

The results of our research indicate that generative taxonomic quantitative traits of all populations vary less than the vegetative characters. The length and width of a petal, the length of a sepal apex, hypanthium stigma, and anther appear to be quite essential for dis-

criminating the authentic differences between morphotypes. Other employed features are most variable.

In most cases, the mean values of quantitative generative characters in populations correspond to the traits described for the same species. All mean values of characters' CV were higher than 11.2 in *Oe. biennis* populations from Germany and lower than 12.3 in the Ukrainian populations. The most variable characters were the lengths of a sepal apex and stigma. The least variable characters were the lengths of a petal and hypanthium.

Quantitative traits of some populations under different geographical conditions have close values of CDC, i.e., despite their considerable geographic distances between these populations, and their traits have a similar structure (Table 1). The summarized CDC for the populations ranged from 1.35 (in *Oenothera biennis* s. str., population N1) to 19.37 (in *Oenothera glazioviana*, population N23) (see Table. 2).

Fig. 1 shows clear separation of *Oe. glazioviana* from other studied populations, as results from the discriminant analysis of the flower's traits: (Fig. 1).

Most of the studied populations of *Oe. biennis* s.str. differed insignificantly from the standard population by their CD of generative characters (Table 1). However, the traits of some *Oe. biennis* s.str. populations deviated even more than the traits of some species (population N6, length of a stigma; populations N12, length of a sepal apex). Thus, the variation in morphological traits of populations may be of the same magnitude as in some single species. The populations' variability of morphological characters studied is mainly coincident. Several populations, however, have some distinctive traits (e.g., the populations No. 6, 12, 20, 21, 34). Populations of other morphotypes had the largest differences from the standard population of *Oe. biennis*, and so did the populations of *Oe.biennis* s.str. (according to K.Rostanski's species concept) from Poland and Germany (populations N2, N11 and N6, the divergence coefficients are 11.34; 10.32 and 6.63) (Table 2).

Oe. biennis L. s.l. morphotype (including the species treated as *Oe. biennis*, *Oe. fallax*, *Oe. hoelscheri*, *Oe. pycnocarpa*, and *Oe. rubricaulis*) differed more than some widely circumscribed species (population N30, the coefficient of divergence is 11.8).

As it is obvious from Fig. 2, the discriminant analysis of the species *Oe. biennis*, common for all the sites studied, distinctly differentiates the geographic populations between themselves.

To investigate correlation structures, we have determined all the correlation links of six generative, taxonomic features that have been used by us earlier for investigating the populational variation. The data on the differences among z-transformed correlation matrices of the traits studied in different geographic populations of *Oe. biennis* indicate a larger impact of ecological factors on their correlation structure compared to the geographic one. However, the populations from the Czech Republic have very similar characteristics, but for all that the coefficient of features divergence and the coefficient of correlations divergence have sometimes opposite value (populations NN 2, 29, 32, and 35). The factor analysis of the correlations of the morphological traits of evening primroses shows the similarity of their correlations in *Oe. biennis* and *Oe. glazioviana*.

The principal component analysis of correlative structures of morphological traits indicated populations with the most distinctive correlative structures. Resulting from our investigations, the populations NN 1, 6, 12, 22, 26, and 32, which were placed apart from the associated group of populations on the scatter plot, show the most divergent characteristics. Taking into consideration all the coefficients and methods used, we can conclude that the most divergent populations are the populations NN 1,6, 11,12, 31, and 32.

According to the obtained data, the populations from Poland and Ukraine (Fig. 2) have the highest intrapopulational variability. It suggests an impact of the geographic factor on the evolution of populations of *Oe. biennis*. The geographic distances between morphological traits of a flower in Polish and Ukrainian populations (studied in the Ukrainian South-East) considerably exceed the distances between other populations. The variation patterns of floral characters do not support their gradual clinal character of the variation along the wide geographic gradient (Fig. 2). The same results were obtained using the coefficients of characters' divergence. Most likely, these populations have evolved in different directions depending on a complex influence of climatic factors. It was recently revealed that the specific invasion of Evening Primroses was determined by climatic conditions [7].

Based on our data, we can conclude that the coefficient of divergence may be successfully employed to analyze the taxa at the species and supraspecific level. It also allows to range the most divergent plant populations and to assume a microevolutionary character of variation in these populations. The first coefficient (CD) likely reveals the morphologically most isolated populations, and the second coefficient (CDC) indicates, in our opinion, population's adaptation to the environmental conditions as well as the specific morphological structure of characters measured.

The structure of correlation characters indicates certain interspecific differences of correlation links between the morphological traits. The most plastic structure of the correlations was observed in *Oe. biennis* and was apparently related to the range of the ecological amplitude of the species. The correlation structures of *Oe. rubricaulis, Oe. fallax, Oe. biennis, Oe. wienii, Oe. pycnocarpa* (a group of *Oe. biennis*) are similar. The correlation structure of generative characters of *Oe. issleri* considerably differed from that of other species, as well as from those of *Oe. biennis, Oe. glazioviana,* and *Oe. rubricaulis,* which are the closest kin to this group by this characterization (Fig. 2).

The study of the system of correlations of 6 generative characters in 36 different geographic populations of the genus *Oenothera* allows us to make a conclusion of a considerable isolation of the species *Oe. issleri* and some distinctions of *Oe. glazioviana* and *Oe. rubricaulis* from the species investigated. According to our data, Tsarapkin' coefficient of species divergence satisfactorily characterizes morphologically isolated populations, and the coefficient of divergence of correlations and a mean correlation link can show their adaptation to the environmental conditions. A distinct increase or decrease of the strength of the link under extreme anthropogenous conditions have not been observed in species of the genus *Oenothera,* but have been observed in some other species. Simultaneously, the relationships of traits' variability and environment had demonstrated a more complex and complicated mechanism. The geographically distant populations of *Oenothera* very often have a more similar structure of correlations than the neighboring populations under different ecological conditions. A further detailed study of the features and their structure is needed for revealing the internal regularities in populations of alien species under different anthropogenous conditions.

The research of correlation systems of population features is promising in terms of adaptive response of plants to environmental conditions. A larger number of morphological traits, an environmental evaluation, and an analysis of dependence between them are required. All these results obtained can be explained by the microevolutionary processes within these populations, as well as their adaptation to local environments.

The availability of specific changes and adaptation of structures of phenotypic markers in *Oenothera* populations is confirmed, irrespective of the adopted specific concept, because in any case some populations of *Oe. biennis,* as well as the populations of some other species (sensu lato or sensu stricto), could differ from the standard population more than the species studied (Table 2). The hybrid species of *Oenothera* observed in mixed populations of their parental species assume rapid microevolution of the genus in man-made habitats. Moreover, we registered some changes in the structure of different plant organs: the flattering of a stem in *O. biennis, O. rubricaulis,* and *O. depressa* taxa; the duplication of parts of the flower in *O. biennis.* As we know, these morphological changes can result from hereditary changes.

The above large differences of morphological traits among the *Oenothera* populations may be a result of either founder effect or a multiple introduction of weedy species. However, in some cases, these interpopulational differences may be also explained by the introgressive hybridization [8] of some plants in mixed populations, as well as by the displacement of correlative structures of morphological traits in different habitats. It is extremely difficult to determine what formative mechanism prevails in the natural *Oenothera* populations.

Thus, the intensive microevolutionary processes in European populations of Evening Primroses, as well as their variability, can be explained by the microevolutionary transformations and adaptation of plants to different geographical and ecological conditions. These changes may affect the structure of taxonomic quantitative traits and its correlation system. Since all of the taxonomic characters are usually unchangeable and are linked to genetic structures of the species, it is quite probable that these changes may have a genetic background. Obviously, we are observing the formation of new morphotypes, similar to those de-

scribed many times by various researchers as individual taxa and forms in man-made habitats. We quite agree with J.C. Avise [9] in his statement that: "morphometric and crossing evidence is of value in advancing particular hypotheses relating to the evolutionary and ecological history of an organism, but only the direct examination of the genetic material can confirm that such hypotheses are correct". Nevertheless, our investigation of phenotypic markers which are related to genomic complexes allowed us to separate the most divergent *Oenothera* populations to further studies of those combining other approaches, such as common gardening (cultivation) experiment and genetic analysis.

The obtained results suggest a necessity of further development of the taxonomic concept in the genus *Oenothera* subsection *Oenothera*. A concept of a broad species does not provide a possibility to evaluate forms, races, and species s.str. diversity, and sometimes unifies all the differences to the level of *Oe. biennis* sensu latissimo. On the other hand, taxa differing from closely related ones only by one or few insignificant traits should not be regarded as distinct species.

Conclusions

Our data on the quantitative diagnostic morphological characters of *Oenothera* L. species from different geographical territories (the Czech Republic, Germany, Slovakia, Poland, and Ukraine) allow us to conclude that:

1) According to our data, Tsarapkin' coefficient of species divergence satisfactorily characterizes morphologically isolated populations, and the coefficient of divergence of correlations and a mean correlation link in some cases can show their adaptation to the environmental conditions.

2) The system of traits correlations revealed a considerable isolation of the hybrid species *Oe. issleri* and some distinctions of *Oe. glazioviana* and *Oe. rubricaulis* from the studied species. These results support the taxonomic independence of *Oe. issleri*.

3) A concept of a broad species does not provide a possibility to evaluate forms, races, and species s.str. diversity, and sometimes unifies all the differences to the level of *Oe. biennis* sensu latissimo. On the other hand, taxa differing from closely related ones only by one or few insignificant traits should not be regarded as distinct species.

Acknowledgements

LITERATURE

1. Rostanski K., Tokarska-Guzik B. (1998): Distribution of the American epecophytes of *Oenothera* in Poland. *Phytocoenosis,* 10 : 117-130.

2. Wittig R., Lenker K.-H., Tokhtar' V. (1999): Zur Soziologie von Arten der Gattung *Oenothera* L. im Rheintal von Arnheim (NL) bis Mulhouse (F). *Tuexenia,* 19: 447-467.

3. Raven P.H. (1997): *Onagraceae* as a model of plant evolution. In: L.D.Gotlieb & S.K.Jain (ed.), *Plant evolutionary biology,* London,: 85-107.

4. Shmidt V.I. (1984): *Matematicheskiye metody v botanike* (Mathematical methods in Botany), Leningrad, Leningrad University: 1-288.

5. Rostova N.S. (1999): Izmenchivost sistemi korrelaciy morphologicheskich priznakov. 1. Yestestvenniye populyacii *Leucanthemum vulgare* (Asteraceae)) (The variability of correlations systems between the morphological characters. 1. Natural populations of *Leucanthemum vulgare* (Asteraceae)). Botanical Journal, V. 84, N 11: 50-66.

6. Wright S. (1920): The relative importance of heredity and environment in determining the piebald pattern of guinea pigs. *Proc. Nat. Acad. Sci.,* N6: 22-39.

7. Mihulka S. and Pysek P. (2001): Invasion history of *Oenothera* congeners in Europe: a comparative study of spreading rates in the last 200 years. *Journal of Biogeography,* 28: 1-13.

8. Riesenberg L.H., Beckstrom-Sternberg S., Doan K. (1990): *Helianthus annu s* spp. *texanus* has chloroplast DNA and nuclear ribosomal RNA genes of *Helianthus debilis* ssp. *cucumerifolius.* *Proc. National Acad. Science, USA,* 87: 593-597.

9. Avise J.C. (1994): *Molecular markers, natural history and evolution.* Chapman & Hall, London.

**Morphological distances of characters measured in *Oenothera* L. populations:
according to the list of populations given in Table 3;
N15 population is a standard population**

N of Popula-Tion #	Standardized deviations of characters						Summari-zed coef-ficients of fea-tures divergence
	Petal length	Petal width	Sepal apices length	Hypan-thium Length	Stigma Length	Anther length	
1	0,9	-1,8	-0,4	-0,7	1,7	1,2	1,35
2	-11,9	-18,7	-0,4	-5,0	-9,3	-6,5	11,34
3	-1,2	-1,7	0,3	-1,5	-1,9	-1,1	1,52
4	-1,5	-3,0	0,4	-2,1	5,0	-4,7	3,55
5	-3,5	-7,7	-0,6	-3,2	6,5	-7,1	5,91
6	-4,6	-10,8	-0,8	-5,1	6,5	-3,5	6,63
7	-2,5	-2,70	-2,5	-4,1	0,2	-1,8	2,6
8	-1,4	-1,3	-1,1	-3,3	-0,2	-2,6	1,4
9	-3,4	-4,3	-0,8	-3,0	0,3	-2,4	2,7
10	0,3	-0,8	0,6	-2,6	5,3	-4,3	3,32
11	-8,8	-10,3	0,0	-4,6	-3,3	-17,8	10,32
12	-2,1	-2,4	3,2	-1,0	12,5	-2,5	6,06
13	-1,4	-1,7	0,6	-1,0	-2,5	-2,0	1,81
14	-3,5	-4,1	0,6	-2,2	-1,7	-2,8	2,99
15	**0 ,0**	**0 ,0**	**0 ,0**	**0 ,0**	**0 ,0**	**0 ,0**	**0 ,0**
16	-6,6	-13,5	-3,4	-4,6	-7,0	-4,3	8,08
17	-5,5	-11,3	-2,8	-1,4	-6,7	-0,6	6,53
18	-4,9	-12,1	-3,2	-5,7	-7,3	-6,4	7,85
19	-7,0	-13,6	-5,0	-2,6	-10,0	-6,1	8,98
20	-4,9	-11,9	-2,4	-3,9	-1,2	-4,8	6,496
21	-1,6	-4,6	-0,2	-2,1	4,8	-3,2	3,52
22	-2,6	-4,9	-0,8	-3,9	-0,5	-0,7	3,0
23	11,7	4,6	3,8	-4,7	40,2	7,5	19,31
24	14,02	11,4	0,1	-2,95	23,3	9,7	13,9
25	-5,5	-10,4	-1,6	-2,1	8,3	-6,5	7,18
26	-9,7	-10,0	-7,3	-6,8	-1,0	-3,8	7,6
27	-9,3	-15,7	-4,2	-8,1	-1,6	-3,0	9,1
28	-8,0	-15,1	-0,4	-3,3	-8,0	-5,8	8,95
29	-4,9	-9,9	-0,2	-6,5	-0,3	-4,2	6,04
30	-10,7	-19,2	0,2	-5,0	-7,0	-11,6	11,77
31	-9,5	-17,9	-2,4	-4,9	-2,2	-13,5	11,198
32	-7,7	-15,9	-2,7	-	6,0	-11,7	9,98
33	-7,3	-14,9	-2,8	-3,9	-5,8	-13,2	10,06
34	-11,9	-18,7	-0,4	-5,0	-9,3	-6,5	11,37
35	-8,2	-16,1	0,8	-5,3	-7,3	-4,2	9,23
36	-11,5	-19,1	-2,6	-6,0	-5,2	-15,4	12,67

Table 2

Degree of divergence of *Oenothera* L. populations from different geographical territories ranked according to the degree of divergence from standard population

| N of population	Name of *Oenothera* taxa s.str.	Summarized coefficients of features divergence (CD)	Name of *Oenothera* taxa s.l.
23	*Oe.glazioviana*	19,37	*Oe.glazioviana*
24	*Oe.glazioviana*	13,90	*Oe.glazioviana*
36	*Oe. wienii*	12,67	*Oe.biennis x villosa*
30	*Oe. pycnocarpa*	11,77	*Oe.biennis*
34	*Oe.subterminalis*	11,37	*Oe.parviflora*
2	*Oe.biennis*	11,34	*Oe.biennis*
31	*Oe. rubricaulis*	11,20	*Oe.biennis*
11	*Oe.biennis*	10,32	*Oe.biennis*
33	*Oe.rubricaulis*	10,06	*Oe.biennis*
32	*Oe.rubricaulis*	9,98	*Oe.biennis*
35	*Oe.subterminalis*	9,23	*Oe.parviflora*
27	*Oe.issleri*	9,10	*Oe. biennis x oakesiana*
19	*Oe.fallax*	8,98	*Oe.biennis x glazioviana*
28	*Oe.pycnocarpa*	8,95	*Oe.biennis*
16	*Oe.fallax*	8,08	*Oe.biennis x glazioviana*
18	*Oe.fallax*	7,85	*Oe.biennis x glazioviana*
26	*Oe.issleri*	7,60	*Oe. biennis x oakesiana*
25	*Oe.hoelscheri*	7,18	*Oe.biennis*
6	*Oe.biennis*	6,63	*Oe.biennis*
17	*Oe.fallax*	6,53	*Oe.biennis x glazioviana*
20	*Oe.fallax*	6,49	*Oe.biennis x glazioviana*
12	*Oe.biennis*	6,06	*Oe.biennis*
29	*Oe.pycnocarpa*	6,04	*Oe.biennis*
5	*Oe.biennis*	5,91	*Oe.biennis*
4	*Oe.biennis*	3,55	*Oe.biennis*
21	*Oe. fallax*	3,52	*Oe.biennis x glazioviana*
10	*Oe.biennis*	3,32	*Oe.biennis*
22	*Oe. fallax*	3,00	*Oe.biennis x glazioviana*
14	*Oe.biennis*	2,99	*Oe.biennis*
9	*Oe.biennis*	2,70	*Oe.biennis*
7	*Oe.biennis*	2,60	*Oe.biennis*
13	*Oe.biennis*	1,81	*Oe.biennis*
3	*Oe.biennis*	1,52	*Oe.biennis*
8	*Oe.biennis*	1,40	*Oe.biennis*
1	*Oe.biennis*	1,35	*Oe.biennis*
15	***Oe.biennis***	**0,00**	***Oe.biennis***
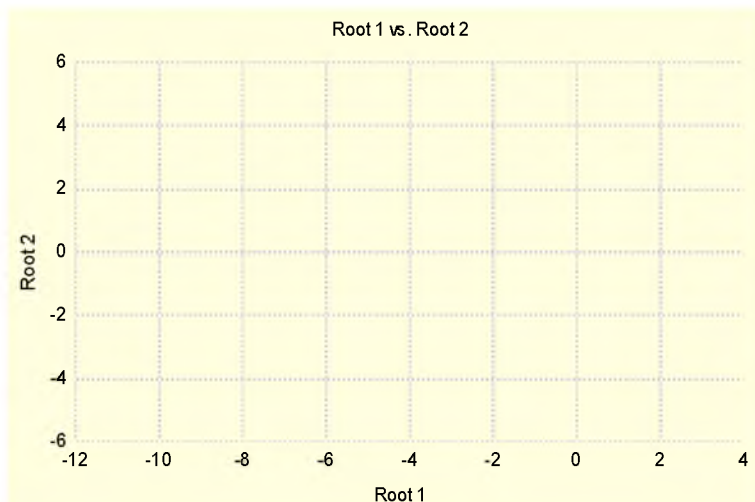
Fig.1. Discriminant analysis of flowers measured in *Oenothera* populations:
every point reflects the position of a flower in the scatterplot: points on the left part
of the scatterplot belong to *Oe.glazioviana*, points on the right part are the rest species
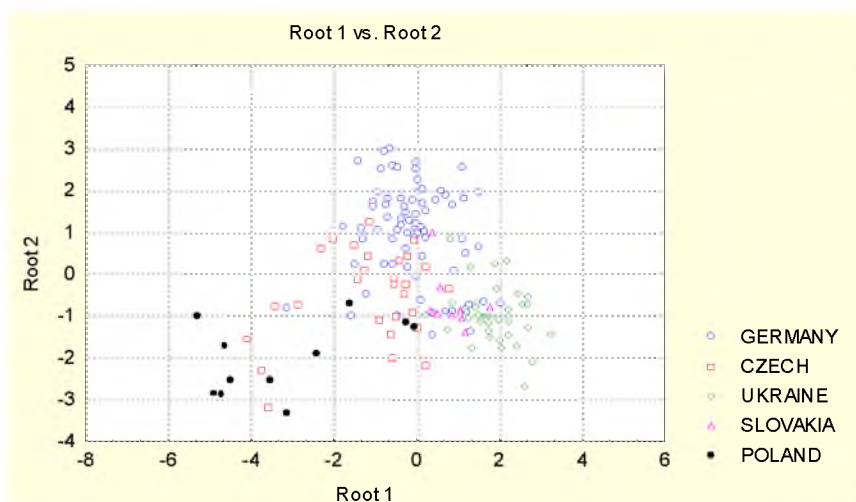

Fig.2. Geographical variability of flowers in *Oenothera biennis* populations between discriminant
roots: every point in the scatterplot characterizes a flower under different condition

ДИВЕРГЕНЦИЯ МОРФОЛОГИЧЕСКИХ ПРИЗНАКОВ ЦВЕТКА
В ЕВРОПЕЙСКИХ ПОПУЛЯЦИЙ *OENOTHERA* L.

В.К. ТОХТАРЬ [1]
ВИТТИГ РЮДИГЕР [2]

[1] *Белгородский государственный университет*

[2] *Francfurt-on-Main, Institute of Botany*

e-mail: tokhtar@bsu.edu.ru

В результате проведенных исследований была изучена структура стабильных, диагностических фенотипических маркеров в 36-ти популяциях 9-ти видов рода Oenothera L. в Чешской республике, Германии, Польше, Словакии и Украине. Изучение морфологических признаков различных географических популяций позволяет говорить о существенных отличиях структуры мофрологических признаков и системы их корреляций у ряда видов: Oe. issleri,Oe. glazioviana, Oe. rubricaulis. Дискриминантный анализ популяций наиболее распространенного в Европе вида Oenothera biennis свидетельствует о существенных отличиях морфологической структуры различных географически удаленных популяций. Очевидно, что дивергенция морфологических признаков в популяциях видов рода Oenothera может быть объяснена микроэволюционными процессами в пределах этих изолированных географически популяций и их адаптацией к локальным условиям окружающей среды.