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ЭВОЛЮЦИЯ ИНВАЗИВНОСТИ У ЭНОТЕР

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Род *Oenothera* L. (subsect. *Oenothera*, Onagraceae) является очень удобным модельным объектом для изучения эволюции инвазивности заносных видов в природные местообитания. Это связано с генетическим механизмом размножения, который присущ энотерам (механизм перманентной гетерозиготной транслокации), который способствует тому, что в результате гибридизации двух видов может образовываться константный третий. В результате анализа оригинальных и литературных данных о распространении гибридных и парентальных видов и их инвазивности в различных частях Европы были установлены некоторые особенности микроэволюции инвазивности у видов. Группа «очень инвазивных» гибридных видов чаще всего происходила от родителей из группы «очень инвазивных» парентальных видов. Изучение происхождения парентальных видов свидетельствует о том, что наиболее инвазивные гибриды образовались в результате гибридизации между североамериканскими и европейскими видами. Частота встречаемости парентальных видов также как и генетические особенности близких морфологически видов также являются значимыми характеристиками, влияющими на степень инвазивности видов.

Ключевые слова: *Oenothera*, эволюция, инвазивность, гибриды.

Invasive species are of great interest to evolutionary biologists and ecologists because they represent historical examples of dramatic evolutionary and ecological change [1]. The genus *Oenothera* L. (subsect. *Oenothera*, *Onagraceae*) is one of the most widespread genera of American origin in Europe. *Oenothera* species are successful invaders of disturbed riverbanks, ruderal places, parks, roads, sandy dunes, natural reserves and sea coasts in Europe [2, 3]. In result of their intercontinental spread many species and forms have been originated in Europe that has resulted in a number of taxonomic problems in the genus (Table 1). The species possess a special breeding system in Evening Primroses (permanent heterozygous translocation (PTH) mechanism) which promotes the hybridization (also introgressive one) among several species resulting in the formation of a stable (constant) third taxon [4, 5]. 14 chromosomes of oenotheras from the subsection can merge by different way and form rings during meiosis (so called Renner's rings). And many combinations of these rings can be formed in hybrid plants. Therefore, this genus is a good object for research of microevolutionary changes and adaptation of plants and evolution of their invasiveness.

Material and methods

Hybridization among species may serve as a stimulus for the evolution of invasiveness and leads to critical evolutionary changes that create an opportunity for increased invasiveness [1]. The analysis of hybrid species distribution in Europe shows existence of groups with different degree of invasiveness (Table 2). The hybrid Evening primroses were analyzed by the following criteria which can related to evolution of their invasiveness: 1) time of origin of hybrid, 2) degree of invasiveness of the parental species, 3) geographical origin of parental species, 4) frequency of occurrence of parental species, 5) their invasiveness, 6) genetic factors (heterosis; possibility of hybridization between: cultivated and natural species, ring formed and bivalent species), 7) environmental factors (climatic and ecological), 8) biological peculiarities (life history traits and morphology) of newly created species, 9) presence of accompanying organisms on hybrids (EICA hypothesis). Some of the mentioned traits are analyzed in the Table 2.

Results and discussion

The time of origin is not determined factors in plant invasiveness of Evening primroses. It is perhaps connected with the fact that majority of species have been originated practically

simultaneously in time. Therefore, considering this criterion there are no sufficient differences on in the plant group.

The degree of invasiveness of the parental species is influential but not good understood trait impacting to invasiveness of hybrids. Our analysis shows that in the group of "very invasive" hybrid species there are also "very invasive" parental species (table 2). One of the basic species for such hybrids often is *Oe. biennis*. And there is only one exception from the rule with *Oe. punctulata* which are not invasive at the moment and their parental species belong to "very invasive" species group. However it also can be connected with the lack of reliable data on distribution of the species in Europe.

The analysis of the parental species origins testifies that the most invasive hybrids are created from crossing among North American and European species. In result of hybridization the heterosis effect can arise among isolated lines promoting viability of newly created species.

The frequency of the parental species is of important value for the invasiveness of hybrid species because the hybridization probability between parental species is increased with frequency of their presence at the same habitat.

Sometimes the resulting hybrids are morphologically similar to the parental species and, at the same time, are very different by genetic nature. The invasiveness of all these species is also distinguished from one another. In this case evolution of invasiveness depends on genetic nature of the species most of all.

Table 1

Oenothera species in Europe based on literary data

Oenothera species	Origin	Remarks
1	2	3
acutifolia	Europe, *Oe. silesiaca* × *rubricaulis*	Crossing between European species
affinis	South America	
albipercurva	Europe, *Oe. biennis* × *ammophila*	Crossing between European and North American species
ammophila	N America	
angustissima	N. America	= *Oe. rubricuspis*, introduced before 1900, species escaped from gardens
biennis s.str.	Europe (Rostanski), N.America (Raven et al.)	
braunii	hybrid origin	crossing between European and N. American species
britannica	*Oe. glazioviana* × *cambrica* (R., 2003)	crossing between N. American species
cambrica	N. America	= *Oe. nova-scotiae*
canovirens	North America	= *Oe. renneri*, introduced in 20th century, after II World War
chicaginensis		= *Oe. pycnocarpa*
coronifera	Perhaps *Oe. parviflora* × *glazioviana* (R., 2003)	crossing between N. American species
cruciata	N. America	= *Oe. atrovirens*, introduced before 1900, species escaped from gardens
deflexa	North America, Europe	= *Oe. lipsiensis*, introduced in 20th century, after II World War
depressa	North America	= *Oe. salicifolia*, introduced before 1900, species escaped from gardens
drawertii	*Oe. depressa* × *suaveolens*	crossing between European and N. American species
ersteinensis	N. America	= *Oe. perangusta*
erythrosepala	N. America	=*Oe. glazioviana*
fallax	*glazioviana* × *biennis*	crossing between European and N. American species
flaemingina	Europe	related with *Oe. rubricaulis*
flava	?	?
glazioviana	North America	= *Oe. erythrosepala*, introduced before 1900, species escaped from gardens

The end of the table 1

1	2	3
hoelscheri	*rubricaulis* × *depressa*	crossing between European and N. American species
indecora	South America	
issleri	*biennis* × *oakesiana*	crossing between European and N. American species
italica	?	?
jamesii	N. America	introduced before 1900, species escaped from gardens
jueterbogensis	Europe (Germany)	hybrid origin, recently noted in Poland
laciniata	N. America	
longiflora	?	?
missouriensis	N. America	
moravica	Europe, *fallax* × *victorini*	
nuda	N. America	= *Oe. nutans*, introduced in 20th century, after II World War
oakesiana	North America	= *Oe. syrticola*, introduced before 1900, species escaped from gardens
oehlkersii	Europe, *glazioviana* × *suaveolens*	crossing between European and N. American species
paradoxa	Perhaps *Oe. depressa* × *subterminalis* (R., 2003)	crossing between N. American species
parviflora	North America	introduced before 1900, species escaped from gardens
perangusta	N. America (Rost., 2003)	= *Oe. ersteinensis*
perennis	N. America ?	
Oe.polgari	*Oe. suaveolens* × *depressa* (R., 2003)	crossing between N. American species
punctulata	*Oe. biennis x pycnocarpa*	crossing between European and N. American species
purpurans	*Oe. glazioviana* × *depressa* (R., 2003)	=*Oe. hungarica*, crossing between European and N. American species
		crossing between European species
pycnocarpa	North America	=*Oe. chicaginensis*, introduced in 20th century, after II World War
rigirubata		
rosea	South America	pink flowers, different sect.
royfraseri	N. America	= *Oe. turoviensis*, introduced in 20th century, after II World War
rubricalix	N. America	
rubricaulis	East European species (Rostanski, 2003)	Recently originated
salicifolia		= *Oe. depressa*
silesiaca		= *Oe. subterminalis*
stricta	South America	
stuchii	Perhaps *Oe. jamesii* × *suaveolens* (R., 2003)	crossing between N. American species
suaveolens	South Europe (Rostanski, 2003)	
subterminalis	North America	= *Oe. silesiaca*
syrticola	N. America	= *Oe. chicaginensis*
tacikii	*Oe. suaveolens* × *rubricaulis*	Crossing between European species
tetragona		
tetraptera		
turoviensis		= *Oe. royfraseri*, introduced in 20th century, after II World War
victorini	North America	=*Oe. nissensis*, = *Oe. rostanskii* Jehlik, introduced in 20th century, after II World War
wienii	*Oe. rubricaulis* × *depressa*	crossing between European and N. American species

Table 2

Analysis of European *Oenothera* species on different invasiveness groups

Invasiveness	Name of hybrid	Parental species	Frequency of occurrence of hybrids related to parental species	Frequency of occurrence of hybrids	Origin of parental species	Invasiveness of parental species and their distribution	Predominant distribution of hybrid
Very invasive	× *Oe. fallax*	*Oe. biennis* s.str.	=	Often	Europe	Very invasive (E)	WE, CE
		× *Oe. glazioviana*	>		?	Sometimes invasive (WE, CE)	
	× *Oe. issleri*	*Oe. biennis* s.str.	<	Often	Europe	Very invasive (E)	Mostly WE and less in CE
		× *Oe. oakesiana*	>			Non-invasive or rare-invasive (WE, CE)	
	× *Oe. hoelscheri*	*Oe. rubricaulis*	=	Often	Europe	Invasive (CE, EE)	CE, EE
		× *Oe. depressa*	=		NA	Invasive (CE, EE)	
Middle-invasive	× *Oe. oehlkersii*	*Oe. suaveolens*	=	Not often	Europe	Middle invasive (WE, CE, EE)	WE, CE, EE
		× *Oe. glazioviana*	<		NA	Middle invasive (WE, CE)	
	× *Oe. acutifolia*	*Oe. rubricaulis*	<	Not often	Europe	Invasive (CE, EE)	CE
		× *Oe. silesiaca*	<		Europe	Invasive (WE, CE)	
	× *Oe. paradoxa*	?	?	Not often	?	?	CE
Non-invasive, Locally distributed	× *Oe. drawertii*	*Oe.depressa*	<	Rare	NA	Non-invasive (WE, CE)	WE, CE
		× *Oe. suaveolens*	<		Europe	Middle-invasive (WE, CE, EE)	
	× *Oe. punctulata*	*Oe. biennis* s.str.	<	Not often	Europe	Very invasive (E)	WE, CE
		× *Oe. pycnocarpa*	<		NA	Very invasive (WE, CE)	
	× *Oe. wienii*	*Oe. rubricaulis*	<	Rare	Europe	Invasive (CE, EE)	CE, EE
		× *Oe. depressa*	<		NA	Invasive (CE, EE)	
	× *Oe. coronifera*	*Oe. glazioviana*	<	Rare	NA	Middle invasive (WE, CE)	CE
		× *Oe. parviflora*	<		NA	Non-invasive (WE, CE, EE)	
	× *Oe. moravica*	*Oe. fallax*	<	Not often	Europe	Very invasive (WE, CE)	CE
		× *Oe. victorini*	?		?	Non-invasive (CE, FE)	
	× *Oe. jeterbogensis*	?	?	Very rare	?	?	CE

WE –West Europe, CE – Central Europe, EE – East Europe, FE – Far East, E – everywhere, NA – North America.

Oe. glazioviana also has presumable hybrid nature. And there are a lot of hybrid species with undetermined status and unclear range of distribution and putative parental species. These species are very difficult to recognize them reliably without experience. Many of them are recently originated and locally distributed, mostly from places where they were described.

Beside those hybrid species, which were noted in the table 2 K. Rostanski reported also 33 hybrid species locally distributed in Europe. Sometimes such species are known only from one locality: *Oe. braunii* Doell, *Oe. brevispicata* Hudziok, *Oe. canovertex* Hudziok, *Oe. clavifera* Hudziok, *Oe. coloratissima* Hudziok, *Oe. compacta* Hudziok, *Oe. conferta* Renner, *Oe. editicaulis* Hudziok, *Oe. flaemingina* Hudziok, *Oe. inconspecta* Hudziok, *Oe. indivisa* Hudziok, *Oe. macrosperma* Hudziok, *Oe. mediomarchica* Hudziok, *Oe. obscurifolia* Hudziok, *Oe. octolineata* Hudziok, *Oe. pseudocernua* Hudziok, *Oe. rigirubata* Renner ex Gutte et Rostanski (all are distributed in Germany), *Oe. adriatica* Soldano, *Oe. fallacoides* Soldano et Rostanski, *Oe. marinella* Soldano, *Oe. pedemontana* Soldano, *Oe. pellegrinii* Soldano, *Oe. sesitensis* Soldano, *Oe. stuchii* Soldano (all are distributed in Italy), *Oe. pseudochicaginensis* Rostanski, *Oe. tacikii* Rostanski, *Oe. wratislaveinsis* Rostanski (all are distributed in Poland), *Oe. polgari* Rostanski, *Oe. purpurans* Borbas (Hungary), *Oe. carinthiaca* Rosanski, *Oe. heiniana* Teyber (Austria), *Oe. slovaca* Jehlik et Rostanski (Slovakia), *Oe. britannica* Rostanski (Great Britain). That is why there are many perspectives to provide new insights studying invasiveness in this, very suitable for these goals, plant group in future.

Conclusions

The analysis of hybrid species distribution in Europe shows existence of groups with different degree of invasiveness. The degree of invasiveness of the parental species is influential but not good understood trait impacting to invasiveness of hybrids. Our analysis shows that in the group of "very invasive" hybrid species there are also "very invasive" parental species. The analysis of the parental species origins testifies that the most invasive hybrids are created from crossing among North American and European species. In result of hybridization the heterosis effect can arise among isolated lines promoting viability of newly created species. The frequency of the parental species is of important value for the invasiveness of hybrid species because the hybridization probability between parental species is increased with frequency of their presence at the same habitat. Sometimes the resulting hybrids are morphologically similar to the parental species and, at the same time, are very different by genetic nature. The invasiveness of all these species is also distinguished from one another. In this case evolution of invasiveness depends on genetic nature of the species most of all.

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EVOLUTION OF INVASIVENESS IN *OENOTHERA*

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The genus *Oenothera* L. (subsect. *Oenothera*, Onagraceae) is very convenient modelling object for evolution studying of inadventive invasiveness species in natural habitats. It is connected with the genetic mechanism of reproduction, which is inherent oenotheras (the mechanism of a permanent heterozygotic translocation) which promotes that as a result of hybridization of two kinds the third can be formed constant. As a result of the analysis of original and literary data about distribution of hybrid and parental species and their invasiveness in various parts of Europe some features of microevolution invasiveness at species have been established. The group «very invasiveness » hybrid species more often occurred from parents from group «very invasiveness» parental species. Origin studying parental species testifies that most invasiveness hybrids were formed as a result of hybridization between North American and European species. Frequency of occurrence of parental species as well as genetic features of species close by morphology is also the significant characteristics influencing on degree of species invasiveness.

Key words: *Oenothera*, evolution, invasiveness, hybrids.