

Microevolution and Invasiveness of *Oenothera* L. Species (Subsect. *Oenothera*, Onagraceae) in Europe

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Abstract—A comparative analysis of *Oenothera*'s hybrid species was carried out. The genus *Oenothera* L. (subsect. *Oenothera*, Onagraceae) is one of the most widespread American genera in Europe. These species possess a special breeding system (permanent translocation heterozygosity) which promotes the hybridization (also introgressive one) among any species resulting in formation of a hybrid with a constant complex of morphological characteristics.

The analysis of hybrid species distribution in Europe using published and original data proved the existence of groups with different degrees of invasiveness. A positive correlation between the degree of invasiveness of the parental species and the invasiveness of hybrid ones was shown. As a rule, the aggressive hybrids originated from aggressive parents. The most aggressive hybrids were formed after a crossing of North American with European species; perhaps such hybridization leads to the heterosis effect among normally isolated genes. The invasiveness of morphologically similar hybrids correlates both with their genetic features and with the abundance of the parental species. The new evolution branch of ring-forming species of Evening primroses is distinguished by high invasiveness in comparison with bivalent species. The invasiveness of the model species depends on plant cytotypes.

Keywords: *Oenothera* L., microevolution, hybridization, invasiveness, Europe.

INTRODUCTION

At present, the problem of nonindigenous distribution of organisms can be solved only at the international level. Therefore, their influence on the biosphere is acquiring global significance. Local measures do not produce positive results, because there are no borders for expansion of nonindigenous species.

Study of microevolution mechanisms and survivability of invasive species during introduction into natural populations is especially important, because of increasing anthropogenic effects and a progressively increasing number of damaged and quasi-natural ecotopes. Presently, it is doubtless that invasiveness of a certain species depends on interaction of its biological features with geographic, climatic, and ecological environmental conditions. The complex of these factors may lead to alteration (evolution) of this species invasiveness in a time-dependent manner. The basic principles of this process were revealed not so long ago (Vinogradova, 1992). However, the problem of hybridization has not been properly studied thus far. Nevertheless, it was reported that hybridization may work as a stimulus for the increase in invasive activity of species and often leads to critical evolutionary changes in ecosystems that result in irreversible modifications (Ellstrand and Schierenbeck, 2000).

For a long time, geographic isolation was recognized as the most important limiting factor for hybridization. However, it is presently known that closely related taxa can contact one another through a number of anthropogenic "corridors" (Williamson, 1996). For example, interregional migration occurs during introduction of plants into gardens that is followed by unintended transfer of plant pests and pathogens (Heywood, 1989). Moreover, introduction can be frequent and repeated, which significantly increases the immigration flow.

One of the potential consequences of hybridization is that a hybrid can be introduced into a territory which was not able to be colonized by parental species. It is suggested that the increase in competitiveness and invasiveness of hybrids may be due to changes in distribution of resources by forces of selection in a new environment, which leads to fast changes in the relative stability of species (Blossey and Nötzold, 1995; Blossey and Kamil, 1996).

MATERIALS AND METHODS

The *Oenothera* L. (subsect. *Oenothera*, Onagraceae) genus, which was used as a model object of our study, is the most widespread genus of American origin in Europe. *Oenothera* L. plants are characte-

alized by considerable invasive capacity owing to a special genetic mechanism (permanent heterozygous translocation) (Renner, 1917; Cleland 1964; Dietrich et al., 1998), which provides the formation of hybrids with constant morphological features as a result of crossbreeding. It was shown that chromosomes of some species may be fused in meiosis to form circular Renner complexes, so that genetic information is transferred from ancestors to descendants in an attached manner (Renner, 1917). Homozygous plants die because of the presence of a balanced lethal complex, whereas hybrid plants develop successfully. In mixed populations of microspecies, *Oenothera* L. plants are capable of both direct and back crossing, which may occur several times. Therefore, an overwhelming number of species, microspecies, and races adapted to the local environmental conditions with unclear taxonomic status were formed in Europe. Genotypic differences between the species refer to the size and number of chromosomal rings and bivalents, the normal quantity of which is $2n = 14$. The main sources for development of new forms and species of *Oenothera* L. are the exchange by chromosome regions with subsequent back crossing, gene exchange between Renner rings, and reciprocal translocations that lead to the formation of new ring and bivalent combinations of different shape (Grant, 1981). The *Oenothera* L. genus is quite complex because of intense speciation. Therefore, there are several taxonomic versions of it (Rostański, 1982, 1998; Skvortsov, 1996; Dietrich et al., 1998; Wittig et al., 1999; Wittig and Tokhtar, 2002, 2003; Rostański et al., 2004).

A number of new species were described in Europe after *Oenothera* L. species occurred there before. For example, more than 100 new taxa were described in Germany (Hudziok, 1968), which allows us to suggest that this country is us of the centers of formation of a secondary range of the genus. New species were also found in Italy (Soldano, 1979), the Czech Republic and Slovakia (Jehlík and Rostański, 1995), Germany (Gutte and Rostański, 1971), the United Kingdom (Rostański, 1982), Lithuania (Rostański et al., 2004), and other countries. Therefore, the genus is considered to be an appropriate model that allows following the features of distribution and evolution of species invasiveness in Europe.

A comparative analysis of invasiveness of hybrids and parental species was carried out. The inheritance of invasive capacity of species in different environmental and climatic conditions was studied. This approach allowed us to come closer to understanding the invasiveness evolution mechanism in plants with respect to their genetic features.

The voluminous literature and herbarium sources about *Oenothera* species in Western and Eastern Europe were chronologically analyzed. A number of locations were studied in Germany (Northern Rhine-Westphalia, Hessen, Baden-Württemberg), France (Alsace) (Wittig et al., 1999; Wittig and Tokhtar, 2002,

2003; Tokhtar, 2003), the Czech Republic, Slovakia, Poland, Ukraine, and Russia (Rostański et al., 2004). Herbaria of the Komarov Institute for Botany, Russian Academy of Sciences (St. Petersburg, LE); Central Botanical Garden, Russian Academy of Sciences (Moscow, MHA); Moscow State University (Moscow, MW); Moscow State Pedagogical University (Moscow, MOSP); Southern Federal University (Rostov-on-Don, Russia, RV); Kholodny Institute for Botany, National Academy of Sciences of the Ukraine (Kyiv, Ukraine, KW); Donetsk Botanical Garden (Donetsk, Ukraine, DNZ); University of Silesia (Katowice, Poland, KTU); Institute for Botany, Academy of Sciences of the Czech Republic (Pruhonice, Czech Republic, PR); Berlin-Dahlem Botanical Garden (Berlin, Germany, B); Sekenbergianum Museum (Frankfurt om Main, Germany, SNG); and Natural Museum (Wiesbaden, Germany) were analyzed.

We studied *Oenothera* species in accordance with Rostański's concept, because it allows to provide more detailed analysis of *Oenothera* invasion in Europe regardless of the taxon status. Therefore, Latin names of plants are given as they appear in (Rostański, 1998; Rostański et al., 2004).

The increase in species invasiveness and its evolution may be retraced by analysis of chronological features of parental species and their hybrid descendants. We performed a comparative analysis of the following features of *Oenothera*: (1) period of the species origination; (2) parental species invasiveness; (3) geographical origins of parental species; (4) parental species frequency in mixed populations; (5) genetic factors (heterosis, possibility of crossbreeding between cultural and invasive species, ring-shaped and bivalent species groups); (6) morphological features of newly formed species; (7) cytological types of *Oenothera* in different groups of invasiveness.

To distinguish the species, which demonstrate different strategies of invasion at the present time, they were divided into groups of "actively invasive," "invasive," "naturalizing," and "noninvasive." The group of actively invasive *Oenothera* involves the species which, presently, are intensely increasing their range and colonizing new types of ecotopes. The group of invasive *Oenothera* involves the species which once introduced into natural or anthropogenic plant populations do not tend to invade new types of ecotopes. The group of naturalizing species involves plants which are presently at the initial stage of naturalization. The group of noninvasive species involves locally distributed plants which do not tend to invade natural populations. All the characteristics mentioned are given in Tables 1 and 2.

RESULTS AND DISCUSSION

Analysis of the distribution of the hybrid and parental species in Europe revealed that for *Oenothera* the period of species origination apparently does not

Table 1. Invasive activity of *Oenothera* genus in Europe

Groups of hybridogenetic species divided by their invasive activity		Actively invasive						Invasive						Noninvasive					
Hybrid	Name	× <i>Oe. fallax</i>		× <i>Oe. issleri</i>		× <i>Oe. hoelscheri</i>		× <i>Oe. oehlkersii</i>		× <i>Oe. acutifolia</i>		× <i>Oe. paradoxo</i>		× <i>Oe. moravica</i>		× <i>Oe. wienii</i>		× <i>Oe. coronifera</i>	
	Time of occurrence	>100 years		>100 years		>100 years		>100 years		<50 years		?		<50 years		<50 years		>100 years	
	Frequency	Often		Often		Often		Seldom		Seldom		Seldom		Seldom		Rare		Rare	
	Natural range	WE, CE		WE, CE		CE, EE		WE, CE, EE		CE		CE		CE		CE, EE		CE	
Parental species	Name	<i>Oe. biennis</i> s.str.	<i>Oe. glazioviana</i>	<i>Oe. biennis</i> s.str.	<i>Oe. oakesiana</i>	<i>Oe. rubricaulis</i>	<i>Oe. depressa</i>	<i>Oe. suaveolens</i>	<i>Oe. glazioviana</i>	<i>Oe. rubricaulis</i>	<i>Oe. silesiaca</i>	<i>Oe. depressa</i>	<i>Oe. subterminalis</i>	<i>Oe. fallax</i>	<i>Oe. victorini</i>	<i>Oe. rubricaulis</i>	<i>Oe. depressa</i>	<i>Oe. glazioviana</i>	<i>Oe. parviflora</i>
	Origin	Europe	NA	Europe	NA	Europe	NA	Europe	NA	Europe	Europe	NA	NA	Europe	Europe	Europe	NA	NA	NA
	Secondary range in Europe	EW	WE, CE, EE	EW	WE, CE	CE, EE	EW	WE, CE, EE	WE, CE, EE	CE, EE	WE, CE, EE	EW	WE, CE	WE, CE	CE, EE	WE, CE, EE	EW	WE, CE, EE	WE, CE, EE
	Invasiveness	Actively invasive	Invasive	Actively invasive	Noninvasive	Invasive	Invasive	Naturalizing	Invasive	Invasive	Invasive	Invasive	Invasive	Actively invasive	Noninvasive	Invasive	Invasive	Naturalizing	Noninvasive
Hybrid (1)/parental species (2) frequency ratio		1 = 2	1 > 2	1 < 2	1 > 2	1 = 2	1 = 2	1 = 2	1 < 2	1 < 2	1 < 2	1 < 2	1 = 2	1 < 2	?	1 < 2	1 < 2	1 < 2	1 < 2

Note: WE—Western Europe; CE—Central Europe; EE—Eastern Europe; EW—everywhere, NA—North America; ?—unknown.

Table 2. Chromosomal configuration of cytotypes of different *Oenothera* L. species in meiosis

Species	Chromosomal configuration in meiosis
Noninvasive taxa that do not tend to spread	
<i>Oe. argillicola</i> Mackenz.	7 bivalents ring of 4 chromosomes + 5 bivalents ring of 6 chromosomes + 4 bivalents two rings of 4 chromosomes + 3 bivalents ring of 8 chromosomes + 3 bivalents ring of 10 chromosomes + 2 bivalents
<i>Oe. elata</i> Kunth	7 bivalents
<i>Oe. grandiflora</i> L'Hér.	7 bivalents ring of 4 chromosomes + 5 bivalents ring of 6 chromosomes + 4 bivalents ring of 6 chromosomes + ring of 4 chromosomes + 2 bivalents two rings of 4 chromosomes + 3 bivalents ring of 8 chromosomes + 3 bivalents ring of 10 chromosomes + 2 bivalents ring of 12 chromosomes + 1 bivalent ring of 14 chromosomes
<i>Oe. hirsutissima</i> (A. Gray) Rydb.	7 bivalents ring of 4 chromosomes + 5 bivalents ring of 6 chromosomes + 4 bivalents ring of 8 chromosomes + 3 bivalents two rings of 4 chromosomes + 3 bivalents ring of 6 chromosomes + ring of 4 chromosomes + 2 bivalents ring of 10 chromosomes + 2 bivalents
<i>Oe. hookeri</i> T. & G.	7 bivalents ring of 4 chromosomes + 5 bivalents ring of 6 chromosomes + 4 bivalents
<i>Oe. jamesii</i> Torr. & A.Gray	7 bivalents ring of 4 chromosomes + 5 bivalents ring of 6 chromosomes + 4 bivalents ring of 8 chromosomes + 3 bivalents ring of 10 chromosomes + 2 bivalents ring of 14 chromosomes
<i>Oe. longissima</i> Rydb.	7 bivalents ring of 4 chromosomes + 5 bivalents ring of 6 chromosomes + 4 bivalents ring of 8 chromosomes + 3 bivalents two rings of 4 chromosomes + 3 bivalents
Invasive taxa	
<i>Oe. biennis</i> L.	ring of 14 chromosomes ring of 12 chromosomes + 1 bivalent ring of 10 chromosomes + 2 bivalents
<i>Oe. fallax</i> Renner	ring of 12 chromosomes + 1 bivalent
<i>Oe. glazioviana</i> Micheli	ring of 12 chromosomes + 1 bivalent
<i>Oe. nutans</i> G. F. Atk. & Bartlett	ring of 14 chromosomes ring of 12 chromosomes + 1 bivalent
<i>Oe. oakesiana</i> (A. Gray) J. W. Robbins ex S. Watson & Coulter	ring of 14 chromosomes ring of 12 chromosomes + 1 bivalent ring of 10 chromosomes + ring of 4 chromosomes
<i>Oe. parviflora</i> L.	ring of 14 chromosomes
<i>Oe. strigosa</i> (Rydb.) Mack. & Bush	ring of 14 chromosomes
<i>Oe. stuechi</i> Soldano	ring of 12 chromosomes + 1 bivalent ring of 14 chromosomes
<i>Oe. villosa</i> Thunb.	ring of 14 chromosomes ring of 12 chromosomes + 1 bivalent

significantly affect its invasiveness. This is apparently due to the fast, almost simultaneous, formation of the majority of *Oenothera* species in Europe.

Table 1 shows typical examples which mirror the basic tendencies of invasive activity alteration in parental and hybrid *Oenothera* species. These data confirm the global principles, which we revealed as a result of distribution analysis of 25 species. All nine hybrid species which demonstrated high invasive activity in Europe originated from crossbreeding of highly invasive parental species. Our study revealed that highly invasive hybridogenetic species are more often formed if at least one of the parental species belongs to the group of actively invasive species (Table 1). Cases where a hybrid is not actively invasive regardless of high invasive capacity of one of the parents may be, in our opinion, explained by recent formation of the hybrid, and a future increase in its invasiveness may be expected. It was shown that the presence of *Oe. biennis* L. as one of the parents of a hybrid helps increase its invasiveness (Table 1). Analysis of parental species origins revealed that the most aggressive hybrids originated from crossbreeding of North American and European species geographically remote from each other. In their hybrid progeny, an effect similar to heterosis upon crossbreeding of remote geographically isolated lines is often observed (Table 1).

We also found that the frequency of parental species is important for realization of the potential probability of hybridization, because in that case the probability of crossbreeding between parental species is significantly increased. This observation is confirmed by our studies of mixed *Oenothera* L. populations in Europe (Wittig et al., 1999; Wittig and Tokhtar, 2002, 2003), where a number of hybrid plants is usually present alongside with parental species. The distribution of parental species in Europe as well as their frequency was also assessed on the basis of data published in (Rostański et al., 2004, 2010).

Despite a similarity of morphological traits of closely related *Oenothera* species, their invasive capacities may differ significantly, which is apparently due to genetic features of the species. For example, *Oe. fallax* Renner, which is the hybrid of *Oe. glazioviana* Micheli and *Oe. biennis*, is known to be one of the most invasively active species of Western Europe, whereas *Oe. moravica* V. Jehlík et Rostański, which is closely related to it, is distributed locally in several regions of Moravia (Czech Republic). *Oe. glazioviana* is quite common in Western Europe and a little bit rarer in Eastern Europe, while *Oe. coronifera* Renner, which is closely related to it, was found only in some areas of Europe. A large population of this species has for a long time been known to inhabit Germany in the suburbs of Berlin in the Brandenburg region, though it has recently been found in South Bohemia (Czech Republic) (Mihulka et al., 2003). The most striking examples of this phenomenon are the hybridogenetic species, which are often morphologically similar to

parental ones, though they differ from them both genetically and invasively. Therefore, the invasive capacity of hybrid and parental *Oenothera* species depends significantly on their genetics. On the basis of the example of *Oenothera*, it may be concluded that the establishment of the invasive capacity of a species, microspecies, or race may be one of the taxonomic criteria to support a particular species concept.

It was shown that, although 33 hybrid species are locally distributed in Europe, some of them are known from only one or several locality: *Oe. braunii* Doell, *Oe. brevispicata* Hudziok, *Oe. canovortex* Hudziok, *Oe. clavifera* Hudziok, *Oe. coloratissima* Hudziok, *Oe. compacta* Hudziok, *Oe. conferta* Renner, *Oe. editi-caulis* Hudziok, *Oe. flaemingina* Hudziok, *Oe. inconspicua* Hudziok, *Oe. indivisa* Hudziok, *Oe. macrosperma* Hudziok, *Oe. mediomarchica* Hudziok, *Oe. obscurifolia* Hudziok, *Oe. octolineata* Hudziok, *Oe. pseudocernua* Hudziok, *Oe. rigirubata* (Renner) Gutte & Rostański (distributed in Germany), *Oe. adriatica* Soldano, *Oe. fallacoides* Soldano & Rostański, *Oe. marinella* Soldano, *Oe. pedemontana* Soldano, *Oe. pellegrinii* Soldano, *Oe. sesitensis* Soldano, *Oe. stuchii* Soldano (Italy), *Oe. pseudochicaginensis* Rostański, *Oe. tacikii* Rostański, *Oe. wratislaveinsis* Rostański (Poland), *Oe. polgari* Rostański, *Oe. purpurans* Borbas (Hungary), *Oe. carinthiaca* Rostański, *Oe. heiniana* Teyber (Austria), *Oe. slovacica* Jehlík et Rostański (Slovakia), *Oe. britannica* Rostański (UK) (Rostański, 1982, 1998; Rostański and Tokarska-Guzik, 1998; Rostański et al., 2004).

It is suggested that evolution of the genus was initially realized through hybridization of two ancestral species subgroups: (1) species with a normal diploid genetic system and (2) species with a ring-shaped genetic system (Grant, 1981). There is also a primitive intermediate group which involves species that sometimes form very big chromosomal rings. It is postulated that ring-forming species originated from more primitive bivalent species, among which relict plants with archaic features, which preferred a mild humid climate, prevailed (Grant, 1981). Being a new branch of evolution, ring-forming species are exceptionally aggressive with respect to colonization of territories of any kind and are considered to be weeds even in their native habitation area. Apparently, this genus originated from some regions of Mexico and Central America, from where primitive forms migrated northward (Cleland, 1964). It is suggested that *Oe. argillicola* Mack., *Oe. grandiflora* L'Hér., and *Oe. hookeri* Torr. et A. Gray originated from this very ancestor population, which gave rise to the ring-forming species via hybridization. Later on, they migrated to Europe, where they underwent evolution for several hundred years.

Natural populations of *Oenothera* contain plants that have rings of different size in their genome, which consists of 4–14 chromosomes. In some cases, plants which have small rings in their genomes may be fre-

quently found in populations because of some selective advantage of heterozygotes.

Cytogenetic data analysis revealed that bivalents can be formed in the following species: *Oe. hookeri*, *Oe. argillicola*, *Oe. grandiflora*, and *Oe. elata* (Table 2). According to contemporary concepts, they are the very ancestors of the ring-forming species: *Oe. parviflora*, *Oe. biennis*, *Oe. strigosa*, and *Oe. glazioviana*. In some populations of *Oe. hookeri*, *Oe. jamesii*, and *Oe. longissima*, small and medium size rings can be formed. Sometimes, these populations carry balanced lethality as well, thus occupying an intermediate position between two major subgroups.

Several components of the genetic system of permanent heterozygosity of the *Oe. glazioviana* group vary by translocations in a species-dependent manner. One of such variable components is the ring size. The ring of *Oe. glazioviana*, which consists of 12 chromosomes, is atypical of the group as a whole. In one of the populations of *Oe. irrigua*, which is located in New Mexico, a ring consisting of eight chromosomes and three bivalents is constantly formed. In microspecies that populate central and eastern parts of the United States, a 14-chromosome ring is more often formed. Considering the genotypic level of species organization, it may be noted that aggressive ring-forming species usually have advantages in distribution capacity. They inhabit tilled fields and penetrate northern regions. Most of them form only a small number of cytotypes in meiosis and their genotype usually consists of ring-shaped chromosomes and only a few bivalents. In some cases only one ring, which consists of all 14 chromosomes, can be formed. For example, *Oe. glazioviana*, which was formed in the Hugo de Vries Garden as a result of a single nucleotide mutation and actively spread through the railways in Denmark, in meiosis forms a ring, which consists of 12 chromosomes and one bivalent.

Plesiomorphic plants, such as *Oe. hookeri*, *Oe. argillicola*, *Oe. grandiflora*, and *Oe. elata*, which populate mostly the American continent have not become invasive, apparently, because of the specificity of their genetic system. In meiosis, these species form a large number of cytotypes, in which up to 14 chromosomes may be involved in bivalents. If they form only one cytotype, as in *Oe. elata* Kunth., it totally consists of bivalents (Table. 2).

On the contrary, invasive *Oenothera* species more often form only few cytotypes, in which the majority of chromosomes can fuse in meiosis to form rings. They also differ in their distribution activity in anthropogenic ecotopes (Table 2).

A comparative analysis of cytogenetic data on the species of the *Oenothera* genus with the data on their distribution and invasiveness allowed us to conclude that their invasiveness depends on their genetic features. Those species that in meiosis have the majority of their chromosomes in bivalents demonstrate plesiomorphic traits and do not tend to actively spread

(Table 2). Usually, this group involves plants with large flowers that appear directly from the rosette, and the stem is often absent. The range of these species is limited and stable, and the species themselves are sometimes considered to be relict. The ring-forming species whose chromosomes mostly form Renner rings in meiosis appear to be active aggressors and tend to invade new territories. These are the very species that have colonized wide territories in Europe. This may be due to their heterozygous genotypes that are typical of plants that form Renner rings in meiosis, which makes them more competitive and resistant to difficult environments.

Considering the ring-forming species group in more details may lead to the conclusion about some specific features of their genetic apparatus which, apparently, affect the invasiveness of a species. In this group, a larger invasive capacity is demonstrated by those species that have fewer cytotypes (for example, *Oe. biennis*—3 cytotypes; *Oe. oakesiana*—3 cytotypes; *Oe. parviflora*—1 cytotype; *Oe. villosa*—2 cytotypes) (Table 2). Species which have a larger diversity of cytotypes (more than five) in natural populations usually do not demonstrate invasive activity in Europe. These are, for example, *Oe. argillicola*, *Oe. grandiflora*, *Oe. hirsutissima*, *Oe. jamesii*, and *Oe. longissima* (Table 2). At the same time, one of the cytotypes of these species is represented by seven bivalent chromosomes.

Among the species with a small number of cytotypes a not strict but nevertheless quite obvious tendency can be observed. These plants demonstrate a higher invasive capacity in the case where one of the cytotypes of the *Oenothera* species is represented by a single ring consisting of 14 fused chromosomes.

Although it was previously shown that parental genotypes did not affect the distribution of specific features of species of the genus *Oenothera* subsect. *Oenothera* (Mihulka et al., 2006), our data suggest that further detailed investigations of the dependence of *Oenothera* invasiveness on its cytogenetic features are necessary. Undoubtedly, the presence of a permanent heterozygous translocation mechanism in the *Oenothera* genus helps formation of a number of new taxa of different rank, and this, in and of itself, provides adaptive and competitive advantages for their survivability and distribution under new environmental conditions. Analysis of cytogenetic features and invasiveness of *Oenothera* in Europe allowed us to reveal a quite obvious tendency: the more evolutionarily specialized and modernized the genetic apparatus of a species, the higher its invasiveness. The new branch of ring-forming *Oenothera* demonstrates higher invasiveness compared to that of bivalent species. Ring-forming plants possess higher invasiveness, the smaller the number of cytotypes and the more fused chromosomes are typical of the taxon. Although not only the *Oenothera* subsect. *Oenothera* species but also the parental plants of this group of plesiomorphic

species were analyzed in our study, the dependence of invasive activity on the cytotype characteristics was quite obvious. Therefore, to understand fully the nature and mechanisms of these phenomena, not a simple analysis of the Renner ring structure of parental and hybrid species but detailed investigations of the genetics of *Oenothera* using contemporary approaches of genetic marking are required.

Therefore, the analysis of the distribution of parental and newly formed hybrid species of the *Oenothera* genus in Europe provides evidence that (1) in *Oenothera*, the speciation time apparently does not significantly affect their invasiveness; (2) highly invasive hybrids are often formed when at least one of the parental species belongs to the group of actively invasive species; in *Oenothera* hybrids, the invasiveness promoter role often belongs to the parental species *Oe. biennis*; (3) the most aggressive hybrids are often formed as a result of crossbreeding of geographically remote North American and European species; (4) the invasive activity of hybridogenetic and parental *Oenothera* species depends considerably on their genetics, because these plants are often morphologically similar; and (5) the group of ring-forming *Oenothera* species is characterized by higher invasiveness compared to bivalent species. The ring-forming plants demonstrate higher invasiveness, the smaller the number of cytotypes and the more fused chromosomes they possess. The obtained data suggest that the invasive capacity of *Oenothera* is determined by its genetic features, which is apparently due to the high fraction of heterozygosity of the ring-forming species, which are known to be successful colonizers of new territories and possess the highest invasive capacity within the studied group of plants.

The study of species, microspecies, and races of *Oenothera* revealed also that their invasive activity may be one of the criteria for taxonomic decisions to accept or reject a particular species concept.

A correlation between the invasiveness of hybridogenetic and parental *Oenothera* species undoubtedly exists, though it is not linear and depends on many factors.

In the future, study of adventive for Europe Evening primroses not only may help reveal the principles of invasion evolution in this group of plants, but it also will make it possible to extrapolate the obtained data over the whole Onagraceae family and the species with similar genetic mechanisms of reproduction or trait inheritance, including clonal species.

CONCLUSIONS

It was shown by example of the *Oenothera* genus that the frequency of hybrids is increased in the secondary range. This suggests that indigenous species run the risk of assimilation extinction. This is especially important because taxa that are the most sensi-

tive to introgression and hybridization have small populations and limited range (Levin et al., 1996).

The results of our study showed that it is necessary to study genetic structure of populations into which invasive species are introduced in order to reveal whether they can undergo hybridization and introgression. Moreover, the data on the relative stability of phytocenoses will provide the possibility of forecasting invasive species introduction into natural populations. This information will make it possible to predict whether it is possible to substitute nonindigenous species for indigenous.

Analysis of cytogenetic features and invasiveness of *Oenothera* in Europe allowed us to reveal an obvious tendency: the more evolutionarily specialized and modernized the genetic apparatus of a species, the higher is its invasiveness. The new branch of ring-forming *Oenothera* demonstrated higher invasiveness compared to bivalent species. The ring-forming plants demonstrated a higher invasive capacity, the smaller the number of cytotypes and the larger the number of fused chromosomes in the taxon. Therefore, the invasiveness of *Oenothera* plants is determined by their genetic features, which is apparently due to high level of heterozygosity of the ring-forming species.

ACKNOWLEDGMENTS

This work was supported by the Program for the Support of Fundamental Research of the Presidium of the Russian Academy of Sciences "Biodiversity and Gene Pool Dynamics" and by the Russian Foundation for Basic Research, project no. 08-04-00239.

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