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Invasion history of *Oenothera* congeners in Europe: a comparative study of spreading rates in the last 200 years

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Abstract

Aim The dynamics of spread of some representatives of *Oenothera*, a genus of New World origin and alien to Europe, was analysed.

Location Distribution data from six European countries., i.e. Austria, Czech Republic, Hungary, Portugal, Serbia and UK were used.

Methods Floristic records covering the last 200 years were collated and the cumulative number of localities was plotted against time. A correction of the number of localities, taking into account the intensity of floristic research in particular countries, was applied based on the total number of available herbarium specimens to make comparisons of the rate of spread in particular countries possible.

Results In total, 35 alien taxa of the genus have been reported from the countries considered, the majority of which has only a limited distribution. So far 1800 records of *Oenothera* species have been reported from the six countries analysed since 1780, with *O. biennis*, *O. erythrosepala, O. salicifolia, O. stricta, O. cambrica, O. rubricaulis,* and *O. chicaginensis* having more than 50 localities. There is a highly significant negative correlation between the total number of localities in Europe and the year of the first introduction. Marked differences were found in the taxonomical pattern of invasion in particular countries.

Main conclusions Multivariate analyses have shown that in Europe, there are two distinct groups of species of North and South American origin, respectively, whose invasion is determined by climatic conditions, namely temperature and precipitation. The South American group is represented by perennial and annual species preferring oceanic climate (e.g. *O. rosea, O. stricta*), while the North American group consists of biennial representatives (*O. biennis* and others) better adapted to inland conditions with lower mean temperature and more balanced monthly precipitations. In addition, there is a transitional group of species, including namely *O. erythrosepala* and *O. fallax,* preferring regions with sufficient rainfall and higher temperatures. The relatively hot climate of Balkan Peninsula seems to prevent invasion by *Oenothera* representatives. Pattern of invasion of particular taxa corresponds well to the climatic conditions in the regions of their natural distribution.

Keywords
Plant invasions, floristic records, herbaria, *Oenothera*, congeners, spread dynamics, historical reconstruction, rate of invasion.

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INTRODUCTION

Actual distribution of invasive species is usually supposed to be a good predictor of their invasive potential (e.g. Daehler & Strong, 1993; Williamson, 1996). However, when we compare a broad spectrum of invasive species across a higher taxonomical level (such as a whole flora of some territory), the relationship may be biased by intrinsic characteristics of particular taxa, different time of introduction and other factors. Whether and how precisely it is possible to determine the date of an alien species arrival to a new territory depends on how good are the relevant historical records, i.e. on the tradition of floristic research in the country (Pyšek & Prach, 1993).

Further, there is an interpretational problem associated with actual species ranges as it is usually impossible to determine whether the range we observe is of maximum possible extent (in the context of the characteristics of species and their environment) or not. Ranges of many alien species are still increasing while those of others seem to have reached their potential size. Unfortunately, studies of existing plant community patterns provide only correlative evidence for factors that control plant distribution. Experimental approaches play an important role in this research but seldom tell whether a factor such as competition is sufficient to explain observed distributions (Richardson & Bond, 1991).

Research of invasive species provides us with certain advantages in this respect. We can assume, at least in some cases, that species have not yet reached their maximum potential distribution, simply because of the lack of time. Consequently, the research on the dynamics of spread of invasive species can bring about important implications to the problem of range development and distribution limits. Moreover, invasive species have been exposed to a new environment without the presence of co-adapted fauna and flora, representing hence a suitable model for testing the role of interspecific interactions. Finally, invasions are often relatively well documented, especially if the invading species is economically important (Richardson & Bond, 1991).

Considering larger sets of alien species brings about some difficulties which can be partially eliminated by phylogenetic corrections methods (Harvey & Pagel, 1991). Another possibility is to compare a taxonomically limited set of closely related species. This approach was successfully used in previous studies (e.g. Forcella *et al.*, 1986; Perrins *et al.*, 1993; Pyšek & Prach, 1993; Frean *et al.*, 1997; Weber, 1998). Studies on closely related species with varying invasive success have a great potential for prediction of future behaviour and impact of actual and potential invaders (Weber, 1998).

Invasive plants continue to be introduced to new regions over all continents but the mechanisms underlying successful plant invasion are still poorly understood (Crawley, 1989) although new promising theories do emerge (Davis *et al.*, 2000). Still, the prediction of a successful invasion remains difficult (Weber, 1998) and rates of introduction of new invasive species can be only vaguely estimated (Forcella, 1985).

The process of invasion consists of several phases (Newsome & Noble, 1986; Kowarik, 1995; Weber, 1998) affected to varying extent by human activities. At each step, the species must overcome specific barriers (Richardson *et al.*, 2000). The mode of introduction plays an important role in the process of invasion (Auld & Coote, 1980; Forcella *et al.*, 1986; Kowarik, 1995), and increase in the area occupied by invasive species was found to be faster when the spread began with several smaller populations rather than with one large population (e.g. Auld & Coote, 1980; Auld & Tisdell, 1986; Forcella *et al.*, 1986; Kowarik, 1995).

The present paper describes and compares the dynamics of spread of alien *Oenothera* species in six European countries. This genus is of a New World origin (see Dietrich *et al.*, 1997) and its numerous representatives were introduced into Europe where they grow with varying success, from casual to naturalized to invasive (see Richardson *et al.*, 2000 for terminology). This, together with an available qualitative data on distribution over a wide range of the introduced range, makes the genus a very suitable model for a detailed comparative historical study of invasion among a set of congeners. The study aims at answering the following questions: (1) What is the generic pattern of invasion in *Oenothera* spp. introduced to Europe? (2) Are there any differences between countries in the extent of invasion by *Oenothera* species and if so, can they be related to environmental factors? (3) Do particular species differ in the rate of their invasion over the past two centuries and if they do, can these differences be related to their ecological requirements?

METHODS

The study genus

The genus *Oenothera* L. (Onagraceae), consisting of *c.* 120–200 species (e.g. Dietrich *et al.*, 1997; Jehlík, 1997; Mabberley, 1997), is considered to have originated in Central America. Its representatives are native to Central, North and South America and the genus also includes a number of species that are now naturalized world-wide (Dietrich *et al.*, 1997). Most of the invasive species, especially those invading into temperate regions, belong to the section *Oenothera* subsection *Oenothera*. From Europe, approximately 70 species of the genus have been reported, 59 of which belong to the subsect. *Oenothera* (Rostański, 1982). Twenty-nine *Oenothera* species have been reported as planted in Europe (Cullen *et al.*, 1997).

Most species of the genus occur in primarily or secondarily open habitats, including old fields and roadsides, stream sides or dunes (Dietrich *et al.*, 1997). This pattern of occurrence is also typical of the regions into which they were introduced. Most of the introduced representatives are biennial and have high requirements for light needed for seeds to germinate (e.g. Gross & Werner, 1982; Kachi & Hirose, 1983; Gross, 1985).

Chromosomes of some *Oenothera* species are arranged in rings, which are passed through to next generations without any recombination. Newly originated combinations of rings give new genotypes with sometimes startling morphological features (Cleland, 1972; Mabberley, 1997). This specific pattern of chromosomes together with commonly occurring self-pollination and frequent hybridization leads to true breeding (i.e. offspring have the same traits as their parents if the parents are self-fertilized) with a high survival rate, but with gene flow being essentially eliminated by genetic reproductive barriers (Cleland, 1972; Dietrich *et al.*, 1997). Consequently, there are native populations covering enormous area consisting exclusively of isolated true-breeding self-pollinating heterozygotes (Cleland, 1972) and the taxonomical status of such populations is inevitably unclear. Most of the species of *Oenothera* that have become naturalized outside their natural range and all of the naturalized species that have achieved a wide secondary distribution are of such chromosomal pattern (Dietrich *et al.*, 1997).

Data sources

The present paper is based on analysis of previously published data. Because of taxonomic complexity within the genus and resulting possible misdetermination, only data from monographers were considered as reliable and used for analysis. Common floristic papers from botanical periodicals were omitted. Complete lists of localities of all *Oenothera* species are available for the following European countries: Austria, Czech Republic (= Czechia), Hungary, Portugal, Serbia and UK (see Table 1 for data sources). These data were used to reconstruct the spread of particular *Oenothera* representatives from the time of their introduction up to the present. In each country, all *Oenothera* species reported to occur there were considered. A database was created storing information on species, country, and the year of the report. Repeated reports on the occurrence of a species from the same locality were omitted.

Resulting set of countries is representative in terms of European climatic conditions, covering latitudinal range of 37–61° N, and longitudinal range from 9° W 23° E (Table 1).

Each 'national' list of localities represents a summarized source of information based on revised herbarium collections. Except Serbia (Zlatković; *et al.*, 1998), these surveys were all carried out by monographer K. Rostański or his colleagues (Rostański, 1966; Jehlík & Rostański, 1979, 1980; Rostański & Forstner, 1982; Rostański, 1982, 1991). This makes the data extremely valuable for comparative analyses both in terms of particular species and their spread in different countries. This point is very important because of the complicated taxonomical situation in the genus *Oenothera*. There are at least two alternative taxonomical approaches, i.e. Anglo-Saxon, based mostly on cytogenetical studies (e.g. Munz, 1965; Cleland, 1972; Dietrich *et al.*, 1997), and central-European, which is population-based and takes into account Renner's chromosomal complexes and 'constant' phenotypes. The latter approach is represented by K. Rostañski and followed in the present study. Papers using

Table 1 Overview of countries analysed in the present study with respect to the occurrence of *Oenothera* species. Geographic coordinates, total area and climatic characteristics were taken from official internet sources of given countries. Total number of *Oenothera* species and that of abundant representatives reported from the given country is shown. A species for which there are more than five reported localities was considered as 'abundant'

Country	Latitudinal range	Longitudinal range	Mean annual temperature (°C)	Mean annual precipitaition (mm)	Mean altitude (m a.s.l.)	Area (km^2)	No. of reported *Oenothera* species	No. of abundant *Oenothera* species	Total no. of *Oenothera* localities	Data sources
Austria	46–49° N	10–17° E	8.3	921.2	437.8	83 858	20	7	402	Rostański & Forstner, 1982
Czech Republic	49–51° N	12–19° E	8.2	563.5	291.3	78 703	20	8	703	Jehlík & Rostański, 1979, 1980
Hungary	46–49° N	16–23° E	10.2	558.9	153.0	93 030	5	4	118	Rostański, 1966
Portugal	37–42° N	9–7° W	15.2	790.3	208.2	92 391	11	4	114	Rostański, 1991
Serbia	42–46° N	19–23° E	13.0	952.0	134.3	88 412	4	2	67	Zlatković *et al.*, 1998
UK	50–61° N	8° W–2° E	9.1	753.9	59.5	244 820	16	9	403	Rostański, 1982

these two approaches are simply incompatible because of different taxonomical treatment.

Data analysis

For each country, the cumulative number of localities was plotted against time (hereafter termed invasion curves, see Pyšek & Prach, 1993) for each *Oenothera* species with more than five localities reported from the given country. In addition to the species level, invasion curves based on cumulative numbers of localities of all *Oenothera* species were constructed for each country.

Because of the character of the data, which are represented by point records in an *a priori* defined geographical area, it was not possible to use the size of the area occupied by a species or another size-related measure of invasion success (Hengeveld, 1989; Pyšek & Prach, 1993). Exponential regression models were therefore fitted to the cumulative numbers of localities plotted against time and the slope b was used as a measure of the invasion rate (Trewick & Wade, 1986; Pyšek, 1991; Pyšek & Prach, 1993, 1995). Differences in slopes were tested by analysis of covariance (ANCOVA) using the test of parallelism of regression lines (Zar, 1984).

To compare the course of invasion of particular species between the countries, data were standardized with respect to the intensity of floristic research in the given region. The number of herbarium specimens available in the national herbaria was taken as a convenient measure of the intensity of floristic research. In order to obtain the information on the rate of accumulation of herbarium specimens in the country, their number was recorded based on three subsequent editions of the Index Herbariorum (Lanjouw & Stafleu, 1956; Holmgren & Keuken, 1974; Holmgren *et al.*, 1990). All specimens stored in the indexed national herbaria up to the given year were summed up to yield the total number of specimens for each country. Exponential regression models were then fitted to the cumulative numbers of herbarium specimens plotted against time (i.e. using the values from three editions of Index Herbariorum) for each country on the log/log scale. Based on this model, numbers of herbarium specimens accumulated up to a given year were predicted. Finally, the numbers of localities for each year were corrected by the predicted numbers of herbarium specimens by using the following equation:

$$\text{Standardized cumulative number of localities} = (\text{number of localities}/\text{number of herbarium specimens}) \times 100\,000$$

Invasion curves using the standardized cumulative numbers were then constructed (further termed 'standardized invasion curves'). The advantage of such an approach is that (i) it considers the dynamics of accumulation of herbarium specimens in the given country, and (ii) makes the area of the country irrelevant as the relative frequency of occurrence of primrose species in the flora can well be expressed by their contribution to the herbaria regardless of the size of the country. It also can be assumed that the larger the country is, the more herbarium specimens are located in its herbaria.

Statistical analyses were carried out by Statistica 5.5 software (Statsoft, 1998). Redundancy analysis (RDA) with log-transformed data was performed using CANOCO for Windows 4.0 software package (ter Braak, 1988). Total number of localities of particular species reported in the given country were used as input data for multivariate analysis and all species were included into computation. The following environmental variables were obtained for each country and used as explanatory variables in the multivariate analysis: mean altitude, distance from the nearest seashore, mean latitude and longitude (taken as a medium values between the two extreme coordinates), maximum and minimum mean monthly temperature, mean annual precipitation, mean human population density, maximum and minimum mean monthly temperature, mean annual temperature. Climatic data were obtained by calculating average values from selected meteorological stations located within the territory of the given country.

RESULTS

Overall generic pattern of *Oenothera* invasion in Europe

At the generic level, i.e. considering all representatives of the genus *Oenothera* together, the highest number of localities has been reported from the Czech Republic, UK and Austria (Table 1). Using standardized invasion curves reveals that the rate of invasion (expressed as the regression coefficient b) was highest in the Czech Republic ($b = 0.023 \pm 0.0011$) and Portugal ($b = 0.018 \pm 0.0008$), followed by Austria ($b = 0.017 \pm 0.0008$), Hungary ($b = 0.013 \pm 0.0005$), Serbia ($b = 0.012 \pm 0.0004$) and UK ($b = 0.004 \pm 0.00008$). Multiple range comparison revealed that the rates of invasion in particular countries were significantly different from each other at $P < 0.001$, except of Hungary and Serbia. In Austria, Czech Republic and Serbia, there is a remarkable increase in the standardized cumulative number of localities since the 1960s (Fig. 1).

In total, 35 taxa of *Oenothera* have been reported from the six countries. Of this number, five taxa are of hybrid origin (Table 2). Three species (*O. biennis*, *O. erythrosepala*, and *O. salicifolia*) occur in each country, another eight species occur in three countries, and remaining 24 taxa occur only in one or two countries. *Oenothera biennis* was the first species introduced into Europe in 1780 (UK) (Table 2). Since the first half of the 19th century, there was a fast steady increase in the number of alien *Oenothera* species known from Europe up to the given year followed by a rather slower increase in the twentieth century (Fig. 2). Unlike the trend in species number, the increase in the cumulative number of localities of *Oenothera* species reported from Europe has been steeper and more consistent over the whole study period, and the slopes describing the increase in the number of species and that of localities were significantly different at $P < 0.001$ (Fig. 2).

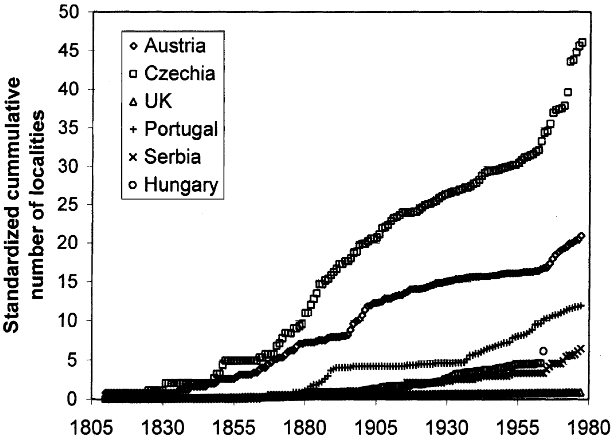

Figure 1 Invasion of representatives of the genus *Oenothera* in selected European countries.The figures represent an increase over time in the standardized cumulative number (i.e. the number of records standardized by the floristic intensity expressed by the number of herbarium specimens in the country, see Methods for details) of localities of all representatives of the genus reported from the given country.

In total 1800 records of *Oenothera* species have been reported from the six countries in the last 220 years. The highest number of records was reported for *O. biennis* (794, i.e. 44.1% of the total number of records for the whole genus) and *O. erythrosepala* (229, i.e. 18.8%). Another group of species with more than 50 localities follows (*O. salicifolia, O. stricta, O. cambrica, O. rubricalis, O. chicaginensis*). Only 12 species contribute with at least 1% to the total number of localities in Europe (Table 2).

Pooled data on the occurrence of particular species were used to assess their rate of invasion in Europe (Fig. 3). The fastest spread was found in *O. erythrosepala* ($b = 0.035 \pm 0.0013$), followed by *O. biennis* ($b = 0.031 \pm 0.0008$) and *O. stricta* ($b = 0.026 \pm 0.0011$) (Table 3, Fig. 5).

There was a highly significant negative correlation between the total number of localities recorded up to present and the year of introduction into Europe ($r = -0.55$, $F = 14.31$, d.f. = 133, $P < 0.001$). This relationship remained significant even when the first introduced and most represented species *O. biennis* was excluded from the analysis ($r = -0.43$, $F = 7.27$, d.f. = 132, $P < 0.01$).

Species invasion in particular countries

By inspecting the invasion curves and the number of localities particular species have reached up to present, two distinct groups of countries can be recognized with respect to the most invasive *Oenothera* species (Fig. 4). While in Austria, Czech Republic, Hungary, and Serbia *O. biennis* is most frequent, usually followed by *O. erythrosepala*, a different pattern was observed in seashore countries with a more moderate, oceanic climate such as the UK and Portugal. In both the latter countries, *O. erythrosepala* is also important, being the most frequent in UK since the 1950s, but the role of *O. biennis* is minor. The most abundant invasive *Oenothera* species in Portugal is *O. stricta* (Fig. 4), a species native to Mediterranean-like habitats in Southern Chile and Argentina (Table 2).

Comparison of spreading rates of particular species in the countries with higher number of invasive representatives of the genus shows that *O. erythrosepala*, *O. biennis* and *O. syrticola* spread at highest rate in Austria, *O. biennis* in the Czech Republic and *O. erythrosepala* in the UK (Table 4a).

The rate of spread and the number of localities of *Oenothera* species in particular countries varies (see Table 4b for statistical differences). Standardized invasion curves were used to compare the rate of spread of each species among countries (Fig. 5). It appears that biennial species, namely *O. biennis* and *O. erythrosepala* spread faster in countries with temperate climate. *Oenothera erythrosepala* invades massively also in countries with oceanic climate, i.e. UK and Portugal. *Oenothera stricta*, a perennial species of South American origin (Table 2), occurs in more than five localities only in the latter two countries, and its rate of spread is higher in Portugal, i.e. the warmest country of all (Table 1).

Factors determining the pattern of *Oenothera* invasion across Europe

Figure 6 shows relationships among *Oenothera* species, countries invaded and selected environmental characteristics. The first two ordination axes explained 63.8% of variation in the data set. First ordination axis corresponds to the gradient of mean annual temperature, minimum mean monthly temperature, and oceanic character of climate. This gradient decreases from Portugal to Czech Republic. Species of South American origin such as *O. stricta* or *O. rosea*, which occur in warmer territories and in scrubland habitats, prefer coastal countries with higher mean annual temperature and higher minimum monthly temperature (Portugal, UK). Occurrence of group of biennial species of North American origin (e.g. *O. biennis, O. chicaginensis*) and of taxa of presumed recent hybrid origin (e.g. *O. acutifolia, O. issleri*) is positively correlated with altitude and distance from the seashore. In this group, species such as *O. erythrosepala* or *O. fallax* tend to form a transition between markedly inland central European species and those species preferring oceanic type of climate with higher mean temperatures and lower weather fluctuation. Their occurrence is positively correlated with minimum mean monthly precipitations.

DISCUSSION

The nature of the data set

Several studies focusing on the dynamics of plant invasions compared the rates of alien species increase using floristic data from various regions (Auld *et al.*, 1982; Forcella & Harvey, 1982, 1986; Frean *et al.*, 1997; Stadler *et al.*, 1998; Weber, 1998). Knowledge of the actual distributions of some species and the number of recorded localities are

Table 2 Overview of alien *Oenothera* representatives reported from the six European countries analysed in the present study. For each taxon, the following information is given: section to which it belongs; origin (i.e. from where it has been introduced or which are the parental species in the case it originated in the adventive distribution area); life form (A = annual, B = biennial, C = perennial); date of the earliest report from Europe; the country from which it was first reported, total number of localities recorded in the 6 countries considered; and the number of countries in which the taxon was recorded

Taxon	Author	Section	Life form	Origin	Date of first record in Europe	Country of the first introduction	Total number of localities	Number of countries
O. acutifolia	Rostański	*Oenothera*	B	*ammophila* × *rubricaulis*	1975	Czechia	1 (0.1)	1
O. affinis	Camb. in St-Hil.	*cf. Raimannia* (Rose) Munz	A	S. America	1880	Portugal	11 (0.6)	2
O. × *albipercurva*	Renner ex Hudziok	*Oenothera*	B	*ammophila* × *biennis*	1899	Czechia	2 (0.1)	1
O. × *albivelutina*	Renner	*Oenothera*	B	cf. *biennis* × *erythrosepala*	1875	UK	13 (0.7)	2
O. ammophila	Focke	*Oenothera*	B	cf. N. America	1848	Czechia	27 (1.5)	2
O. biennis	L.	*Oenothera*	B	N. America	1780	UK	794 (44.1)	6
O. × *britannica*	Rostański	*Oenothera*	B	*erythrosepala* × *cambrica*	1956	UK	11 (0.6)	1
O. cambrica	Rostański	*Oenothera*	B	cf. Canada	1833	UK	82 (4.6)	1
O. carinthiaca	Rostański	*Oenothera*	B	cf. N. America	1970	Austria	6 (0.3)	1
O. chicaginensis	De Vries	*Oenothera*	B	N. America	1917	Austria	60 (3.3)	2
O. × *drawertii*	Renner ex Rostański	*Oenothera*	B	*salicifolia* × *suaveolens*	1964	Hungary	1 (0.1)	1
O. erythrosepala	Borbás	*Oenothera*	B	N. America	1866	UK	339 (18.8)	6
O. fallax	Renner emend. Rostański	*Oenothera*	B	*biennis* × *erythrosepala*	1892	UK	47 (2.6)	3
O. hoelscheri	Rostański	*Oenothera*	B	*rubricaulis* × *salicifolia*	1969	Austria	5 (0.3)	2
O. indecora	Camb. in St-Hil.	*cf. Raimannia* (Rose) Munz	A	S. America	1954	Portugal	8 (0.4)	1
O. issleri	Rostański	*Oenothera*	B	*biennis* × *syrticola*	1949	Czechia	15 (0.8)	2
O. laciniata	Hill	*Raimannia* (Rose) Munz	A/P	N. America	1903	UK	8 (0.4)	2
O. longiflora	L.	*Raimannia* (Rose) Munz	A/B	S. America	1865	Portugal	3 (0.2)	2
O. missouriensis	Sims	*Megapterium* (Spach) Munz	P	N. America	1913	Czechia	3 (0.2)	1
O. nuda	Renner ex Rostański	*Oenothera*	B	cf. N. America	1943	Portugal	2 (0.1)	1
O. oehlkersi	Kappus	*Oenothera*	B	*erythrosepala* × *suaveolens*	1953	Portugal	1 (0.1)	1
O. parviflora	L.	*Oenothera*	B	N. America	1871	Austria	4 (0.2)	3
O. × *punctulata*	Rostański et Gutte	*Oenothera*	B	*biennis* × *chicaginensis*	1972	Czechia	1 (0.1)	1
O. renneri	H. Scholz	*Oenothera*	B	N. America	1907	UK	9 (0.5)	3
O. rosea	Ait	*Hartmannia* (Spach) Munz	P	warm N., C. & S. America	1876	Portugal	17 (0.9)	3

O. rubricaulis	Klebahn	*Oenothera*	B	N. America	1846	Austria	68 (3.8)	3
O. rubricuspis	Renner ex Rostański	*Oenothera*	B	N. America	1906	Austria	3 (0.2)	2
O. salicifolia	G. Don	*Oenothera*	B	N. America	1836	Hungary	108 (6.0)	6
O. silesiaca	Renner	*Oenothera*	B	N. America	1900	Austria	3 (0.2)	2
O. stricta	Ledeb.	*Raimannia* (Rose) Munz	A/B	Chile, S. America (cf. *odourata* × *ravenii*)	1825	Czechia	91 (5.1)	3
O. suaveolens	Persoon	*Oenothera*	B	cf. N. America	1862	Hungary	26 (1.4)	3
O. syrticola	Bartlett	*Oenothera*	B	N. America	1888	Austria	23 (1.3)	3
O. tetragona	Roth	*Kneiffia* (Spach) Munz	P	N. America	1884	Czechia	1 (0.1)	1
O. tetraptera	Cav.	*Hartmannia* (Spach) Munz	P	C. America	1932	UK	1 (0.1)	2
O. turoviensis	Rostański	*Oenothera*	B	N. America	1951	Austria	6 (0.3)	2

The percentage of the total number of localities reported from Europe is indicated in parentheses.

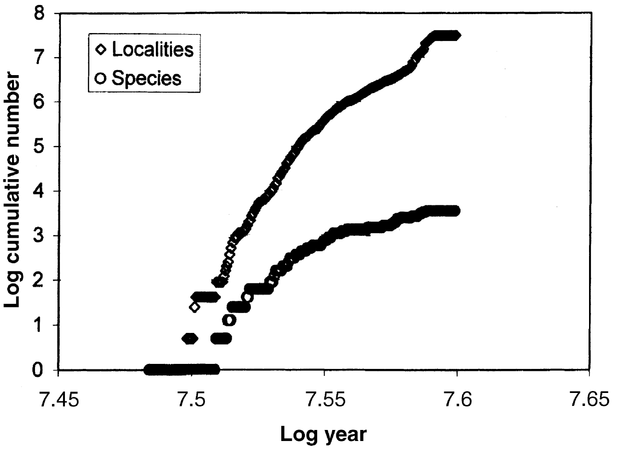

Figure 2 Increase in the cumulative number of *Oenothera* species ($b = 0.018 \pm 0.0009$), and in the total number of localities ($b = 0.038 \pm 0.0012$) reported from the six European countries in the last two centuries. The slopes are significantly different at $P < 0.001$. The stagnation at the end of the invasion curve is an artifact caused by the data for particular countries being available up to different time (depending on date of publication of source data for particular countries, see Table 1).

inevitably influenced by the intensity of floristic research in a given region or country. However, in previous studies no attempts have been made to use a correcting factor on floristic data. As the floristic activity and consequently the amount of data available for analysis largely differ among particular countries and regions (e.g. Rich & Woodruff, 1992), taking this limitation into account and treating it by using some correction factor allows a more exact comparison of the rate of alien species invasion in different countries. We believe that the number of herbarium specimens accumulated within the country is a convenient measure of floristic intensity and represents a synthetic characteristic reflecting both the number of collectors involved, size of the geographical area sampled, and diversity of the local flora.

The present paper deals with a genus very complicated from the taxonomical point of view (see Cleland, 1972; Dietrich, 1977) and makes advantage from the fact that all the data it is based on were collected in the same manner, i.e. by the same monographer. This provided us with an opportunity to conduct a comparative study of congeners of unusually wide range both in terms of taxonomic identity and geographical distribution.

Distribution pattern, habitat preferences and mode of dispersal

Species of *Oenothera* recorded in the six European countries represent relatively variable set of herbaceous life strategies. However, they have ecological features in common: almost all of them prefer open habitats with light, sandy or gravelly, frequently disturbed soils. Such habitats used to be rare in the landscape and are randomly dispersed in space and time. Nevertheless, the frequency of such habitats has been

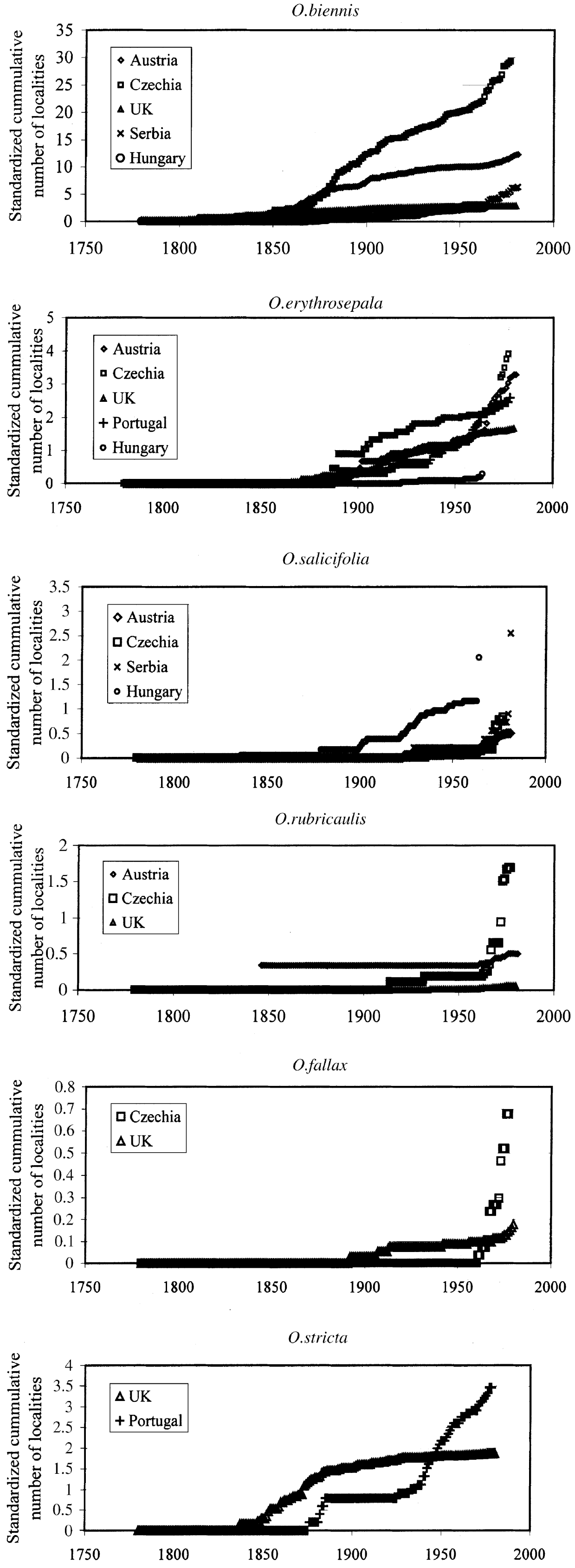

Figure 3 Invasion curves of the most represented *Oenothera* species in particular European countries. Pooled data showing cumulative increase in the number of localities reported from the six analysed countries are used. Only species occurring in more than one country with more than 5 localities are displayed.

increasing because of human activities. The character of habitats preferred by *Oenothera* representatives is further determined by the prevailing mode of seed transport. *Oenothera* seeds seem to have a great potential for long-term dispersal in time (Darlington & Steinbauer, 1961), but lack special adaptation for long distance dispersal (Hall *et al.*, 1988). Therefore it can be supposed that their spread is strongly dependent on human activities rather than on natural dispersal agents (Frean *et al.*, 1997). This corresponds to the pattern of occurrence found in the countries studied. Most of *Oenothera* localities are situated in human-made habitats, on disturbed soils, in industrial sites, along railways and in waste places of various kind, which are occupied by early successional species. Several *Oenothera* species are often planted as ornamentals and they are escapes from cultivation (e.g. *O. missouriensis*, *O. erythrosepala*).

A striking difference in the rate of increase in species numbers and that of their localities in Europe indicates that only few representatives are successful in terms of increasing abundance while the majority of species remain only scattered and rare (Kowarik, 1995). Given similar ecology and habitat preferences of European *Oenothera* species and their common evolutionary history, competitive relationship can be also supposed, at least among biennial species of the subsect *Oenothera*. During the initial phase of invasion, number of localities was increasing at a similar rate as that of newly introduced (or originating) taxa (Fig. 5). Approximately since the beginning of the twentieth century, the few

Table 3 Rate of spread of *Oenothera* species in Europe represented by the six countries studied. Invasion rate was expressed as a value of slope *b* from the regression equation Cumulative number of localities = exp (a + b × year). Pooled data from all countries were used. Slopes with their confidence intervals are given for each species. Slopes that were not significantly different are bearing the same letter. The species are arranged according to decreasing rate of invasion

Species	Slope *b*
O. erythrosepala	0.035 ± 0.0013 a
O. biennis	0.031 ± 0.0008 b
O. stricta	0.026 ± 0.0011 c
O. salicifolia	0.025 ± 0.0008 cdef
O. cambrica	0.024 ± 0.0006 d
O. syrticola	0.021 ± 0.0013 defgh
O. ammophila	0.020 ± 0.0010 g
O. suaveolens	0.020 ± 0.0007 h
O. fallax	0.018 ± 0.0013 gh
O. rubricaulis	0.018 ± 0.0014 degh
O. rosea	0.017 ± 0.0008 i
O. chicaginensis	0.016 ± 0.0020 bc

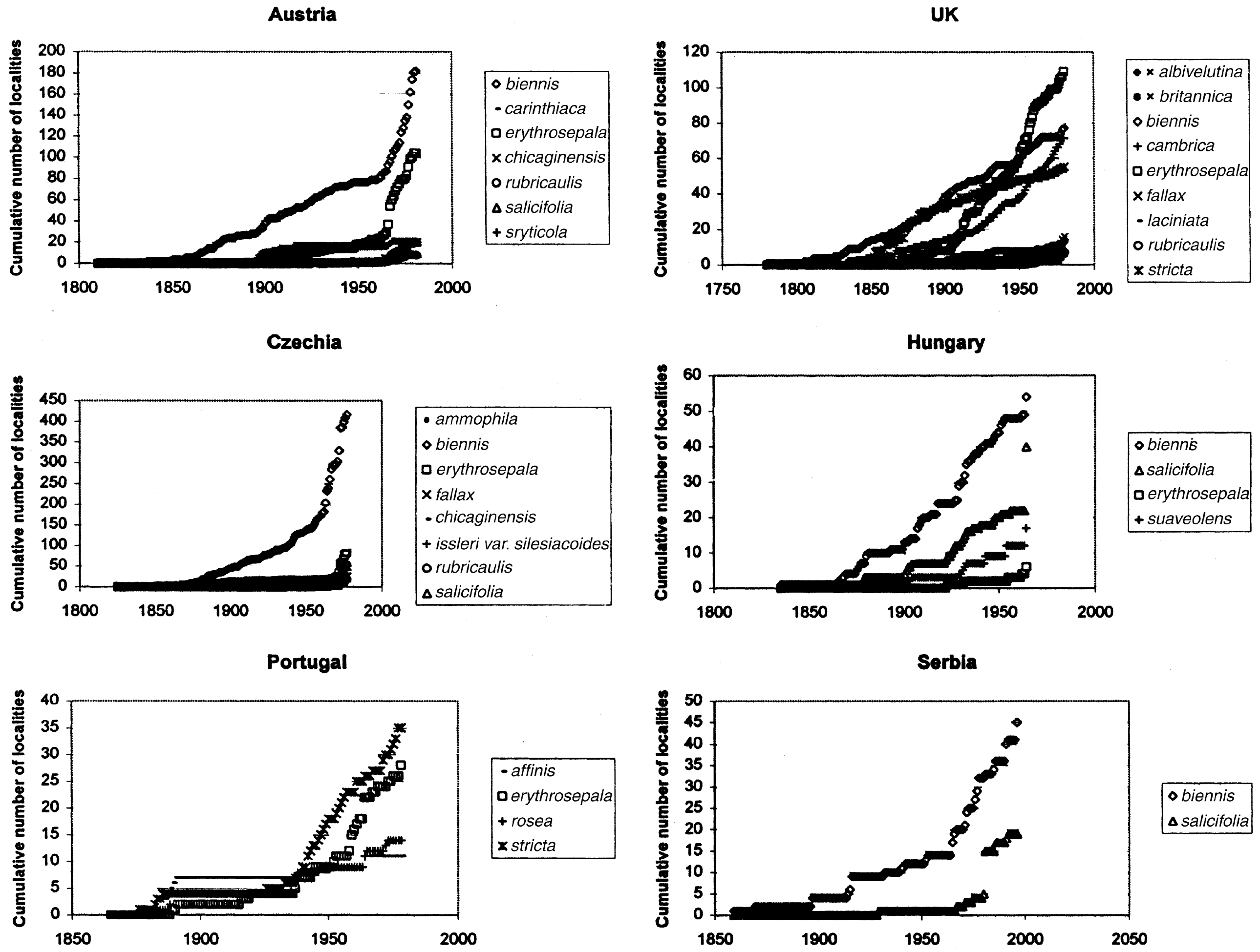

Figure 4 Dynamics of invasion of particular *Oenothera* species shown for individual countries. Increase in the cumulative number of localities over the last two centuries is shown. Only species with more than five localities recorded in the given country are shown. Species are arranged in alphabetical order. See Table 4a for statistical evaluation.

successful species started to increase their abundance and occupy disproportionaly large number of available niches.

Pattern of invasion in Europe

The multivariate analysis has shown that in Europe, there are two distinct groups of species of Central and South American origin, whose invasion is positively correlated with low temperature and higher annual precipitations. Both these climate characteristics represent key features distinguishing between oceanic and inland character of regional climate. One of the groups is represented by species confined to the oceanic regions (e.g. *O. rosea, O. stricta*), which have been reported as successful invaders from another parts of world with similar type of climate (e.g. South Africa – Frean *et al.*, 1997). In these species, perennial or annual life cycle prevails (Dietrich, 1977; Frean *et al.*, 1997). The other group, consisting of biennial representatives of invasive *Oenothera*, seems to be adapted to the inland landscape with lower mean temperature and more balanced monthly precipitations. Another group of species, including namely *O. erythrosepala* and *O. fallax*, seems to represent a transition between those confined to either inland or oceanic climate. In fact, their occurrence is positively correlated with minimum mean monthly precipitations. These species prefer regions with sufficient rainfall, in addition to higher mean temperatures. Positive correlation of this group with the latitudinal gradient appears to be an artifact of specific influence of the Gulf stream, which affects European climate on the global scale. The climate of Balkan Peninsula, with the high maximum mean month temperatures, represented in our data set by Hungary and Serbia is apparently not suitable for invasion of representatives of the genus *Oenothera*.

We showed that the invasion of primrose representatives proceeded at the highest rate in central Europe (Czech Republic, Austria). This can be explained by climatic requirements of *Oenothera* species. Central Europe probably represents the most appropriate climatic region for biennial *Oenothera* species from sect. *Oenothera* subsect. *Oenothera* as it corresponds well to the climate in their primary

Table 4 Rate of spread of *Oenothera* species in the countries considered. Invasion rate was expressed as a value of slope *b* from the regression equation Cumulative number of localities = exp (a + b × year). Slopes with their confidence intervals are given for each species. Slopes that were not significantly different column-wise (real numbers) and row-wise (standardized numbers, see Methods) bear the same letter. Differences in slopes were tested using ANCOVA (Zar, 1984). Slopes referring to the species spreading at highest rate in a given country (a) and to countries in which the given species spreads at a highest rate (b) are shown in bold

Species	Austria	Czechia	Hungary	Portugal	Serbia	UK
(a) Based on the real number of localities						
O. × *albivelutina*						0.016 ± 0.0008 a
O. × *britannica*						0.004 ± 0.0008 b
O. *affinis*				0.018 ± 0.0027 a		
O. *ammophila*		0.022 ± 0.0018 a				
O. *biennis*	0.028 ± 0.0011 a	**0.039 ± 0.0012 b**	**0.030 ± 0.0012 a**		0.023 ± 0.0006 a	0.020 ± 0.0008 g
O. *cambrica*						0.025 ± 0.0007 f
O. *carinthiaca*	0.004 ± 0.0013 b					
O. *chicaginensis*	0.012 ± 0.0016 b	0.028 ± 0.0014 c				
O. *erythrosepala*	**0.029 ± 0.0014 a**	0.008 ± 0.0021 acd	0.026 ± 0.0010 b	**0.032 ± 0.0012 a**		**0.030 ± 0.0013 d**
O. *fallax*		0.011 ± 0.0028 bd				0.012 ± 0.0008 c
O. *isslerii*		0.007 ± 0.0015 e				
O. *laciniata*						0.014 ± 0.0011 a
O. *rosea*				0.021 ± 0.0016 b		
O. *rubricaulis*	0.008 ± 0.0009 c	0.016 ± 0.0021 adf				0.006 ± 0.0009 bc
O. *salicifolia*	0.013 ± 0.0017 b	0.011 ± 0.0019 def	0.012 ± 0.0014 d		0.020 ± 0.0022 b	
O. *stricta*				0.029 ± 0.0018 a		0.026 ± 0.0014 e
O. *suaveolens*			0.022 ± 0.0008 c			
O. *syrticola*	0.025 ± 0.0018 a					
(b) Based on the standardized number of localities						
O. × *albivelutina*						0.001 ± 0.0001
O. × *britannica*						0.0001 ± 0.000008
O. *affinis*				0.008 ± 0.0011		
O. *ammophila*		0.013 ± 0.0013				
O. *biennis*	0.014 ± 0.0007 a	**0.021 ± 0.0011 b**	0.011 ± 0.0003 c		0.014 ± 0.0004 a	0.006 ± 0.0003 d
O. *cambrica*						0.005 ± 0.0001
O. *carinthiaca*	0.0002 ± 0.00008					
O. *chicaginensis*	0.001 ± 0.0002 b	**0.011 ± 0.0006 a**				
O. *erythrosepala*	0.008 ± 0.0005 b	0.001 ± 0.0003 e	0.007 ± 0.0004 c	**0.012 ± 0.0005 a**		0.006 ± 0.0003 d
O. *fallax*		**0.002 ± 0.0005 a**				0.001 ± 0.00005 b
O. *isslerii*		0.001 ± 0.0002				
O. *laciniata*						0.001 ± 0.00007
O. *rosea*				0.008 ± 0.0006		
O. *rubricaulis*	0.002 ± 0.0002 b	**0.003 ± 0.0005 a**				0.0002 ± 0.00003 c
O. *salicifolia*	0.001 ± 0.0002 b	0.001 ± 0.0003 d	0.001 ± 0.0002 c		**0.008 ± 0.0012 a**	
O. *stricta*				**0.012 ± 0.0007 a**		0.007 ± 0.0004 b
O. *suaveolens*			0.004 ± 0.0003			
O. *syrticola*	0.009 ± 0.0006					

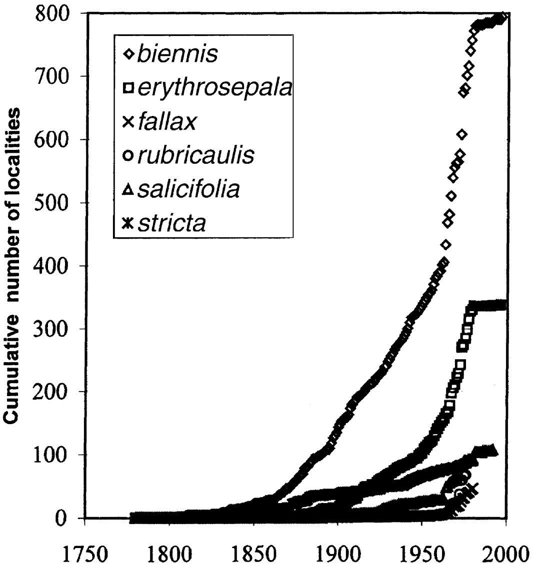

Figure 5 Invasion of selected *Oenothera* species in the countries considered. Only species occurring in more than one country with more than five localities are displayed. Increase in the cumulative number of localities (i.e. the number of records standardized by the floristic intensity expressed by the number of herbarium specimens in the country, see Methods for details) over the last two centuries is shown. See Table 3 for statistical analysis of spreading rates among species in a given country. The stagnation at the end of some invasion curve is an artifact caused by the data for particular countries being available up to different time (depending on date of publication of source data for particular countries, see Table 1).

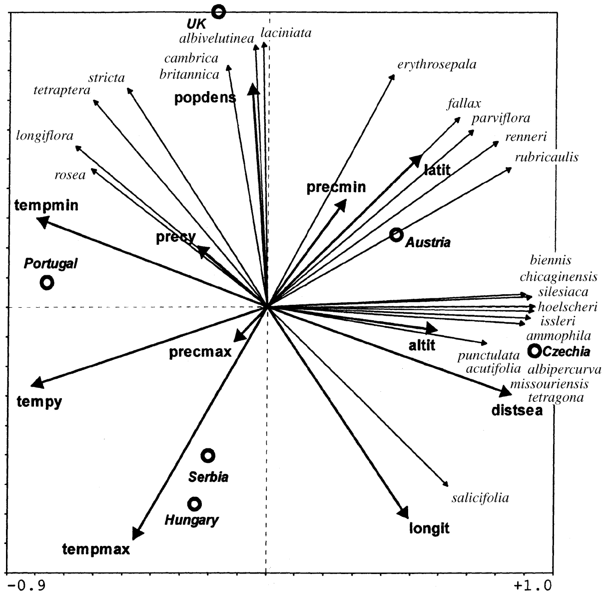

Figure 6 Redundancy analysis ordination diagram (showing first and second ordination axes) displaying the relation of species (thin arrows) and countries (circles) in the primary data set and the correlation pattern of selected environmental characteristics of countries (thick arrows): altit – mean altitude, distsea – distance from the nearest seashore, latit – mean latitude, longit – mean longitude, precmax – maximum mean monthly temperature, precmin – minimum mean monthly precipitation, precy – mean year precipitations, popdens – human population density, tempmax – maximum mean monthly temperature, tempmin – minimum mean monthly temperature, tempy – mean annual temperature.

distribution range. These species are the most successful colonizers of this genus on the global scale (e.g. Dietrich *et al.*, 1997; Frean *et al.*, 1997) and their localities represent major part of total number of localities in central European countries. Conversely, in the countries with oceanic climate with lower rate of increase of *Oenothera* localities these biennial species are not that successful.

The lowest rate of increase of *Oenothera* localities in the UK is probably, at least in part, because of the long and heavy floristic research in this country. High absolute numbers of localities are overridden by an extremely high number of herbarium specimens accumulated in this country.

Remarks on invasion by particular species

Oenothera biennis has been invading most successfully in central Europe (Czech Republic and Austria), and there was a marked acceleration of invasion rate in the 1960s which can be interpreted by increasing building activity, namely in the former country, and creating an array of suitable habitats.

A similar pattern of invasion as in *O. biennis* was found in *O. erythrosepala*, including the sudden acceleration of spreading rate in the 1960s. The main distinction between both species is the better performance of the latter in countries with oceanic climate such as Portugal and UK. The rates of increase of *O. erythrosepala* in these countries are less abrupt than in central Europe but a steady linear increase in the number of localities has been the case since the 1910s.

The invasion of *O. stricta*, a species characteristic of warmer regions with Mediterranean climate, was faster in Portugal than in the UK. The interesting pattern of its invasion curve in the UK (Fig. 5) may reflect a rapid 'saturation of environment' by this species as early as in the second half of the nineteenth century while in Portugal, the invasion has been continuous at a steady rate up to now. This species seems to be tolerant to a relatively wide gradient of ecological conditions within Mediterranean environment. Rostañski (1982) mentions *O. stricta* as a species of maritime sands and various waste places in UK. Frean *et al.* (1997) emphasize the capability of *O. stricta* to invade grasslands, coastal vegetation, fynbos, as well as semidesert areas in South Africa.

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