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Invasiveness of *Oenothera* congeners alien to Europe: Jack of all trades, master of invasion?

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Abstract

The genus *Oenothera* includes a number of species alien to central Europe, which differ in their invasion success. The present study was designed to investigate how fecundity, growth rate of seedlings and competitive ability contribute to the invasion potential within this genus. The relative growth rate and response to interspecific competition from neighbouring vegetation were determined for 15 species. Relations between these characteristics and other species traits identified in previous studies (germination, seed production and seed mass) were examined and used to explain the invasion success of particular species in Europe. Ability to germinate in the light was the only significant predictor of invasion success in six European countries. Fecundity is another trait contributing to invasion success. The most successful invaders within the genus are poor at competing with native vegetation, and an ability to escape from competition seems crucial for invasion success. *Oenothera biennis*, the most successful invader, is not outstanding in any of the characteristics assessed but is well placed in most of them. We suggest that a 'Jack-of-all-trades' strategy may be beneficial for an invader. The parental chromosomes of the species studied had no effect on the distribution of traits; hence the conclusions drawn at the species level are not biased by the specific banding pattern within the genus (permanent translocation heterozygosity). The present study indicates that comparative studies of closely related species may indicate the determinants of invasion success if they include many characteristics of the complete life cycle.

Keywords: Competitive ability; Fecundity; Germination; Growth rate; Invasion success; Seeds

Introduction

Invasions by alien plant species are recognized as a serious threat to global biodiversity, crucially affecting native species and communities (Elton, 1958; Drake et al., 1989; di Castri et al., 1990; Pyšek et al., 1995; Williamson, 1996; McNeely et al., 2001; Chytrý et al., 2005). Attributes of successful invaders and invasible communities have attracted the attention of researchers in the last decade (Crawley, 1987; Noble, 1989; Rejmánek, 1989; Richardson and Bond, 1991; Daehler and Strong, 1993; Rejmánek, 1996; Lonsdale, 1999; Richardson and Pyšek, 2006).

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The invasion potential of alien species has been related to the possession of a particular set of plant traits (Baker, 1974; Bazzaz, 1986; Roy, 1990; Williamson and Fitter, 1996) including life-history, physiological, demographic and genetic characteristics. Such generalizations, often based on correlative studies, unavoidably suffer from many exceptions that limit their predictive ability (Crawley, 1987; Roy, 1990; Thébaud et al., 1996). It is also suggested that the success or failure of alien species depend on their interactions with other species in the plant community (D'Antonio, 1993; Pyšek and Pyšek, 1995; Williamson, 1996). Such a view implies that small differences in biological and ecological traits and their interaction with the environment can critically affect species' invasion success (Thébaud et al., 1996).

Studies on closely related alien species, similar in morphological and ecological characteristics, may be used to evaluate this concept (Pyšek et al., 2003; Pyšek and Richardson, 2007). Key differences in biology of congeners and otherwise related taxa can be revealed by comparative analyses of species with different invasion success, and there is also a potential for predicting future spread and impact of alien species (Forcella and Harvey, 1983; Weber, 1998; Radford and Cousens, 2000; Mihulka and Pyšek, 2001). These differences can be relatively minor but still sufficient to explain the observed pattern of invasion success, as shown for life-history characteristics within *Impatiens* species (Perrins et al., 1993) or regeneration potential within the genus *Reynoutria* (Pyšek et al., 2003). For this reason, comparative studies of closely related species should focus on numerous characteristics of the whole life cycle when attempting to identify those related to invasion success (Radford and Cousens, 2000).

Although there are examples of pairs or groups of congeneric species, introduced into the same region, differing in invasiveness (Baker, 1974; Kruger et al., 1986; Macdonald et al., 1991; Weber, 1998), they have been rarely studied (Weaver, 1984; Forcella et al., 1986; Perrins et al., 1993; Thébaud et al., 1996; Radford and Cousens, 2000; see Pyšek and Richardson, 2007 for a review). The genus *Oenothera* is one of a few alien genera in central Europe that includes species differing in their invasion success, reflected in their current distributions, which range from widespread to rare. Most are biennials, a life cycle well-adapted to the colonization of open, irregularly disturbed habitats (Hart, 1977; Grime, 1979; Silvertown and Lovett Doust, 1993). Population dynamics of these monocarpic species depend crucially on seed production, dispersal and seedling establishment (Kachi and Hirose, 1990). Biennial plants are generally not strong competitors; they must reach a minimum critical size before reproduction (Werner, 1975; Baskin and Baskin, 1979; Gross, 1981; Wesselingh et al., 1994), and the time of reproduction is more closely correlated with size than age (Lacey, 1986).

In the present study we (i) examine relative growth rate and response to interspecific competition from neighbouring vegetation in selected *Oenothera* taxa, and (ii) relate these characteristics and other species traits known from a previous study (germination, seed production and seed mass; Mihulka et al., 2003) to their invasion potential in Europe (as determined by Mihulka and Pyšek, 2001, see below). We hypothesize that higher seed production, faster relative growth rate of seedlings and relative resistance to competition contribute to invasion potential within the genus *Oenothera*.

Study genus

Species of *Oenothera* (Onagraceae) are native to Central, North and South America. Several are naturalized worldwide (Dietrich et al., 1997; Pyšek et al., 2002) and approximately 70 taxa have been reported from Europe; nearly 90% of those belong to the sect. *Oenothera* subsect. *Oenothera* (Rostański, 1982). While European authors recognize numerous species in this subsection, American authors (Dietrich et al., 1997) recognize only *O. biennis* and do not distinguish taxa within this subsection as separate species. In this paper we follow the European approach of the Polish monographer K. Rostański (cf. Jehlík and Rostański, 1979; Rostański, 1982, 1991; Rostański and Forstner, 1982). Most invading species, including those from the subsect. *Oenothera* are biennial. In their native range, most species, biennials in particular, occur in primarily or secondarily open habitats such as old-fields, roadsides, stream sides, arroyos and dunes (Dietrich et al., 1997). Similar habitats are occupied by *Oenothera* species in their invaded range. In Europe, *Oenothera* species differ in their invasion status; the majority are casual aliens, but some are considered naturalized or invasive (Table 6). We follow the criteria of Richardson et al. (2000) and Pyšek et al. (2004): 'casual alien species' do not regularly reproduce in the wild and rely on repeated introduction of propagules, 'naturalized aliens' form self-sustaining populations and reproduce outside cultivation independently of man, and 'invasive aliens' quickly spread over a large geographical area.

Seeds of the biennial species of *Oenothera* require light for germination, and their seedlings grow on a wide range of bare soil types (Gross and Werner, 1982; Kachi and Hirose, 1983; Gross, 1985), whereas those of the perennial species also germinate in the dark (Mihulka et al., 2003). Seed mass has only a temporary effect on seedling size and rosette diameter in *O. biennis*, but soil type generally affects growth rate, final plant size and

Table 1. List of alien *Oenothera* species analyzed in the present study

Taxon	Life form	Origin	Number of populations	Experiments performed	LocNo	Seed production	Seed mass (mg)	*Q*-index
O. ammophila Focke	B	N America?	1	RGR, COMP	27	4,580	0.46	0.944
O. biennis L.	B	N America	7	RGR, COMP	794	15,000	0.587	0.917
O. caespitosa Nutt.	P	N America	1	—	0	227	3.80	−0.766
O. coronifera Renner	B	new European genotype?	1	RGR, COMP	0	52,629	0.39	0.082
O. erythrosepala Borbás	B	N America	5	RGR, COMP	339	22,466	0.34	0.415
O. fallax Renner em. Rostański	B	hybrid genotype *biennis* × *erythrosepala*	2	RGR, COMP	47	19,081	0.53	0.232
O. issleri Rostański	B	hybrid genotype *biennis* × *syrticola*	1	RGR, COMP	15	14,956	0.62	0.886
O. lipsiensis Rostański et Gutte	B	New European genotype?	1	—	0	11,897	0.53	−0.027
O. missouriensis Sims	P	N America	1	COMP	3	177	20.98	−0.647
O. moravica Jehlík et Rostański	B	New European genotype?	1	RGR, COMP	0	6,627	0.54	0.121
O. parviflora L.	B	N America	1	COMP	4	7,481	0.54	0.484
O. pycnocarpa Atkinson et Bartlett	B	N America	3	RGR, COMP	60	32,629	0.39	0.959
O. rosea Ait.	P	Trop and subtrop N, C and S America	1	RGR, COMP	17	8,075	0.06	0.525
O. scabra Krause	A	S America	1	RGR, COMP	0	9,565	0.14	0.414
O. tetragona Roth	P	N America	1	RGR, COMP	1	3,436	0.13	0.288

For each taxon, the following information is given: life form (A, annual; B, biennial; P, perennial), origin (from where it was introduced or where appropriate genotypes are supposed to have originated), and number of populations analyzed (see Table 2 for sampling details). As a measure of invasion in Europe, total number of localities recorded in six European countries (Austria, Czech Republic, Hungary, Portugal, Serbia, UK) is shown (LocNo; taken from Mihulka and Pyšek, 2001). Data on seed production, mass and germination response, expressed as *Q*-index (see text for details), are taken from Mihulka et al. (2003). The experiments conducted are indicated: RGR, seedling growth rate; COMP, interspecific competition. For technical reasons it was not possible to obtain complete data on some species; they are listed here as they were used in analyses of invasion success. Information on the regions of origin was taken from Jehlík and Rostański (1979). For presence/absence of PTH system see Table 6.

reproductive output (Gross and Kromer, 1986). Seed production in species of the genus *Oenothera* is very variable (Table 1). Species from the subsect. *Oenothera* usually have a robust biennial or short-lived perennial habit with stems up to 3 cm in basal diameter and their seed production is many times higher than that of species in other sections of the genus (Dietrich et al., 1997). In unfavourable conditions, such as low water and/or nutrient levels, some may persist in the rosette stage for several years and the length of this period depends on rosette size (Kachi and Hirose, 1983).

Oenothera flowers are insect-pollinated and facultative self-pollinated. Most information is available on *O. biennis*. Hall et al. (1988) reported that an average plant produces 140 capsules, each containing 180 seeds. Seed production per plant ranges from 5000 to 12,000 seeds (Gross, 1980; Hall et al., 1988). Dormant seeds may remain viable in soil for up to 80 years (Darlington and Steinbauer, 1961). Seedlings emerge in summer and a strong tap root is formed during the first year. Acaulescent vegetative rosettes are poor competitors for light (Gross and Werner, 1982). Plants overwinter as either rosette buds or dormant seeds. Critical rosette diameter for flowering the following year is 14 cm (Gross, 1981) and mortality of rosettes in old-fields is low (Gross and Werner, 1982). Maximum root growth occurs in early summer of the second year. Seeds are produced by the end of the second growing season (Hall et al., 1988). Flowering may be delayed by one year, but by the third year all plants have either flowered or died (Gross, 1981). Flowering plants always die after seed set (Gross, 1980), and clonal reproduction has not been reported in *O. biennis* (Hall et al., 1988).

The complicated taxonomy of the genus *Oenothera* partly results from a specific breeding system. Chromosomes of some *Oenothera* species are arranged in a specific pattern of rings, which pass through to later generations without recombination. These species are complete translocation heterozygotes, which breed predominantly true, because of a balanced lethal system, self-pollination and hybridization, and have a high survival rate (Cleland, 1972; Hall et al., 1988). Consequently, there are populations consisting of many different but continuous genotypes, each of which is an inbreeding line (Steiner and Levin, 1977). Each of the two sets of chromosomes of these species produces a distinct and contrasting phenotype. Hybrid vigour seems to be a significant factor in the invasion success of these species (Levin et al., 1972). 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 have this chromosomal pattern (Dietrich et al., 1997).

Material and methods

Seed production

Twenty-eight populations representing 15 *Oenothera* species (Tables 1, 2) were planted in light, sandy soil in the experimental garden of the University of South Bohemia, České Budějovice (48°59′N, 14°36′E). In May 1999, 100 seeds from each population were sown on bare soil. After seedling emergence, some individuals were removed randomly to achieve a density of 10 plants m^{-2}. Plots were weeded but not fertilized or watered during the growing period. In mid-November 2000, five randomly selected mature plants from each population were sampled to estimate seed production. On each plant, all fruits were counted, 10 intact ripe fruits were randomly selected and all seeds in these fruits counted. If the number of fruits borne by a selected plant was less than or equal to 10, all of them were considered. Average seed production for each population was determined as the average number of seeds per fruit multiplied by the number of fruits per plant.

Relative growth rate

In spring and summer 2000, 24 populations of 11 *Oenothera* species were tested for seedling growth (Tables 1, 2). Four species (*O. caespitosa, O. lipsiensis, O. parviflora, O. missouriensis*), each represented by one population, were not considered because of poor germination and high seedling mortality. Ten even-aged seedlings from each population were planted immediately after germination, one per $10 \times 10\,\mathrm{cm}^2$ pot filled with sand. The basic Rorison solution (Hunt et al., 1993) was used as the initial nutrient source. The pots were positioned randomly and incubated in a growth chamber. Light and temperature conditions corresponded to normal field conditions in early summer, when *Oenothera* seedlings grow in the wild (day: 14 h, 25 °C; night: 10 h, 15 °C). Pots were watered every 2 days.

Five seedlings were harvested 7 and 21 days after planting, following the standard method for RGR evaluation (Hunt et al., 1993). The root length was measured with computer programme ROOTARCH (P. Šmilauer, unpubl. data), and the leaf area with Adobe Photoshop™ 5.0 software, using images of seedlings scanned immediately after the harvest. Relative growth rates (RGR) of root elongation (RE) and increase in leaf area (LA) were calculated based on fresh material using the following equations:

$$\mathrm{RGR_{RE}} = [\ln(\mathrm{RE}_2) - \ln(\mathrm{RE}_1)]/(t_2 - t_1),$$

$$\mathrm{RGR_{LA}} = [\ln(\mathrm{LA}_2) - \ln(\mathrm{LA}_1)]/(t_2 - t_1).$$

Table 2. Overview of the populations analyzed and localities and habitats where seeds were collected

Population	Locality	Latitude	Longitude	Habitat
Amm	Prague, Czech Republic	50°05′	14°25′	Gravel site, ruderal place
Bi1	Prague, Czech Republic	50°05′	14°25′	Track, local railway station
Bi2	Zliv, Czech Republic	49°04′	14°22′	Track, local railway station
Bi3	České Budějovice, Czech Republic	48°58′	14°28′	Sandy site, ruderal place
Bi4	Prague, Czech Republic	50°05′	14°25′	Gravel site, ruderal place
Bi5	České Budějovice, Czech Republic	48°58′	14°28′	Waste land, ruderal place
Bi6	Nové Homole, Czech Republic	48°56′	14°24′	Track, local level crossing
Bi7	Prague, Czech Republic	50°05′	14°25′	Ruderal place near river bank
Cae	Prague, Czech Republic	50°05′	14°25′	Ruderal place near garden
Cor	Berlin, Germany	52°31′	13°20′	Waste land near abandoned tracks
Ery1	Plzeň, Czech Republic	49°44′	13°22′	Waste land, ruderal place
Ery2	Vroutek, Czech Republic	50°10′	13°22′	Waste land, ruderal place near garden
Ery3	Zliv, Czech Republic	49°04′	14°22′	Waste land, ruderal place near garden
Ery4	České Budějovice, Czech Republic	48°58′	14°28′	Ruderal place near garden
Ery5	Prague, Czech Republic	50°05′	14°25′	Garden cultivation
Fal1	Rabí, Czech Republic	49°16′	13°37′	Ruderal place near river bank
Fal2	Leipzig, Germany	51°20′	12°23′	Ruderal place near garden
Iss	Zliv, Czech Republic	49°04′	14°22′	Track, local railway station
Lip	Leipzig, Germany	51°20′	12°23′	Ruderal place near garden
Mis	Prague, Czech Republic	50°05′	14°25′	Ruderal place near garden
Mor	Prague, Czech Republic	50°05′	14°25′	Gravel site, ruderal place
Par	Leipzig, Germany	51°20′	12°23′	Ruderal place near garden
Pyc1	Prague, Czech Republic	50°05′	14°25′	Gravel site, ruderal place
Pyc2	Prague, Czech Republic	50°05′	14°25′	Gravel site, ruderal place
Pyc3	Prague, Czech Republic	50°05′	14°25′	Gravel site, ruderal place
Ros	Leipzig, Germany	51°20′	12°23′	Ruderal place near garden
Sca	Leipzig, Germany	51°20′	12°23′	Ruderal place near garden
Tet	Leipzig, Germany	51°20′	12°23′	Ruderal place near garden

Codes for populations are derived from initial letters of species names (see Table 1).

Dry biomass of treated seedlings was not determined as they were too small for accurate measurements.

Competition with neighbouring vegetation

Twenty-six populations of 13 *Oenothera* species (Tables 1, 2) were used in an experiment carried out in the experimental garden during summer 1999 to assess the response of seedlings to competition from neighbouring vegetation. Two species (*O. caespitosa*, *O. lipsiensis*), each represented by one population, were excluded from the analysis due to high seedling mortality.

We used $30 \times 30\,\text{cm}^2$ plots in established, mesotrophic grassland vegetation, dominated by *Crepis biennis*, *Holcus lanatus*, *Vicia cracca*, *Glechoma hederacea*, *Hypericum perforatum*, *Plantago lanceolata*, *Poa pratensis*, *Potentilla reptans*, *Veronica chamaedrys* and *Taraxacum officinale* agg. These were mown three times per year. One week old seedling was planted into the central $5 \times 5\,\text{cm}^2$ part of each plot from which the vegetation was removed prior to planting. Three replicate plots were used for each population. The plots were arranged in a randomized block design. For each population, three control plots of the same size were established with above-ground vegetation completely removed prior to the planting of the seedling in the centre. These plots were maintained without vegetation until late autumn. In all plots, seedlings were regularly watered but not fertilized, during the growing period (from May to October). A design consisting of 2 treatments × 3 replicates × 26 populations was used, giving a total of 156 experimental plots.

For each seedling, the length and width of the biggest leaf were measured 3, 6 and 9 weeks after planting. Idealized 'leaf area' was computed as the product of length and width of the measured leaf.

Data on invasiveness in Europe

Number of localities of the *Oenothera* species reported from six European countries were taken from Mihulka and Pyšek (2001; see primary references therein) and used as the measure of invasiveness, which was related to the information on traits. The data on traits obtained in the present study were supplemented by those from

Mihulka et al. (2003; see next section for details). This enabled us to evaluate the effect of a large set of traits.

Statistical analysis

Competition experiments were analysed using ANOVA with repeated measures. The factors were species, competition and time, and the dependent variables were number of leaves and leaf area.

To characterize the effect of interspecific competition, linear regression models were fitted to the values from final measurements and the slope *b* was used as a measure of the intensity of competition. The number of leaves and leaf area recorded for particular treatment levels were regressed on competition and density levels. Differences in slopes within treatments and densities were tested by analysis of parallelism of regression lines (Zar, 1984). Data were analysed using Statistica 99 software.

We used regression models to evaluate the effect of species traits on invasion success. Number of localities in Europe (LocNo; Table 1)—the response variable—was taken from Mihulka and Pyšek (2001). The following predictors were used: seed production, seed mass (Table 1), percentage germination in the light (GermLight) and in the dark (GermDark), *Q* index (measure of germination preferences based on GermLight and GermDark; Table 1), reduction in leaf area (InterLA) and number (InterLN) as measures of interspecific competition, and $\mathrm{RGR}_{\mathrm{LA}}$, $\mathrm{RGR}_{\mathrm{RE}}$, $\mathrm{RGR}_{\mathrm{TOT}}$, and RGR ratio as measures of growth rate (seed mass and germination characteristics were determined by Mihulka et al., 2003; data on reduction in leaf number by Mihulka, 2001). *Q* index was calculated as Yule's *Q* coefficient (Yule, 1912) expressing the preference for pairs of contrast variables with values range from −1 to 1. Using the Box-Cox method (Crawley, 1993, pp. 220–223), the response variable LocNo was transformed as $(\mathrm{LocNo}+1)^{-0.3}$. The predictor variables were standardized (zero mean, variance one) to achieve, in absolute terms, a comparable influence of their effects. The strength of the effects is not directly comparable unless standardized, because the predictors were measured on different scales.

Multiple regressions, that enabled us to assess the relationships between the response variables and each of the predictors, adjusting for the remaining predictors, were fitted separately for (1) seed characteristics, using the predictors seed production, seed mass and *Q* index, (2) interspecific competition, using the predictors InterLA and InterLN, and (3) growth of seedlings, with predictors $\mathrm{RGR}_{\mathrm{LA}}$, $\mathrm{RGR}_{\mathrm{RE}}$, $\mathrm{RGR}_{\mathrm{TOT}}$ and RGR ratio. The ordinary additive models of multiple regressions, where all the explained variation in the response variable is assumed to be due to the additive effects of the response variable, were applied. Significance of the response variables were adjusted for multiple comparisons by Bonferroni correction. The relationship between the response variable LocNo and the predictors GermDark and GermLight was examined by a multiplicative model of multiple regression, which included the interactive effect of GermDark and GermLight on LocNo (Quinn and Keough, 2002, pp. 130–133). Standardized partial regression slopes were plotted following Quinn and Keough (2002, pp. 123–124).

Models of multiple regressions with significant ($P<0.05$) and marginally significant ($P<0.1$) predictor terms were simplified by deletion tests to determine the minimal adequate models. In these models, all predictors were at least marginally significantly different from zero and from each other, and all non-significant predictors were removed. This was achieved by a stepwise process of model simplification, beginning with the maximal model (containing all predictors), then proceeding by the elimination of non-significant predictors (using deletion tests from the maximal model), and by retention of significant and marginally significant predictors (Crawley, 1993).

The adequacy of transformations was checked by comparing the raw and the transformed data by plotting standardised residuals of the models against fitted values and against explanatory variables, and the ordered residuals against expected order statistics (Crawley, 1993). The homogeneity of variance was checked by Cochran's test (Underwood, 1997). Collinearity in multiple regressions was checked by examining a matrix of correlation coefficients and by assessing tolerance values (Quinn and Keough, 2002, p. 128). Calculations were made in commercial statistical software GLIM 4 (Francis et al., 1994).

The role of parental genotypes

To consider the specific banding of chromosome rings within the genus, we identified combinations of parental genotypes for each species where applicable (Jäger and Werner, 2002) and tested all measured characteristics for correlation with parental genotypes by using two-way ANOVA. In total, 13 parental genotypes were involved in the genetic make up of the 10 species studied, which possessed the PTH mechanism (Table 1). None of the results appeared significant, presumably because of the high heterogeneity of parental chromosomes involved and the fact that very few of the species tested shared the same parental chromosome set. The taxonomically defined species included in this study therefore represent convenient entities for investigating population ecological parameters, and the conclusions drawn at the species level are not biased by the specific banding pattern within the genus.

Results

Seed production

Seed production varied two-fold among the species studied. *Oenothera coronifera* exhibited the highest fecundity while *O. missouriensis* and *O. caespitosa* were the least productive species (Table 1). Of the species represented by more than one population, *O. biennis* and *O. erythrosepala* showed remarkably high among-population variation in seed production: the most productive population of the former species produced approximately 7.5 × more seeds than the least productive and the among-population coefficient of variation (*CV*) was 90.7%. In *O. erythrosepala*, the most fecund populations produced 3.5 × more seeds than the least productive ($CV = 58.9\%$). Conversely, *O. fallax* and *O. pycnocarpa* showed low within-species variation in the seed production ($CV = 29.8$ and 31.4%, respectively).

Relative growth rate

The study species differed in seedling RGR of below-ground and above-ground plant parts, with *O. moravica*, *O. scabra* and *O. pycnotricha* exhibiting the highest values (Table 3). Both growth characteristics were significantly correlated and regression of leaf area RGR on root elongation RGR ($F_{1,9} = 8.73$; $P = 0.016$) explained 49.2% of the variation.

Competition with neighbouring vegetation

Leaf area differed among species ($F_{12,78} = 21.4$; $P<0.001$; repeated measures ANOVA with species identity, competition and time as factors). In general, it was significantly and negatively affected by competition, with the competition effect ($F_{1,78} = 106.4$; $P<0.001$) gradually increasing over time ($F_{2,78} = 541.1$; $P<0.001$).

Leaf area was reduced in plants exposed to competition from neighbouring vegetation. The difference was apparent at 6 weeks and increased during the following 3 weeks (Fig. 1). Based on their response to competition, species can be divided into three groups with competition effect gradually decreasing: (i) *O. coronifera*, a robust biennial with large rosettes and strong competitive effect, (ii) *O. ammophila*, *O. biennis*, *O. erythrosepala*, *O. fallax*, *O. issleri*, *O. moravica*, *O. parviflora* and *O. pycnocarpa* form a consistent group of biennial species taxonomically related to *O. biennis*, and (iii) *O. missouriensis*, *O. rosea*, *O. scabra* and *O. tetragona* represent a group of annual and perennial species with rather small leaves, which show little effect of competition (Fig. 1).

By comparing the growth characteristics of plants competing with neighbouring vegetation with those not subjected to competition, *O. coronifera*, *O. erythrosepala* and *O. biennis* appear to respond most strongly by reduction in leaf area (Table 4).

Relationship between invasiveness and biological attributes

Number of localities in Europe significantly increased with increasing *Q* index, even when the significance was adjusted for multiple comparisons (Fig. 2). The effects of seed production and seed mass, fitted with *Q* index in the same additive multiple linear regression model, were non-significant (Table 5). No other predictor significantly affected the number of localities (statistical details not shown). Percentage germination in the dark and in the light, fitted on the number of localities in a multiplicative model, did not interact significantly (deletion test: $F_{1,12} = 0.47$; $P>0.05$). Holding germination in the light constant, number of localities significantly decreased with

Table 3. Relative growth rate of leaf area (RGR_{LA}) and root elongation (RGR_{RE}) of seedlings of *Oenothera* species, and ratio of both values

Species	n	RGR_{LA}	RGR_{RE}	RGR_{LA}/RGR_{RE}
O. moravica	10	0.190	0.220	0.87
O. scabra	10	0.200	0.185	1.08
O. pycnocarpa	30	0.168	0.202	0.83
O. biennis	70	0.173	0.194	0.89
O. rosea	10	0.197	0.167	1.18
O. fallax	20	0.175	0.182	0.96
O. ammophila	10	0.174	0.178	0.97
O. erythrosepala	50	0.168	0.181	0.93
O. coronifera	10	0.176	0.168	1.05
O. issleri	10	0.164	0.173	0.95
O. tetragona	10	0.122	0.108	1.13

Leaf area was calculated as length × width of the largest leaf. Ten seedlings from each population (Table 2) were used to measure the growth rate N(n) means ± SD are shown. Species are arranged according to the decreasing sum of both RGR values.

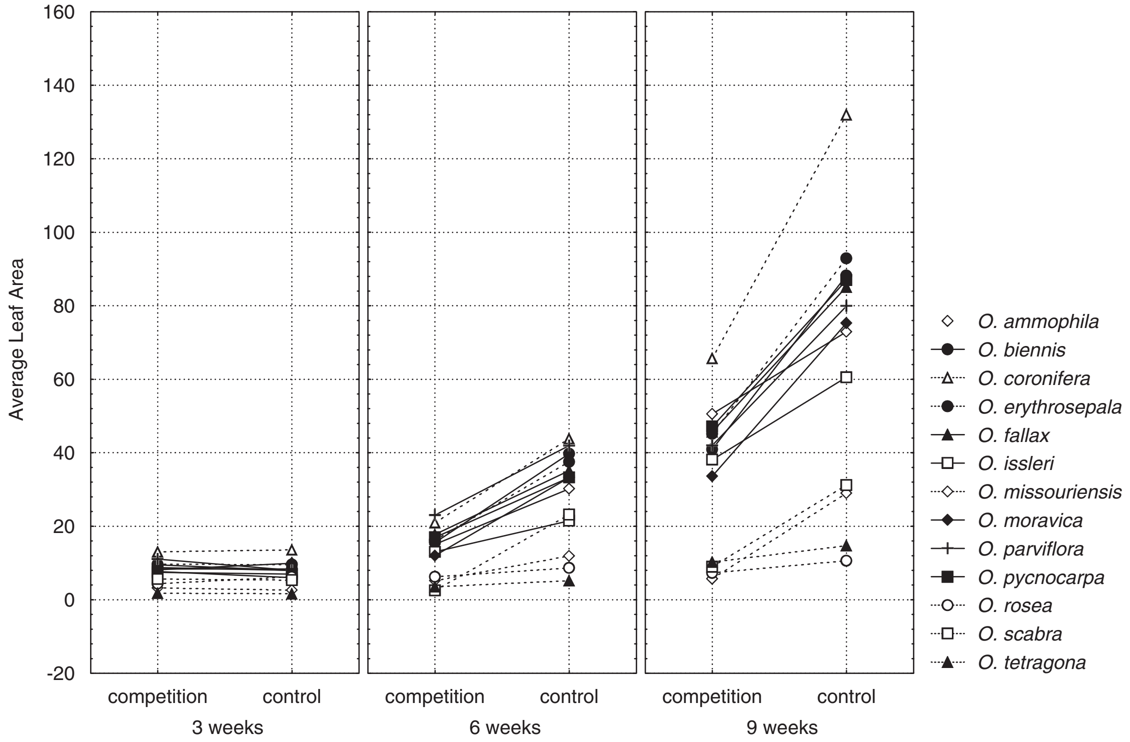

Fig. 1. Effect of competition from neighbouring grassland vegetation on *Oenothera* species. Average leaf area ($n = 3$) of plants in the competition and control treatments for each species at three sampling dates is shown.

Table 4. Effect of competition from neighbouring vegetation measured by the reduction in leaf area

Species	*N*	Slope *b*	
O. coronifera	6	66.2±20.3*	ab
O. erythrosepala	30	47.7±17.0*	abc
O. biennis	42	47.3±10.4*	ab
O. moravica	6	41.7±21.3*	abcd
O. pycnocarpa	18	39.8±18.5*	acd
O. fallax	12	39.4±18.8*	abcd
O. parviflora	6	37.9±39.4	abcde
O. issleri	6	22.4±33.4	abcd
O. ammophila	6	22.4±22.8	a
O. missouriensis	6	23.2±7.2*	ae
O. scabra	6	22.2±14.9*	ade
O. rosea	6	3.3±4.0	ac
O. tetragona	6	4.5±5.3	ae

Number of plants measured is shown for each species (see Methods for details) The effect of competition was described by the value of slope *b* of the linear regression model including two points, representing values obtained at the last measurement, for competition and control. Slopes with their confidence intervals are given for each species. Species are arranged according to the decreasing effect of competition on leaf area. Differences in slopes were tested using ANCOVA (Zar, 1984). Regression slopes significantly different from zero at $\alpha = 0.05$ level, indicating a significant negative effect of competition, are followed by an asterisk. Slopes that were not significantly different between species have the same letter in final column.

germination in the dark, and holding germination in the dark constant, number of localities increased with germination in the light (Fig. 3).

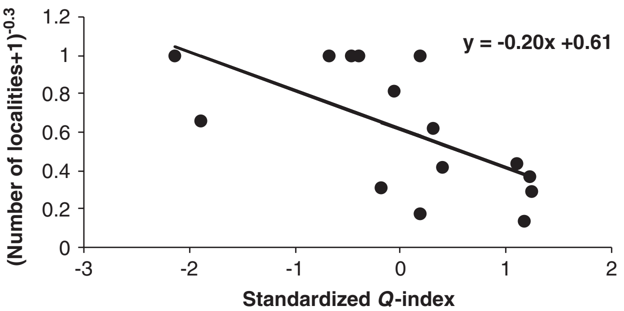

Fig. 2. Minimal adequate model of the relationship between number of localities in six European countries (LocNo) and seed production, seed mass and *Q* index, described by a simple linear regression of $(\text{LocNo}+1)^{-0.3}$ on standardized *Q* index. $F_{1,13} = 8.49$; $P = 0.012$. Five percent level of significance adjusted for multiple comparisons by Bonferroni correction is $P = 0.012$. Note that the negative slope of the transformed LocNo indicates increase in the original scale of untransformed values.

Discussion

Role of species traits and their response to competition

This paper focused on the role that species traits and competitive ability play in determining the success of a number of congeneric species as invaders. Differences in

Table 5. Additive multiple linear regression model of the number of localities for standardized seed characteristics and Q-index

	Estimate	SE	Tolerance	F_s	Explained variance (r^2)
Intercept	0.61	0.066		86.0***	
Seed production	−0.0068	0.070	0.89	0.0095^{ns}	
Seed mass	−0.15	0.085	0.61	3.0^{ns}	
Q-index	−0.29	0.083	0.64	11.9**	0.51

Overall model: $F_{3,11} = 4.09$; $P = 0.03$; $r^2 = 0.53$; df for predictors: 1, 12; ***, $P<0.001$; **, $P<0.01$; $^{\mathrm{ns}}$, not significant. Tolerance values do not indicate collinearity.

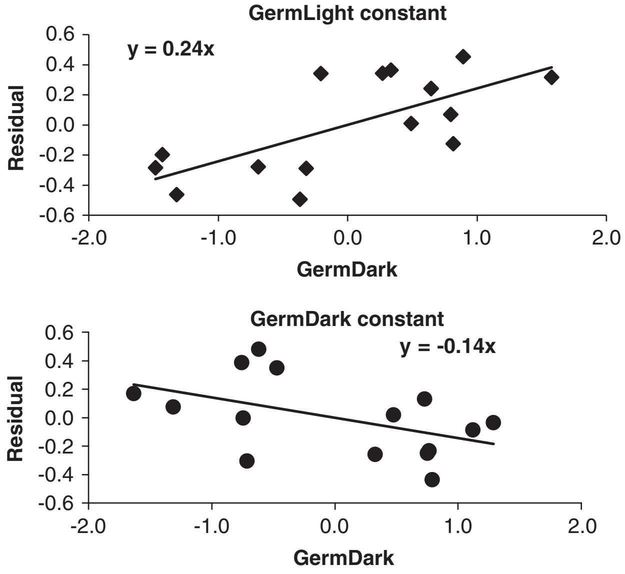

Fig. 3. Minimal adequate model of the relationship between the response variable number of localities in six European countries (LocNo), the predictors percentage germination in the dark (GermDark), light (GermLight), and their interaction (GermDark) × (GermLight). The minimal adequate model is described by the standardized partial regression slope of LocNo on GermDark, holding GermLight constant ($F_{1,13} = 11.0$; $P = 0.0055$), and by the standardized partial regression slope of LocNo on GermLight, holding GermDark constant ($F_{1,13} = 3.83$; $P = 0.072$). The overall significance of the minimal adequate model is $F_{2,12} = 5.84$; $P = 0.017$. Note that the positive slope of the transformed LocNo indicates decrease, and the negative slope increase in the original scale of untransformed values.

the invasion potential of closely related species are thought to be due to differences in their ecology, morphology, life-history or physiology (Roy, 1990; Rejmánek, 1996). Perrins et al. (1993) found that fast germination along with height and shade tolerance were key features in explaining the invasion success of *Impatiens glandulifera* in England compared to *I. capensis* and *I. parviflora*. Thébaud et al. (1996) used minor structural and leaf morphology-related differences to explain differing success of two *Conyza* species. Lonsdale (1994) showed that plant performance, persistence in the field and use as a pasture species were the best predictors of weediness. These examples indicate that in comparative studies of closely related species, it is important to include a broad spectrum of characteristics in order to increase the likelihood of identifying invasive traits (Radford and Cousens, 2000).

The role of competition in the invasion process is still being debated (Crawley, 1987; Willis et al., 2000). It is assumed that interspecific competition, a major force in community dynamics, prevents invasion (Turelli, 1981; Crawley, 1987) and at a small scale, species diversity of resident vegetation increases community resistance to the encroachment of alien species (Tilman, 1999; Shea and Chesson, 2002; Kennedy et al., 2002). Competitive ability together with rapid growth and achene germination in the light were key traits determining invasion success of *Senecio madagascariensis* in Australia (Sindel and Michael, 1992; Radford and Cousens, 2000).

The variation in ecological and morphological characteristics of biennial *Oenothera* species is consistent with their unique cytogenetic features (Cleland, 1972; Dietrich et al., 1997). Competition-related characteristics seem to have varied less in the present study than the germination characteristics determined by Mihulka et al. (2003). However, some species differ substantially in certain traits from the rest of the congeners, such as *O. caespitosa* and *O. missouriensis* in seed production, *O. tetragona* in relative growth rate and *O. coronifera* in response to competition from neighbouring vegetation. Nevertheless, most species are similar in these characteristics or form two distinct groups, e.g. in terms of leaf area organization and response to competition.

Seed production

Seed production is one of the fundamental characteristics distinguishing related rare and common species (Bevill and Louda, 1999) and there is a good evidence that high fecundity and efficient dispersal of seeds promote invasiveness (Richardson et al., 1987; Pyke, 1990; Callaway and Josselyn, 1992; Vila and D’Antonio, 1998; Radford and Cousens, 2000; Perglová et al., 2006; see Pyšek and Richardson, 2007 for review and quantitative assessment). Population dynamics of *Oenothera* species, namely biennial representatives of the subsect. *Oenothera*, are inevitably dependent on seed production and seedling recruitment. Poor invaders, such as *O. caespitosa* or *O. missouriensis*, have remarkably low reproductive outputs while the invasive species (in terms of Richardson et al., 2000), i.e. *O. biennis* and *O. erythrosepala*, exhibit better-than-average seed production. *Oenothera coronifera*, assumed to be a relatively recently evolved microspecies belonging to the *O. erythrosepala* group, is a prolific seed producer. The role of fecundity is further stressed by the fact that in the genus *Oenothera*, there is no special dispersal mechanism; the seeds are released from opening capsules by movement of parental plants caused mostly by wind. Terminal velocity and buoyancy differed little among the species studied (S. Mihulka, unpubl. data) and therefore these variables are unlikely to be related to varying invasiveness.

Relative growth rate

Relative growth rate is often assumed to determine invasion success (Noble, 1989; Roy, 1990; Bazzaz, 1986). A recent review (Pyšek and Richardson, 2007) revealed that in half of eight congeneric pairs, invasive species exhibited a significantly higher seedling growth rate than their native counterparts (Grotkopp et al., 2002; Burns, 2004). In our study, relative growth rate was not a statistically significant predictor of invasion potential at the continental scale. Similarly, Walck et al. (1999) found competitive hierarchies in *Solidago* species to be closely related to plant size, but not to relative growth rate. The values found in *Oenothera* species are rather uniform but distinct groups can be distinguished on the basis of the ratio of above-ground and below-ground RGR. In all biennial species, except *O. coronifera*, the RGR of root elongation was higher than that of leaf area, indicating the allocation of more resources to roots than to photosynthetic structures. The opposite is true for non-biennial species and *O. coronifera*. The strategy of biennial species might contribute to their invasion ability, although we did not find a significant effect of RGR ratio on invasion parameters. However, the statistical power of these analyses was limited by the low number of species for which data were available, which is often the case in comparative ecological studies.

Which factors determine invasion success in the genus *Oenothera*?

The data accumulated in this and previous studies (Mihulka and Pyšek, 2001; Mihulka et al., 2003) allow speculation about the pattern of invasion success within European representatives of *Oenothera*. It must be borne in mind, that species traits based on seeds from populations in the Czech Republic and Germany are used to explain invasion success of species in the whole of Europe. For technical reasons it was not possible to collect seed from all the countries from which the data on the number of localities were obtained (Mihulka and Pyšek, 2001). In the present study, we aimed to sample a range of different habitats to account for the variation in growth characteristics of experimentally grown plants. Also, the plants were grown in optimum conditions in the experimental garden, hence the results may reasonably reflect their growth potential.

Ability to germinate in the light seems to predict invasion success within the genus, and this effect was statistically significant. This response can be considered as an adaptation to disturbed habitats, as species with a high fraction of seeds capable of germinating in response to disturbance and exposure to light, can successfully colonize such habitats. Fecundity, although it did not appear significant in the regression model, is another parameter that seems to separate invasive and naturalized species from casual species (Table 6).

It should be noted that the design of the competition experiments adopted here reflects the fact that *Oenothera* species can only establish themselves if vegetation-free space is available. Removal of vegetation from the immediate neighbourhood of seedlings made the design realistic and reflected the importance of competitive ability of plants with a fugitive strategy. Interestingly, the most successful invaders are poor competitors (Table 4). This holds for *O. biennis* in particular, since this species was among those most severely affected by neighbouring vegetation. These results indicate that in the genus *Oenothera*, low competitiveness of successful invaders is compensated for by high fecundity and a plastic germination response (Table 6). In species with a fugitive strategy, low resistance to competition does not appear to be a constraint to successful invasion. Of the other characteristics, whether a species is cultivated or not, does not seem to be important in determining invasion success (Table 6).

Obviously there are other characteristics that might affect the invasion potential of a species, which were not considered here. For instance range of habitats and their structure in the native distribution area is known to play an important role (Williamson, 1996). Unfortunately, no suitable data are available due to the difference in the central European and American taxonomy of the genus *Oenothera* (Dietrich et al., 1997). On the other hand, the mode of introduction seems to be similar for most species and therefore unimportant as an explanatory variable. Whether the *Oenothera* species studied here are cultivated or not, does not influence their invasion status; both cultivated and accidentally introduced

Table 6. Summary table showing pattern of invasion success within selected European representatives of the genus *Oenothera* and associated attributes

Taxon	InvStat	LocNo	Climatic region	Cult	GermLight	GermDark	Fecundity	RGR	InterComp	Seed mass	PTH	Potential
O. biennis	Invasive	Very high	Temp, cont	No	High	Low	High	High	Low	Medium	Yes	High
O. erythrosepala	Invasive	High	Temp, ocean	Yes	Medium	Low	High	Medium	Low	Medium	Yes	High
O. coronifera	Naturalized	Very small	Temp	No	Medium	Medium	Very high	Medium	Very low	Medium	Yes	High
O. fallax	Naturalized	Medium	Temp, ocean	Yes	High	Medium	High	High	Low	Medium	Yes	Medium
O. pycnocarpa	Naturalized	Medium	Temp, cont	No	High	Low	High	High	Low	Medium	Yes	Medium
O. rosea	Naturalized	Medium	Subtrop, warm, ocean	Yes	High	High	Medium	High	High	Very low	No	Medium
O. ammophila	Casual	Low	Temp, cont	No	High	Low	Medium	High	Medium	Medium	Yes	Medium
O. issleri	Casual	Low	Temp, cont	No	Low	Low	High	Medium	Medium	Medium	Yes	Poor
O. missouriensis	Casual	Low	Temp, cont	Yes	Medium	Medium	Low	—	Medium	Very high	No	Poor
O. moravica	Casual	Low	Temp, cont	No	Medium	Low	Medium	Very high	Low	Medium	Yes	Poor
O. parviflora	Casual	Low	Temp, cont	No	High	High	Medium	—	Low	Medium	Yes	Poor
O. caespitosa	Casual	None	Subtrop, arid	Yes	Low	High	Low	—	—	High	No	Poor
O. lipsiensis	Casual	Very low	Temp, cont	No	Medium	Medium	Medium	—	—	Medium	Yes	Poor
O. scabra	Casual	None	Temp	No	High	High	Medium	Very high	High	Low	No	Poor
O. tetragona	Casual	Very low	Temp	No	High	High	Medium	Low	Low	Low	No	Poor

InvStat, current invasive status in Europe following criteria of Richardson et al. (2000). LocNo, current abundance in Europe. Preferred climatic region is indicated: temp, temperate; cont, continental; ocean, oceanic; subtrop, subtropical. Cult, seed availability in garden stores. GermLight, germination in the light. GermDark, germination in the dark. InterComp, resistence to interspecific competition from neighbouring vegetation. IntraComp, resistence to intraspecific competition. PTH, presence of permanent translocation heterozygosity (Cleland, 1972). The characteristics were evaluated on the basis of the present study and data presented in previous papers (Mihulka and Pyšek, 2001; Mihulka et al., 2003). Potential, prediction of invasive potential for future spread in Europe. Species are arranged according to their invasiveness. Note that information on some attributes is missing for some species.

species occur with comparable frequency among invasive, natural and casual species (Table 6).

The year of introduction is repeatedly identified as an important determinant of the current distribution of alien species (see Pyšek and Jarošík, 2005 for a review) and a previous study found a significant correlation between the number of localities of *Oenothera* species reported for individual European countries and the year of introduction into that country (Mihulka and Pyšek, 2001). Unfortunately, the date of introduction into Europe is not available for six species analysed in the present paper, hence it was not possible to include the year of introduction as a variable in the regression analysis of the number of localities, because the number of species would be too small. It is nevertheless assumed that the current distribution in Europe results from the interplay of invasion potential, determined mostly by germination characteristics of the genus *Oenothera*, and the effect of residence time (Pyšek and Jarošík, 2005).

The summary of analysed species traits (Table 6) allows us to predict that in at least two species, their invasion status (in terms of Richardson et al., 2000; Pyšek et al., 2004) might change in the future. *Oenothera coronifera*, at present a naturalized species but with very few localities in Europe, might be favoured by very high fecundity, although other characteristics are scored medium to low. *Oenothera ammophila*, currently a casual species, germinates rapidly in the light (Mihulka et al., 2003); of species with this characteristic, it is the only one not naturalized yet.

The value of comparative studies increases with the number of species included and the number of traits measured. Our aim was to include traits operating at various stages of the life history, which allows for another interesting conclusion: features of a successful invader in the genus *Oenothera* operate at the very start of the life cycle (germination response), through vegetative growth (competition with other plants) to fruit production. No striking differences were found between *O. biennis*, the most successful invasive species of the genus (Mihulka and Pyšek, 2001) and other species with lower invasion potential. *Oenothera biennis*, the most successful invader, was not found to be superior in any characteristic assessed but is potentially very good in most of them. Unlike other ‘Jacks-of-all-trades’ this species seems to be a ‘master of invasion’.

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