Invasiveness of *Oenothera* congeners in Europe related to seed characteristics

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Abstract

The genus *Oenothera* represents one of a few genera alien to Central Europe comprising a set of species differing in their invasive success, from successful invasion to rare. This study tests the hypothesis that higher seed production, smaller seeds and higher germination rates contribute to invasive potential within the genus *Oenothera*. The study tries to find relations between these species characteristics and their invasive potential and invasion history on a European scale. Measurements and experiments were performed on 15 taxa of this genus representing species of North American origin as well as hybrid taxa which probably originated outside their native range, some of which are invasive. Germination characteristics appear to be more important than pure seed quantity or its weight. In our study, preference for germination in the light was the only significant predictor of invasiveness. Species, which tend to germinate easily in the light, are best invaders.

Introduction

The invasion of alien plant species is recognized as a serious threat to global biodiversity, crucially affecting native species and communities (Drake *et al.* 1989, di Castri *et al.* 1990, Pyšek *et al.* 1995, Williamson 1996, Richardson *et al.* 2000). However, despite growing concern over the negative effects of plant invasion on various scales, we still know surprisingly little about the attributes of successful invaders or what makes a community invasible (Crawley 1987, Noble 1989, Richardson and Bond 1991, Daehler and Strong 1993, Rejmánek 1996, Lonsdale 1999).

The invasion potential of alien species has often been related to their life-history, physiological, demographic and genetic traits (Bazzaz 1986, Roy 1990, Williamson and Fitter 1996). However, such generalizations, mostly based on correlative-like studies, unavoidably suffer many exceptions that decimate their predictive

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ability (Crawley 1987, Roy 1990, Thébaud *et al.* 1996). Recently, it has been concluded that alien species may succeed or fail depending on the context of interactions between the species and the community (D'Antonio 1993, Pyšek and Pyšek 1995, Williamson 1996). Such a view implies that small differences among species in their biology can critically affect their invasion success (Thébaud *et al.* 1996).

Studies focused on groups of closely related alien species, which are generally similar in their morphological and ecological characteristics, have the potential to contribute significantly to this concept. Key differences in the biology of congeners and otherwise related taxa can be revealed by comparative analyses of species with different invasive success, and there is also a potential for prediction of future behavior 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 observed patterns of invasive success (Perrins *et al.* 1993).

Although there are copious examples of pairs or groups of congeneric species introduced into the same regions and differing in their invasive potential (*e.g.* Kruger *et al.* 1986, MacDonald *et al.* 1991, Weber 1998), only a few relevant experimental comparative studies have been conducted (Weaver 1984, Forcella *et al.* 1986, Perrins *et al.* 1993, Thébaud *et al.* 1996, Radford and Cousens 2000). The genus *Oenothera* represents one of a few genera alien to Central Europe whose representatives largely differ in their invasive success, from widespread to rare. Most *Oenothera* are biennials adapted to colonization of open, irregularly disturbed habitats (Hart 1977, Grime 1979, Silvertown and Lovett Doust 1993). Biennial plants often extend their life-history over two growing seasons (Grime 1979) but can also behave as winter annuals in more fertile habitats or as short-lived perennials in infertile habitats (Silvertown 1984, Kachi 1990). Population dynamics of these monocarpic species are substantially affected by seed production, seed dispersal and seedling establishment (Kachi and Hirose 1990) and seed-related characteristics inevitably play key role in their life-histories.

The present study was focused on: (i) examining seed production, seed weight and germination response of 15 selected alien *Oenothera* taxa, and (ii) relating these characteristics to the invasive potential of these species with their invasion history on a European scale. The hypothesis tested was that higher seed production, smaller seeds and higher germination rates contribute to the invasive potential within the genus *Oenothera*.

The study genus

The species of genus *Oenothera* (evening primroses, Onagraceae) are native to Central, North and South Americas. A number of them are now naturalized worldwide (Dietrich *et al.* 1997) and approximately 70 have been reported from Europe, nearly 90% of those belong to the sect. *Oenothera* subsect. *Oenothera* (Rostański 1982).

In their native range, most species of the genus, biennials in particular, occur primarily or secondarily in open habitats such as old fields, roadsides, streamsides, arroyos and dunes (Dietrich *et al.* 1997). Similar habitats are typically invaded by evening primrose in their adventive range (Mihulka and Pyšek 2001).

Chromosomes of some *Oenothera* species are arranged in a specific pattern of rings which are passed through to subsequent generations without recombination. These species are complete translocation heterozygotes which predominantly breed true, because of a balanced lethal system, self-pollination and hybridization with high survival rate (Cleland 1972, Hall *et al.* 1988). Consequently, there are populations consisting of many different, but in fact continuous genotypes, each of which is an inbreeding line (Steiner and Levin 1977). Each of the two sets of chromosomes that constitute these species produces a distinctive and contrasting phenotype. Resulting hybrid vigor 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 with a wide secondary distribution have such a chromosomal pattern (Dietrich *et al.* 1997).

Seeds of biennial evening primroses generally require light to germinate and seedlings establish on a wide range of bare soil types (Gross and Werner 1982, Kachi and Hirose 1983, Gross 1985). In *Oenothera biennis* L., seed weight was found to have only a temporary effect on seedling size and rosette diameter, but soil type affected growth rate, final plant size and reproductive output (Gross and Kromer 1986). Species of the subsect. *Oenothera* usually have robust biennial or short-lived perennial habits with stems up to 3 cm in diameter basally and their seed production is many times higher than other sections of the genus (Dietrich *et al.* 1997). *O. erythrosepala* Borbás may under unfavourable conditions, such as low water and/or nutrient level, persist in the rosette stage for several years, the length of this period being dependent on rosette size (Kachi and Hirose 1983).

Oenothera flowers are insect-pollinated, eventually self-pollinated, producing a capsule type fruit. Ridley (in Hall *et al.* 1988), reported that an average *O. biennis* plant produced 140 capsules, each containing 180 seeds. Data on seed production per plant in *O. biennis* varies between 5,000 and 12,000 seeds (Gross 1980, Hall *et al.* 1988). Dormant seeds of this species can remain viable in soil up to 80 years (Darlington and Steinbauer 1961). Baskin and Baskin (1994) reported that the species has a physiological dormancy, with optimum germination temperature at 30/15ºC and seeds germinated equally well in light and darkness. Germination was independent of seed size (Gross and Kromer 1986). *O. biennis* plants always die after seed set (Gross 1980). No clonal reproduction has been reported for *O. biennis* (Hall *et al.* 1988).

Methods

Seed production

Fifteen selected *Oenothera* species (Table 1) were planted in an experimental garden of the University of South Bohemia, České Budějovice (48º59'N, 14º36'E) in a light, sandy soil. About 100 seeds of each species were sown on bare soil in May 1999. After seedling emergence, some individuals were removed randomly to achieve the density of 10 plants/m^2. Plots were kept weed free and plants were neither fertilised nor watered during growing period. In mid-November 2000, five randomly selected mature plants of each population were sampled to estimate seed pro-

Table 1. List of alien *Oenothera* species included in the present study. For each taxon, the following information is given: origin (i.e. from where it has been introduced or where appropriate genotypes are supposed to originate); life form (A = annual, B = biennial, P = perennial); and summary data from Mihulka and Pyšek (2001): total number of localities recorded in the 6 countries, and invasion rate (expressed as the slope *b* from exponential regression fitted to the cumulative numbers of localities in Europe plotted against time).

Taxon	Author	Life form	Origin	Tot. n. of localities	Inv. rate
O. ammophila	Focke	B	cf. N. America	27	0.020
O. biennis	L.	B	N. America	794	0.031
O. caespitosa	Nutt.	P	N. America	0	0
O. coronifera	Renner	B	new European genotype?	0	0
O. erythrosepala	Borbás	B	N. America	339	0.035
O. fallax	Renner emend. Rostański	B	hybrid genotype *biennis* × *erythrosepala*	47	0.018
O. issleri	Rostański	B	hybrid genotype *biennis* × *syrticola*	15	0.010
O. lipsiensis	Rostański et Gutte	B	new European genotype?	0	0
O. missouriensis	Sims	P	N. America	3	0.008
O. moravica	Jehlík et Rostański	B	new European genotype?	0	0
O. parviflora	L.	B	N. America	4	0.010
O. pycnocarpa	Atkinson et Bartlett	B	N. America	60	0.016
O. rosea	Ait.	P	warm N., C. and S. America	17	0.017
O. scabra	Krause	A	S. America	0	0
O. tetragona	Roth	P	N. America	1	0.005

duction. On each plant, all fruit capsules were counted, 10 intact ripe fruits were randomly selected, and all seeds in these fruit were counted. If the number of fruit borne by the selected plant was less than or equal to ten, 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.

Seed weight and seed germination

Seeds of 15 selected *Oenothera* species were collected in the field from September to October 1999. Nine species were sampled in Czech Republic and 6 in Germany. Mixed samples of freshly matured seeds were collected from each species, seeds were dried for several days at room temperature and then stored over winter in paper bags in the dark in a greenhouse at approximately 5ºC.

Seed weight was determined after winter storage. Because of low weight of individual seeds, they were weighted in random sets of 10. Ten replicates were used for each species and average seed weight calculated.

Germination experiments were performed in spring 2000. Seeds were placed in 90 mm diameter Petri dishes on a single layer of filter paper, wetted with 10 ml of water and subjected to 2 treatments: germination in the light vs. dark under diurnally-fluctuating temperature 30/20ºC. In the light treatment, seeds were incubated in a 14 hr light period and 10 hr dark period (Hendry and Grime 1993). Light conditions were designed to correspond to normal field conditions in May, when these seeds germinate in nature. For the dark treatment, seeds were placed in a paper box. Each treatment consisted of 3 replicate dishes of 50 seeds for each population.

Seeds were incubated in water for 7 days in an incubation chamber. During this period, germination was monitored at 12-hour intervals by counting germinated seeds. A seed with a visible radicle was considered germinated. Monitoring of germination was terminated after one week, a time period proved to be sufficient based on pilot experiments.

Statistical analysis

Yule‘s Q coefficient (Yule 1912) was used to express the preference for the light and dark in the examined species. Q coefficients were computed using average final percentages of germinated vs. non-germinated seeds. The value of the coefficient ranges from –1 to 1, with preferences for a given factor increasing towards the extremes. The following analysis calculated values which were separated into two variables – Qlight which expressed preferences for germination in the light and Qdark which represented preferences for germination in dark.

Significance of relationships between the obtained characteristics (log-transformed seed production, log-transformed seed weight and seed germination) and characteristics related to invasion success of *Oenothera* species were tested using Pearson product-moment correlations (Statistica ’99 software package). Characteristics related to invasiveness were expressed as the rate of invasion (InvRate) and the logarithmically transformed total number of recorded localities in Europe (LogEuroLoc). These characteristics were taken from Mihulka and Pyšek (2001). Significant factors were entered into the model at the $\alpha = 0.05$ significance level.

Principal Component Analysis (PCA) was performed using CANOCO for Windows 4.0 software package (ter Braak 1988) to reveal an overall pattern of seed-related characteristics across all species. Data were log-transformed and fuzzy-coding was used for life-cycle type (annuals, biennials, perennials).

Results

Seed production

Two-fold differences in seed production per plant were found among the species studied. *O. coronifera* Renner, a robust but rare taxon, exhibited highest fecundity while planted and occasionally escaped perennials *O. missouriensis* Sims and *O. caespitosa* Nutt. were the least productive species (Table 2). Most abundant *Oenothera* species (*O. biennis* and *O. erythrosepala*) were among species with the highest production of seeds per plant.

Table 2. Estimated seed production and average seed weight of studied *Oenothera* species. Five plants were sampled for each species. Number of seeds was estimated as the product of the average number of capsules per plant and the average number of seeds per capsule. Means ± S.D. are shown. Species are arranged according to the decreasing fecundity. Ten replicates of 10 seeds were used for each species for estimate of average seed weight.

Species	**Capsules/plant (number)**	**Seeds/capsule (number)**	**Seeds/plant (number)**	**Seed weight (mg)**
O. coronifera	139.6 ± 30.16	377.0 ± 65.83	52629.2 ± 11371.4	0.391
O. pycnocarpa	105.5 ± 32.90	309.3 ± 24.40	32629.6 ± 10230.0	0.386
O. erythrosepala	140.3 ± 70.49	156.2 ± 28.83	22466.3 ± 13220.8	0.341
O. fallax	149.8 ± 45.55	128.0 ± 43.64	19081.5 ± 5684.8	0.527
O. biennis	89.3 ± 57.98	158.0 ± 58.76	15000.8 ± 13601.7	0.577
O. issleri	139.0 ± 87.84	107.6 ± 28.45	14956.4 ± 9452.0	0.622
O. lipsiensis	57.2 ± 17.89	208.0 ± 49.21	11897.6 ± 3722.0	0.526
O. scabra	33.8 ± 8.58	283.0 ± 23.01	9565.4 ± 2429.5	0.141
O. rosea	64.4 ± 14.69	125.4 ± 27.52	8075.8 ± 1842.1	0.064
O. parviflora	59.0 ± 23.63	126.8 ± 16.81	7481.2 ± 2996.6	0.541
O. moravica	55.6 ± 12.97	119.2 ± 11.01	6627.5 ± 1546.4	0.535
O. ammophila	146.8 ± 67.66	31.2 ± 3.83	4580.2 ± 2111.1	0.464
O. tetragona	17.2 ± 6.34	199.8 ± 29.37	3436.6 ± 1266.8	0.127
O. caespitosa	9.8 ± 3.42	23.2 ± 7.56	227.4 ± 79.4	3.805
O. missouriensis	7.2 ± 2.03	24.6 ± 6.58	177.1 ± 74.6	20.985

Seed weight

There are substantial differences of seed weight among the examined species (Table 2). Perennial species *O. missouriensis* and *O. caespitosa* had by far the heaviest seeds of all studied taxa. All biennial species of subsect. *Oenothera* possess seeds of similar shape and weight (about 0.35-0.6 mg per seed). Seeds of perennial *O. tetragona* Roth and annual *O. scabra* Krause weighed about 0.1 mg and the perennial *O. rosea* Ait. had the lightest and smallest seeds.

Seed germination

Final germination percentages varied remarkably between species and treatments (Table 3). Twelve of the 15 species germinated better in the 30/20ºC light treatment. Three species (*O. caespitosa*, *O. lipsiensis* Rostański et Gutte and *O. missouriensis*) achieved higher germination percentage in the 30/20ºC dark treatment. The identical pattern was found as to the species preferences for germination in the light or the dark (Fig. 1).

Relation between seed-related plant traits and invasiveness

Summarizing the pattern of species seed-related characteristics and traits associated with invasiveness by PCA ordination in particular species reveals that invasiveness is correlated with species preferences for germination in light (Fig. 2). The first two ordination axes explain 74.1% of variation in the primary data set (species

Table 3. Final germination percentages for particular species expressed as average value from both light and dark treatments (means and standard errors are shown). Bold value indicates the maximum germination value.

Species	DARK 30/20ºC Mean	SE	LIGHT 30/20ºC Mean	SE
O. ammophila	17.3	1.89	**88.0**	0.00
O. biennis	9.6	7.32	**74.5**	12.68
O. caespitosa	**73.3**	0.00	26.7	0.00
O. coronifera	40.0	9.80	**44.0**	14.97
O. erythrosepala	31.7	32.21	**46.7**	24.97
O. fallax	61.3	30.15	**75.0**	14.59
O. issleri	0.7	0.94	**10.0**	4.32
O. lipsiensis	**48.0**	6.53	46.7	9.98
O. missouriensis	**70.0**	0.00	33.3	4.71
O. moravica	41.3	3.77	**47.3**	0.94
O. parviflora	80.0	3.27	**92.0**	0.00
O. pycnocarpa	7.1	4.82	**73.8**	17.34
O. rosea	81.3	6.80	**93.3**	1.89
O. scabra	82.7	7.54	**92.0**	3.27
O. tetragona	70.7	17.99	**81.3**	4.99

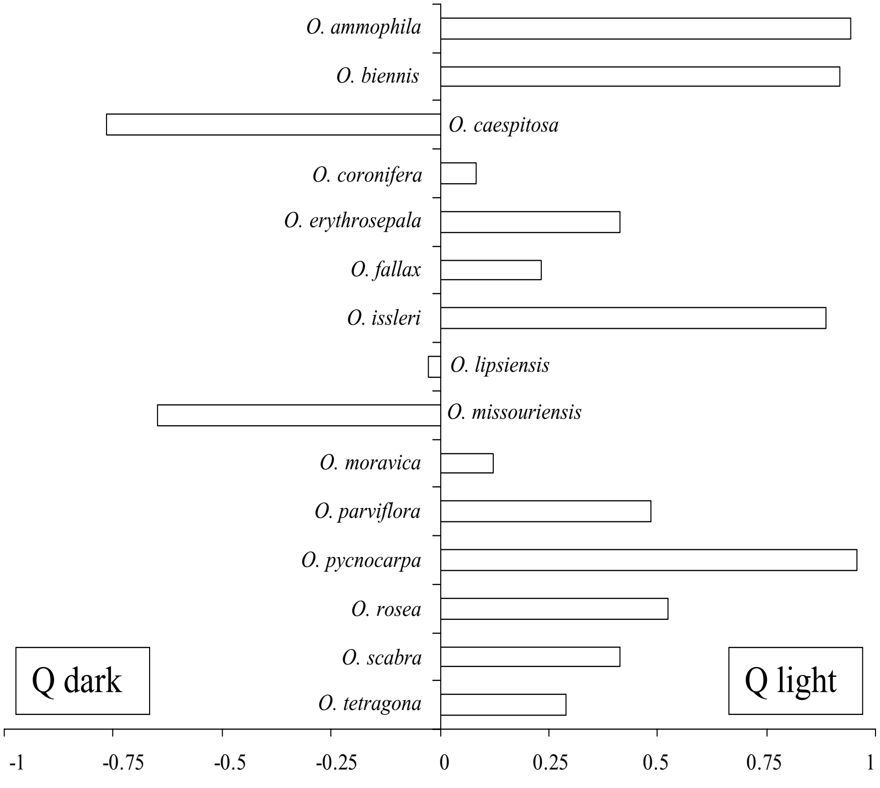

Fig. 1. Preferences of studied population for germination on light vs. dark (expressed as the value of Q index) at 30/20ºC temperature regime. Negative values indicate preference for dark, positive for light.

characteristics). *O. biennis*, *O. erythrosepala*, *O. ammophila* Focke, and *O. pycnocarpa* Atkinson et Bartlett are the most invasive species, measured by the rates of invasion over time and number of localities in six European countries (Mihulka and Pyšek 2001). Other characteristics under study were not correlated with invasiveness. Species with the heaviest seeds, i.e. *O. caespitosa* and *O. missouriensis*, can be considered as representatives of the opposite germination strategy, preferring the dark. The rate of a species' invasion in Europe was significantly positively correlated only with a preference for germination in light (Table 4). The total number of localities recorded in Europe was also positively correlated only with preferences for germination with light.

Comparing particular measured characteristics mutually, increasing seed production was correlated negatively, but seed weight positively with the preference for germination in dark (Table 4). Germination in the dark was further associated with the perennial life form while high seed production was correlated with annual and biennial life form (Fig. 2).

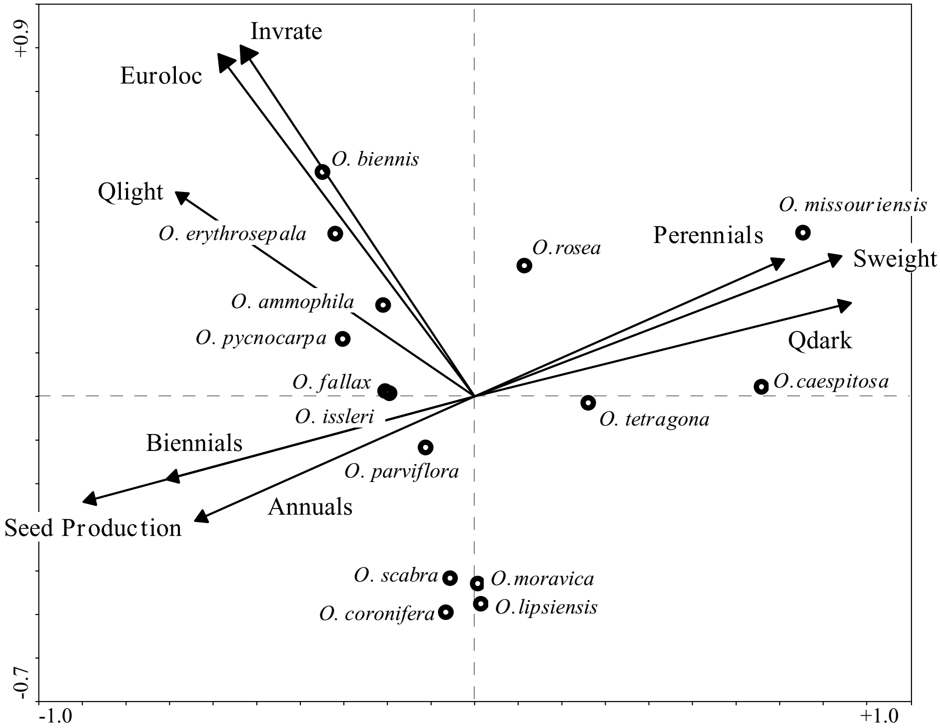

Fig. 2. PCA ordination diagram based on seed-related characteristics (thin arrows) and characteristics related to invasiveness (thick arrows) for 15 selected *Oenothera* species (circles). Euroloc – total number of recorded localities in Europe, Invrate – rate of invasion, Seed production – fecundity, Sweight – seed weight, Qlight – preference for germination in the light, Qdark – preference for germination in dark, Annuals, Biennials, Perennials – dominating type of life cycle expressed as fuzzy variables

Table 4. Correlation between traits related to species' invasiveness and species characteristics. Values of Pearson correlation coefficient are given; number of species analysed n = 15. Bold values indicate significant correlation at $p < 0.05$.

Characteristics	**Seed production**	**Seed weight**	**Pref. for light**	**Pref. for dark**
Invasiveness				
Rate of invasion	0.30	– 0.12	**0.60**	– 0.28
Number of localities	0.35	– 0.14	0.68	– 0.30
Seed-related characteristics				
Seed production	–			
Seed weight	**– 0.72**	–		
Preference for light	0.41	– 0.37	–	
Preference for dark	**– 0.89**	**0.73**	– 0.48	–

Discussion

It has been repeatedly shown that differences in the biology of invasive species, often minor ones, can operate as determinants of their success (Roy 1990, Rejmánek 1996). Comparative studies of closely related species should include as broad a spectrum of their characteristics as possible to identify invasive traits (Radford and Cousens 2000) but among key features, those related to seed production, seed characteristics and germination are most often reported (Forcella *et al.* 1986, Perrins *et al.* 1993). The fact that *Oenothera* includes a number of biennial representatives makes the germination and seed characteristics even more potentially important, since these characteristics are presumed to be key factors directing population dynamics and consequently invasion success of biennial plants (Gross 1984).

Seed production is one fundamental characteristic associated with commonness and rarity (Bevill and Louda 1999) and is often reported among important traits of an "ideal invader" (Noble 1989, Roy 1990). Although in some apparently poor invaders, such as *O. caespitosa* or *O. missouriensis*, reproductive output was remarkably low and in the invasive species (in terms of Richardson *et al.* 2000) *O. biennis* and *O. erythrosepala*, it was above average. Within the whole data set, number of seeds produced did not prove to be a significant predictor of invasive success. The best seed producer was *O. coronifera*, a microspecies belonging to the *O. erythrosepala* group, which is assumed to have originated rather recently and is still rather rare. Negative correlation found between seed production and seed weight indicates that there is a trade-off between these characteristics which makes it difficult to easily relate to the invasion success. Species with the heaviest seeds (*O. missouriensis* and *O. caespitosa*) represent perennial species much less adapted to disturbed habitats. Conversely, the species with the lightest seeds *(O. rosea)*, also a perennial, occurs mostly in less disturbed habitats in warmer regions (Mihulka and Pyšek 2001).

Other characteristics, namely those related to germination appear to be more important for invasiveness than pure seed quantity or its weight. In our study, preference for germination in the light was the only significant predictor of invasiveness. Species, which tend to germinate easily in the light, are best invaders. Dormant seeds of *O. biennis* remain viable buried in the soil for up to 100 years (Darlington and Steinbauer 1961, Baskin and Baskin 1994). As biennial species typically have long-lived seeds (Grime 1979), such longevity can be expected in other biennial representatives of the genus, especially in taxa closely related to *O. biennis*, such as *O. erythrosepala* or *O. fallax* Renner emend. Rostański. The marked germination preference for light, which was correlated with invasiveness, but found only in biennial species (namely *O. biennis*, *O. pycnocarpa* and *O. ammophila*) can have consequences in terms of seed bank formation. A high germination preference for light can be considered as an adaptation for a long-term seed bank, extending germination in time and increasing the species' chance for survival in a new habitat and subsequent establishment and spread.

The invasion of *Oenothera* species seems to be associated with their ability to sense suitable light conditions for germination, and this appears to be more important than the final germination rate (Mihulka and Pyšek 2002). Such a relationship to the light regime can be considered as an adaptation to disturbed habitats, so species with a high fraction of seeds capable of germinating in response to disturbance and exposure to the light, possess a cue for successful spread in such habitats. The most successful *Oenothera* invaders are primarily biennials. Biennial plants solve the problem of mortality risk in the critical period of germination and establishment by delaying flowering and seed production, and becoming a short-lived monocarpic perennial (Grime 1979, van Bremen 1984). Populations of semelparous perennials tend to be volatile, and rely upon a pool of dormant seeds to persist between one disturbance and the next that occurs at the site (Reinartz 1984, Kachi and Hirose 1985, Silvertown and Lovett Doust 1993). The observed patterns of germination response of *Oenothera* biennial species are consistent with the behaviour of other biennial plants with analogous life strategies and annual dormancy cycle (Baskin and Baskin 1994). Moreover, biennials are generally well-adapted to colonization of open, unpredictably disturbed habitats (Hart 1977, Werner 1977, Grime 1979, Gross 1980, Silvertown and Lovett Doust 1993). Most such habitats are under the direct impact of humans, and therefore prone to invasions (Pyšek *et al.* 1998).

This paper involves taxa recognized on the basis of traditional European taxonomy. However, the specific breeding system in the genus (Cleland 1972, Steiner and Levin 1977, Hall *et al.* 1988) opens the possibility to follow the invasive traits beyond the species level, e.g. how they are passed to subsequent generations and therefore to the newly evolving species with specific combinations of chromosome complexes. The present study represents basic information about the relationship between invasiveness and seed-related plant traits, assessed at the species level. Further analysis of present data is needed, taking the specific pattern of evolution of new genotypes within the genus into account.

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