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Comparative study of variously invasive *Oenothera* species
with special emphasis on
phenotypic plasticity of their seedling traits.



COMMON EVENING-PRIMROSE
Oenothera biennis L.
EVENING-PRIMROSE FAMILY

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I honestly declare to have worked out this thesis on my own, with the use of cited references.

Jana Krčmářová

České Budějovice, 24th May 2002

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ABSTRACT

Genus *Oenothera* is one of few alien genera in Central Europe which comprises invasive to rarely occurring species. Since studies on the characteristics distinguishing invaders are thought to be of considerable value for deeper understanding of invasions this genus is a good model for investigating the possible differences in the biology of variously invasive species.

I worked out this study in order to demonstrate that there may be some differences that allow two related species with similar biology and ecology to behave so distinctively in respect to their invasive success.

Williamson (1999) counts in attributes tied with the latter invasive success of a species besides others also the genetic characteristics of a species including the pattern of phenotypic plasticity. In my study I concentrated on this phenomenon, in particular on the sensitivity of morphological and growth-related traits to environmental variables (nutrients levels, light intensity and spectrum, i.e. shading of the neighbouring vegetation). To evaluate the amount of change with the environment I computed an index called phenotypic canalization (PC, an inverse Coefficient of variation of the treatment means, after Milberg 1999) and compared its values in variously invasive species.

Fourteen *Oenothera* taxa were arranged into three groups according to their invasive success, classification being based on number of localities recorded in previous study of Mihulka and Pyšek (2002)

Our hypothesis was that the successful invaders possess more stabilised trait performance, namely in the seedling phase of their life. My results are conformable with this hypothesis.

For some comparisons *Verbascum thapsus* was added, which is sometimes thought of as of the ecological equivalent of *O.biennis*.

1. Introduction

1.1 Invasions

The past decade has seen an explosion of interest in biological invasions, partly because species invasions are enigmatic natural experiments naturally raising academic interest (Thompson et al. 1995) and perhaps more importantly, however, invaders are often claimed to be the second largest threat (globally), after habitat destruction, to biodiversity (Williamson 1999).

A common trend emerging in literature concerning invasive biology is to analyse species characteristics and the predisposition of becoming an invader (Kolar & Lodge 2001). Although some ecologists are sceptical about such approach to predicting plant invasions (Enserink 1999) other studies revealed that some linkage may be detected and that invasive species traits play though partial role in this phenomenon (Sol 2001, Gerlach 2001, Rejmánek and Reichard 2001). Summarised, the actual invasion of an environment by new species is influenced by three factors: the number of propagules entering the new environment (propagule pressure), the characteristics of the new species and the susceptibility of the environment to invasion by the new species (Lonsdale 1999).

Invaded habitat:

Central Europe is a district with long anthropogenic history linked with many habitat disturbances and species range change thanks to the pollution, agricultural practices, urbanization and other threats to biodiversity.

The important role played by disturbances, clearly by eliminating or reducing the cover or vigour of competitors or by increasing resource level (Hobbs 1989, D'Antonio 1993) in facilitating invasions has long been recognised (Elton 1958, Crawley 1987, Lodge 1993) and data exist supporting this view (Hobbs & Atkins 1988; Burke and Grime 1996). Davis et al. (2000) explains such an

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increase in invasibility of a habitat by coherent theory of fluctuating resource availability. The sometimes recorded and emphasised fact that 'r-strategists' are the best invaders has similar basis because the overwhelming majority of plant invasions take place in human and/or naturally disturbed habitats (Rejmánek 1989, Hobbs 1991, Whitmore 1991). Moreover there has been a 'trend' recorded among increasing species in NW Europe to conspicuously inhabit nutrient-rich habitats (Thompson 1994 and Thompson et al. 1995) pointing again on the long human influences in this region.

Invading species:

The attributes of invasive aliens are strongly habitat-dependent (Thompson et al. 1995), which helps to explain the often contradictory nature of lists of predicted attributes of the 'ideal' invader (e.g. Roy 1990).

Majority of species of the alien genus *Oenothera* occurring in Central Europe are representatives of early successional ^{stages} seres such that they are poor competitors for light and they inhabit open and often dry habitats like railway asides, roadside verges, river banks, abandoned fields and sand dunes. Majority of studied species are monocarpic (except *O. rosea* and *O. perennis*) and the persistence of species/population within a plant community depends upon its ability to continually recolonise an area and thus upon distribution and abundance of patches of bare ground therein (Gross and Werner 1982). Their seedling properties correspond with these facts: *Oenothera* species (also *Verbascum thapsus*) possess small elliptical cotyledons and generally oval-elliptical leaves parallel to soil surface. Such a leaf morphology and horizontal habitat of the studied species seedlings thus may decrease their likelihood to establish in denser ground cover types because of the inability of their seedlings to emerge through such cover (Gross and Werner 1982).

1.2 Phenotypic plasticity

Phenotypic plasticity is under genetic control and may be counted as a trait itself, a trait that can be inherited and selected independently of a characteristics it refers to (Bradshaw 1965, Schlichtling and Levin 1986). Phenotypic plasticity- the change of the genotype expression across different environments may buffer against natural selection by partially decoupling genotype and phenotype (Bradshaw 1965, Sultan 1987). It remains uncertain whether an adaptive response when facing heterogenous environment should usually involve a variable(plastic) phenotype or a stable phenotype (Taylor and Aarssen 1988). Natural selection might be expected to favor individuals that experience, on average, the least depression from their maximum potential fitness over the greatest range of suboptimal conditions. Such individuals may be therefore expected to display the least plastic responses to environmental variability in performance characters (e.g. biomass, size) which estimate fitness. Thus phenotypic stability of these characters would be regarded as adaptive, although this may be realised by phenotypic plasticity in other (e.g. physiological) characters which are less direct estimates of fitness (Taylor and Aarssen 1988).

Some experiments have described phenotypic plasticity in invasive/weedy and noninvasive/nonweedy plants (Taylor & Aarsen 1988, Meerts 1995, Williams et al. 1995, Zimmermann 1976) but comparative studies of differently invasive species with emphasis on this characteristics have rarely been carried out (e.g. Weber 1999, Milberg et al. 1999) although understanding the potential of a species for adaptation to new environments through its genetic variation and phenotypic plasticity should contribute to prediction of future spread (Kaufmann and Smouse 2001).

Inspired by the latter mentioned work by Milberg (1999), we conducted this study to test the hypotheses that successful *Oenothera* invaders are more uniform in the seedlings performance along the environmental gradients than native species or less successfull invaders. The comparison was done among alien species of the genus *Oenothera* cooccurring in Central Europe.

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We concentrated on one genus *Oenothera* (*Onagraceae*) to minimize growth form and phylogeny-dependent variability respectively, presupposing that the amount and pattern of plasticity can differ among closely related taxa (Schlichtling 1896).

1.3 Study aims

In my study I asked the following questions (arranged according to their priority level) :

- Are some species able to maintain their trait performance/expression in wider range of conditions? (PC index was used to evaluate the ability to maintain production/expression in our of environments).
- Does the achieved phenotypic canalization correlate with the invasibility, e.g. do the most successful invaders possess the least plastic seedling phenotype?
- Are there some differences between three variously invasive groups, established on basis of previous success of species, in morphometric characteristics (number of leaves, rosette diameter) or in the quantity of shoot and root biomass.
- How do the seedlings of manifold species of the genus *Oenothera* grow under different treatments (shading simulation, nutrient enhancement)?

2 . Materials and methods

2.1 Studied genus

The genus *Oenothera* L. (*Onagraceae*, "evening primroses") is considered to have its origin in Central America, is native to Central, North and South America but it also includes number of species occurring worldwide (Dietrich et al. 1997). From European 70 reported genus representatives nearly 90% belong to the sect. *Oenothera* subsect. *Oenothera* (Rostanski 1982). Species of this subsection usually have sturdy biennial or short perennial habit

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with stems achieving up to 3cm in diameter at the base. Their seed production is many times higher than that of other sections of the genus (Dietrich et al. 1997).

In our study only *O. rosea* stems from South America, whereas majority of studied species are biennial plants from N. America (e.g. *O. biennis*, *O. erythrosepala*, *O. ammophila*) or plants with similar origin but annual (*O. scabra*) or perennial (*O. tetragona*, *O. perennis*) life cycle. Another group that can be distinguished are stable hybrids which originated in Europe from crossing of arriving American species: *O. fallax* Renner em. Rostanski (= *erythrosepala* x *biennis*), *O. ammophila*, *O. moravica*, *O. coronifera*.[†]

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Most species of the genus that are in question in this study occur in primarily or secondarily open habitats like old fields, stream sides, roadsides or dunes (Dietrich et al. 1997) both in their native range and in their secondary range.

Unlike the invasive pattern seen in South Africa region, where the most successful invaders of this genus are perennials like *O. rosea*, which is sometimes called the "weed of almost all tropical and subtropical regions" (Frean et al. 1997) or annuals like *O. stricta* or *O. tetragona*, in Europe these invaders of our studied genus fail to reach similar success in dissemination and establishment and species with this life history occur here very rarely (Mihulka and Pyšek 2001a). Majority of alien representatives of the genus *Oenothera* in Central Europe are biennials. Biennial status of successful *Oenothera* species determines their ecology and consequently invasion success.

Cytogenetic behavior of the genus is unusual. In several species of *Oenothera* (namely the section *Oenothera*) all the chromosomes ($2n=14$, $n=7$) have translocations and during the meiosis they unite to form various numbers of rings (Renner complex). The result of this genetic phenomenon is that paternal and maternal chromosomes are passed through to offspring without mixing and any recombination and that groups of genes and consequently the traits they influence are inherited as a unit. There are populations covering sometimes vast areas consisting of isolated

true-breeding (due to balanced lethal system) self-pollinating heterozygotes (Cleland 1972) and the taxonomical status of such populations is often inevitably unclear (Mihulka and Pyšek 2001b). Most species that became naturalised outside their native range, including species that have achieved a wide secondary distribution, are of such chromosomal pattern (Dietrich et al. 1997).

2.2 Concept of the phenotypic canalization

It is widely accepted that variability (defined as the ability to vary) (Zakharov 1989, 1992; Wagner 1997) results from two antagonistic trends (Palmer 1996): the sources of variation including genetic mutations, environmental effects and developmental errors on one hand and a set of regulatory processes, including buffering and enhancing mechanisms on the other hand.

Canalization was first defined by Waddington (Waddington 1942) as the ability to produce a consistent phenotype in spite of variable genetic and/or environmental features. In parallel, Schmalhausen (Schmalhausen 1949 ^{see} in Debat and David 2001) developed a related concept of "autoregulatory mechanism", i.e. a process that stabilises the morphology against environmental influences and mutations.

Debat and David (~~Debat & David~~ (2001)) provided in their paper definitions from authors dealing with formerly mentioned phenomena, some of them are presented to avoid possible misunderstandings of the used terms:

Canalization

- **Schmalhausen, 1949:** autoregulatory mechanism: "a set of processes historically selected, monitoring developmental path".
- **Thoday, 1953:** developmental flexibility: "an individual organism may be said to possess flexibility either if its genotype is such that it can develop different phenotypes in different environments, each phenotype better adapted than the others to the environment that evokes it, or if its genotype is so balanced that development is buffered against environmental variables and hence apparently the same adaptive phenotype results in a range of environmental conditions".
- **Zakharov, 1992:** Similarity of the expression of the phenotypic character under different conditions of development'
- **Wagner et al., 1997:** 'The suppression of phenotypic variation.'

Plasticity

- **Callahan et al., 1997:** 'The ability of an organism to alter its physiology, morphology or development in response to changes in its environment'.

The latest⁺ review on canalization was done by Gibson and Wagner (2000), who define it simply as 'the reduction in variability of a trait'. They highlighted the difference between genetic and environmental canalization as these two processes are possibly based on different (although potentially overlapping) genetic and developmental systems. In our paper we deal with the environmental canalization defined as the 'insensitivity of a character to environmental factors' (Wagner 1997).

2.3 Coefficient PC

To evaluate variability achieved in chosen characteristics during the experiment or, in other words, the ability to maintain the production in a wide range of environments and compare it easily among the groups, I introduced a coefficient formally called environmental phenotypic canalization (PC, after Stearns 1989, who called it environmental canalization). It is an inverse Coefficient of variation for mean performances of traits in the treatments (computed for the final number of leaves and rosette diameter achieved, for the root and shoot biomass). Thus for each species I obtained four comparable values: *final leaf number PC*, *final rosette diameter PC*, *shoot biomass PC* and *root biomass PC*. Attribute with high PC has small SD relative to the mean of the trait, the trait does not change a lot in various treatments, it has a stabilised performance.

2.4 Studied plant species and measured traits

The study concerns 14 species of the genus *Oenothera* and for some comparisons we included also species *Verbascum thapsus*, which may be counted for a native ecological equivalent of *O. biennis*. Species were selected to comprise both invasive and noninvasive representatives of the genus *Oenothera*. The goal of this selection was to compare the characteristics (including PCs) and the patterns of growth of these so distinctively behaving groups (See **Table 1**).

Table 1. Table of the studied *Oenothera* species. For each species a) the assignment to an invasibility group: E – extremely successful, M – medium successful, U – unsuccessful; taxonomical status; life form: B – biennial plant, P – perennial plant, A – annual plant; and the area of its origin, .

Invasibility	Species	Author	Section	Life form	Origin
E	<i>O. biennis</i>	L.	<i>Oenothera</i>	B	North America
	<i>O. biennis subsp. sulphurea</i>	De Vries	<i>Oenothera</i>	B	North America
E	<i>O. erythrosepala</i>	Borbás	<i>Oenothera</i>	B	North America
M	<i>O. rubricaulis</i>	Klebahn	<i>Oenothera</i>	B	North America
M	<i>O. pycnocarpa</i>	Atkinson et Bartlett	<i>Oenothera</i>	B	North America
M	<i>O. fallax</i>	Renner emend. Rostanski	<i>Oenothera</i>	B	biennis*erythrosepala
M	<i>O. ammophila</i>	Focke	<i>Oenothera</i>	B	cf. North America
M	<i>O. rosea</i>	Ait	<i>Hartmania</i>	P	warm A., C. and S. America
U	<i>O. tetragona</i>	Roth	<i>Kneiffia</i>	P	North America
U	<i>O. moravica</i>	Jehlík et Rostánski	<i>Oenothera</i>	B	cf. New European genotype
U	<i>O. scabra</i>	Krause	<i>Raimania</i>	A	North America
U	<i>O. perennis</i>	L.	<i>Kneiffia</i>	P	North America
U	<i>O. coronifera</i>	Renner	<i>Oenothera</i>	B	cf. new European genotype
	<i>O. stucchii</i>	Soldano	<i>Oenothera</i>	B	North America

b) locality and population labelling, which is used in figures later is shown.

Species	Locality	Population labelling
<i>O. biennis</i>	Hluboká- riverbank	OBIENIS1
	Prague- railway station	OBIENIS2
	Zliv- railway station	OBIENIS3
<i>O. biennis subsp. Sulphurea</i>	České Budejovice, Sádka garden	SULPHUREA
<i>O. erythrosepala</i>	Kladno- abandoned garden	ERYTHRO1
	České Budejovice- Stromovka	ERYTHRO2
<i>O. rubricaulis</i>	Kladno- railroad	RUBRICAU
<i>O. pycnocarpa</i>	Prague, Pruhonice- garden	PYCNOCAR
<i>O. fallax</i>	Prague, Pruhonice- garden	FALLAX1
	Horazdovice- riverbank	FALLAX2
<i>O. ammophila</i>	Prague, Pruhonice- garden	AMMOPHIL
<i>O. rosea</i>	Leipzig(Germany)	ROSEA
<i>O. tetragona</i>	Prague, Troja	TETRAGON
<i>O. moravica</i>	Prague, Pruhonice- garden	MORAVICA
<i>O. scabra</i>	České Budejovice, Sádka garden	SCABRA
<i>O. perennis</i>	Prague, Troja- botanic garden	MINUTISS
<i>O. coronifera</i>	Berlin- railroad (Germany)	CORONIFE
<i>O. stucchii</i>	Livorno- motorway (Italy)	OENOTHER

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There is awareness among plant ecologists enregistered that events which occur during the juvenile stage of the life history of plants are the primary determinants of the distribution of the adults (e.g. Grubb 1977, Harper 1977, Grime 1979) i.e. also of the invasive success, therefore we studied the seedlings characteristics.

(status) (success?)
2.5 Invasibility groups

Number of localities	Invasibility group
< 10	unsuccessful
10 - 100	medium
>100	extreme

Table 2. Classification of the species.

The important aim of this study was to point out possible differences between variously invasive species of the genus *Oenothera*. With respect to the known number of localities

recorded from 6 selected European countries (Mihulka&Pyšek 2001b), the species were arranged (see **Table 2**) into three groups according to their up to now recorded invasive success(see **Table 3**).

Species	Number of localities recorded*	Invasibility(group) <i>status?</i>
<i>O. biennis</i> (3populations)	794	extreme
<i>O. erythrosepala</i> (2populations)	339	extreme
<i>O. rubricaulis</i>	68	medium
<i>O. pycnocarpa</i>	60	medium
<i>O. fallax</i> (2 populations)	47	medium
<i>O. ammophila</i>	27	medium
<i>O. rosea</i>	17	medium
<i>O. tetragona</i>	1	unsuccessful
<i>O. moravica</i>	0	unsuccessful
<i>O. scabra</i>	0	unsuccessful
<i>O. perennis</i>	0	unsuccessful
<i>O. coronifera</i>	0	unsuccessful
<i>O. stucchii</i>	No data available	
<i>O. biennis subsp sulphurea</i>	No data available	

*data obtained from formerly mentioned study Mihulka & Pyšek 2001b

Table 3. Species assignment to three variously invasive groups.

2.6 The experiment arrangement

Seeds of nineteen plant populations representing 14 *Oenothera* taxa and *Verbascum thapsus* were obtained from formerly done experiment (Příkaldě ...) which took place in the experimental garden of the University of South Bohemia, České Budějovice (48°59'N, 14°36') in years 1999-2000.

The seeds were sown on dump sand into Petri dishes and watered sufficiently.

The experiment took place in autumn 2001 in formerly mentioned university experimental garden.

Cca 7 days after emergence 5 seedlings of each species were assigned to each of four treatments. The substrate in each pot consisted of sand and peat-based substrate in rate 5:1. The four treatments consisted of growing under green plastic (simulation of shading by neighbouring plants), two levels of nutrients and control without shading and without enhanced nutrient level. In enhanced nutrients treatments a common fertilizer was used (Univerzální tyčinkové hnojivo, Greenworld) which supplies the plants with elementary and tracer nutrients for a four to six weeks time period. It contains 10% of total nitrogen, 5% of total phosphorus in form of P_2O_5 ; 7% of potassium dissolving in water as K_2O and 2% of magnesium in form of MgO .

The 380 pots were set up in a greenhouse; day and night temperature was about $20^{\circ}C$ and $15^{\circ}C$ respectively. The pots were watered once in 3 days to avoid wilting. No additional fertilizer was used during the experiment.

In the beginning every three days and than, after six initiatory measurements when the rate of growing decelerated, every six days fundamental morphological characteristic were measured. Data on the number of leaves bigger than 0,5cm and the length of two biggest (in order to estimate the extensiveness of the rosette) were collected. The plants were harvested after cessation of the experiment (11 measurements, 46 days). The above- and under-ground biomass was parted and weighted separately.

2.7 Data analysis

Data were treated and analysed with program Statistica 5.1 for Windows. PC indexes were computed in Microsoft Excell. Grafical parts were done partly in the Statistica 5.1 for Windows and in Microsoft Excell 97. Final redundancy analysis (RDA) was done using software package CANOCO for Windows, version 4 (Ter Braak and Šmilauer 1998).

All data were \log_{10} -transformed prior to the analyses to achieve normal distribution and homoscedasticity.

One-way analyses of variance (ANOVA) with treatment as the main effect were performed for each character of each species to investigate their response on given treatments. A significant treatment term indicates that the character in question is plastic.

Two-way ANOVA with species and treatment as the main factors was done to find out if the species vary in their performance and plasticities.

Two-way ANOVA with invasibility group and treatment as the main factors was done to evaluate the average performance of variously invasive groups and plastic responses.

Two-way ANOVA with repeated measurements was done to find possible differences in growth among species (factors: species, treatment and time) and invasive groups (factors: invasibility groups, treatment and time).

One-way ANOVA with invasibility group as the main factor was done to find differences between computed phenotypic canalizations (PCs).

For 'post hoc comparisons' Tukey honest significant difference (HSD) test was used.

3. Results

3.1 Morphological traits

3.1.1. Overall differences

□ Species level

Effect	Species		Treatment		Interaction term	
	F	p	F	p	F	p
final number of leaves	38.51	<< 0.001	77.61	<< 0.001	2.67	<< 0.001
final rosette diameter	76.87	<< 0.001	56.66	<< 0.001	1.84	< 0.001
shoot biomass	40.36	<< 0.001	75.21	<< 0.001	3.21	<< 0.001
root biomass	40.95	<< 0.001	17.26	<< 0.001	1.78	< 0.01

Table 3.1, Two-way ANOVA with species and treatment as the main factors. F-values and the achieved level of significance are shown.

There was found a variance in all measured characteristics both among the species (see **Figure 1**) and among treatments (**Figure 2**). The interaction term was also significant, standing for differences among species for their plastic responses.

Characteristics usually achieved greatest values in fertilised treatments irrespectively of the dosage of the fertiliser (Tukey unsign.), exception was the root biomass, which was greatest in the semi-fertilised treatment. The smallest values of all characters were found in the unfertilised treatments which did not differ between themselves (Tukey unsign.).

The final number of leaves was found to be greatest in *O. rosea* due to its distinctive pattern of growth– forming of alternative rosettes. The lowest number of leaves had *Verbascum thapsus*. Both species differed in the leaf number from all the others (Tukey sign.).

O. tetragona was found to have the grandest rosette while *O. perennis* the smallest (this species was in particular different in this character than other species, Tukey).

The biggest shoot biomass and root biomass was found in one population of *O. erythrosepala* (České Budějovice, Stromovka park), both formerly mentioned characters were smallest in *O. perennis*.

Variances of measured traits in studied species

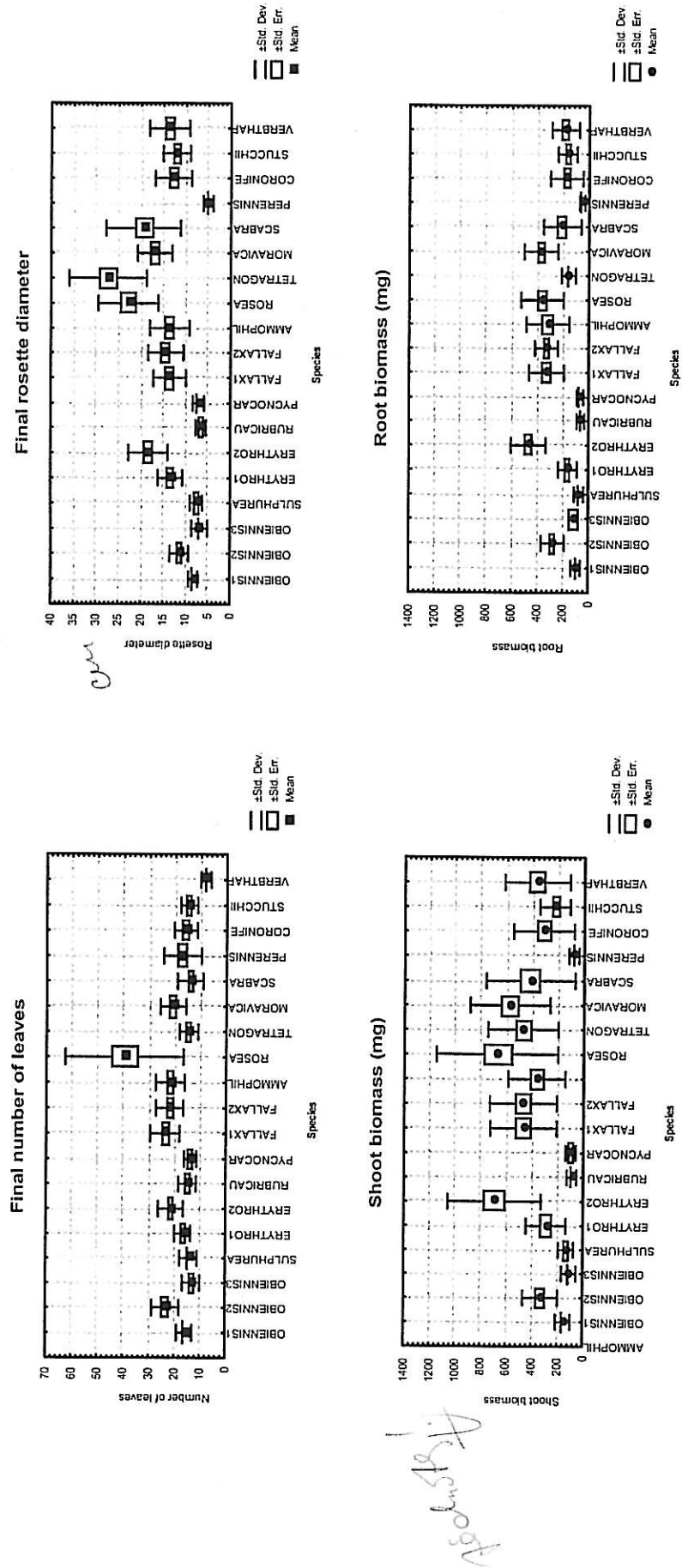


Figure 1. Differences among species in measured characteristics. The species are arranged from the most successful invaders to the least successful invaders. Mean, standard error of mean and standard deviation is shown.

leaf abiotic body + SD

Variability of the chosen characteristics among treatments

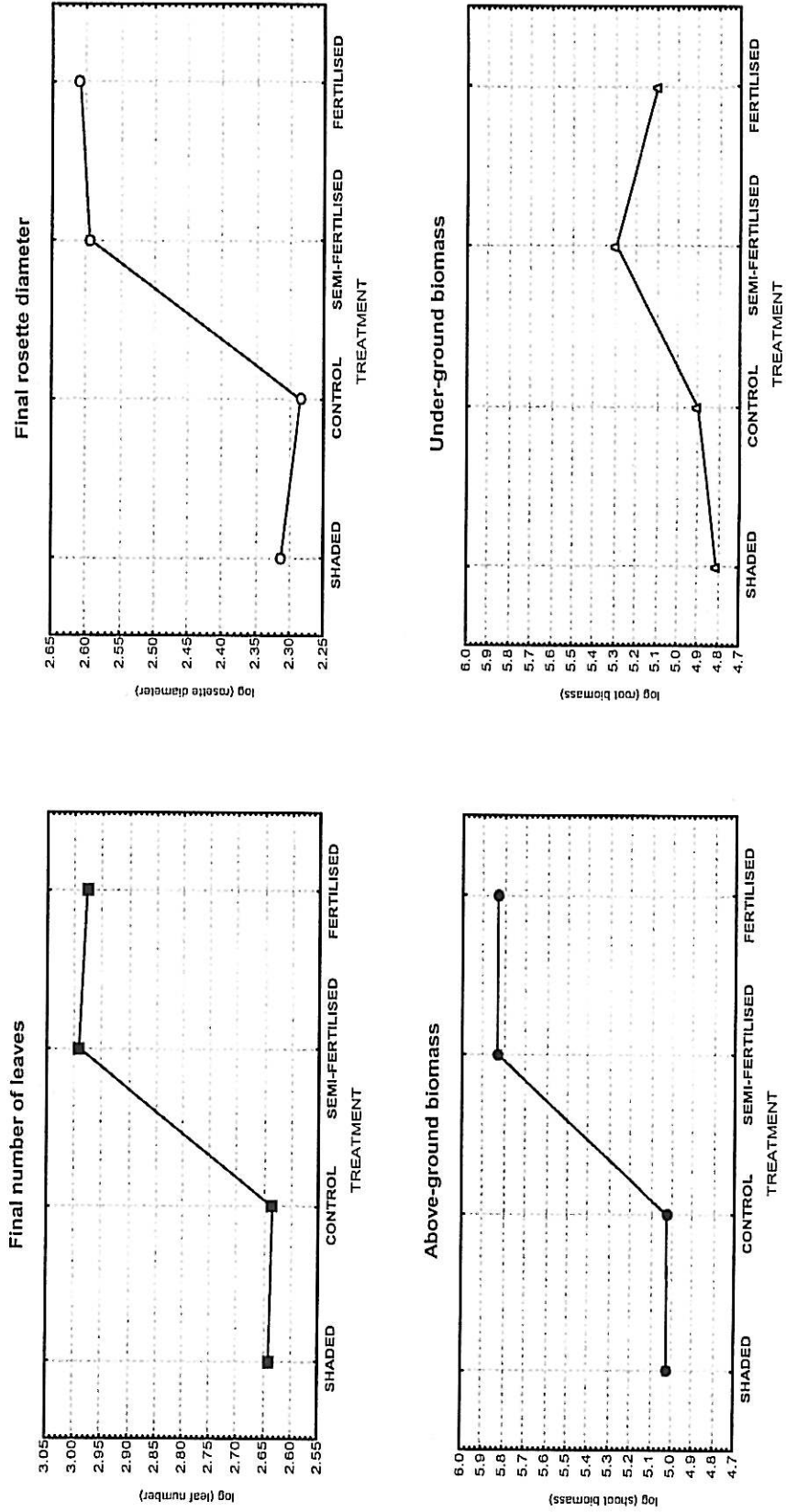


Figure 2. Influence of our chosen treatments on the measured characteristics.

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□ **Group level**

Because we don't have any comparable records (number of localities) for *Verbascum thapsus*, *Oenothera biennis* subsp. *sulphurea* and *O. stucchii* we had to exclude these three from following comparisons concerning the variously invasive groups.

Effect	Invasibility group		Treatment		Interaction term	
	F	p	F	p	F	p
leaf number	16.50	<< 0.001	28.35	<< 0.001	1.52	0.172
rosette diameter	5.30	< 0.01	9.03	<< 0.001	0.80	0.569
shoot biomass	0.10	0.905	23.69	< 0.001	0.88	0.510
root biomass	2.01	0.136	4.37	< 0.01	0.85	0.533

Table 5. Results from the two-way ANOVA with invasibility group and treatment as the main factors. F values and the achieved levels of significance are shown.

The three variously invasive groups (See **Table 5, Figure 3**) significantly differed in the number of leaves and the rosette diameter. Above- and under-ground biomass were similar in all three groups.

There were found differences in all measured characteristics among treatments.

The interaction terms were not significant, signifying that the groups did not differ for their responses.

Significantly greatest number of leaves was found in the group of medium invaders, unsuccessful and extremely successful invaders achieved smaller final number of leaves and were similar in this respect (Tukey unsign.).

The rosette diameter was greatest in the unsuccessful invaders. The extremely successful group had significantly smaller rosette diameter (Tukey, $p < 0,01$) whereas medium achieved intermediate values and did not differ neither from extremely successful nor from the unsuccessful group (Tukey unsign.).

The shoot and root biomasses were similar in all three groups.

Traits of differently invasive groups under various treatments

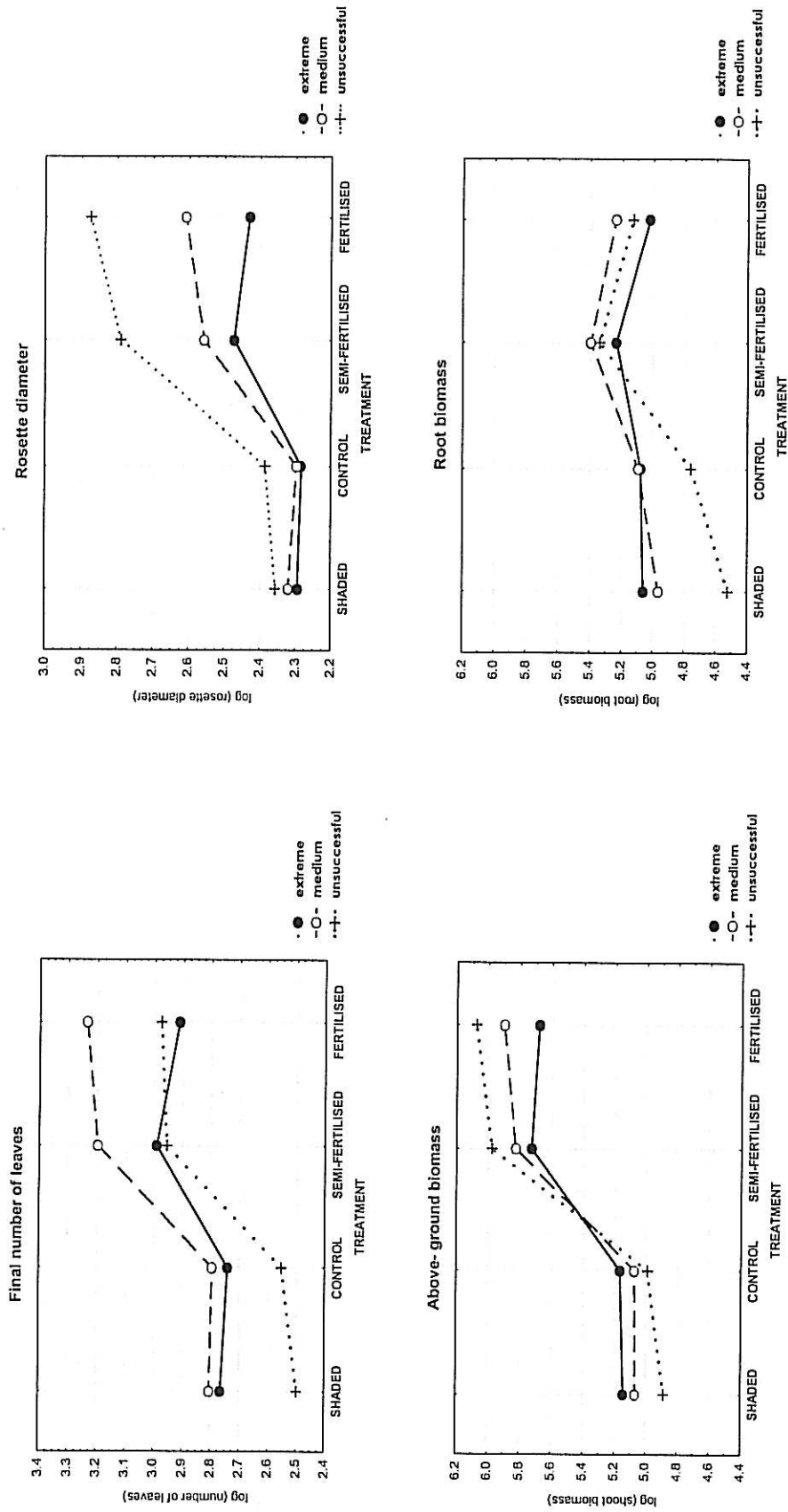


Figure 3.. Reaction norms of variously invasive groups.

3.1.2. Shading and nutrients

Because we actually put the plants through two experiments: shading and nutrient enhancement, I also divided the analysis in order to say how the species/invasibility groups responded to shading and to nutrient enhancement separately.

3.1.2.a Response on shading

□ **Species level**

Results from the one-way ANOVA with treatment effect are compressed in the **Table 6** displaying the variability of chosen traits and also the achieved levels of significance.

In general nothing happened with the selected seedling characters under the shade of a green plastic, the response on shading was not different to the response to non-shading. Exceptions were rare: *O. rubricaulis* increased its number of leaves ($F=7.34$, $p < 0.05$)

□ **Group level**

Effect	Invasibility		Treatment		Interaction term	
	F	p	F	p	F	p
leaf number	0.04	0.850	18.47	<< 0.001	0.36	0.698
rosette diameter	0.45	0.640	0.00	0.985	0.05	0.954
shoot biomass	1.23	0.297	0.16	0.691	0.07	0.928
root biomass	2.007521	0.13607499	4.70	< 0.05	0.25	0.782

Table 7.
Response of variously invasive groups on shading.

There was no difference in the response on shading among the three variously invasive groups (see **Table 7**)

3.1.2 b Response to the nutrient enhancement

The measured characteristics were globally more sensitive to nutrient adding than to the shade simulation.

Variability of chosen characteristics in response to shading

Species	Locality	Number of leaves		Rosette diameter		Shoot biomass		Root biomass	
		F	p response	F	p response	F	p response	F	p response
<i>O. biennis</i>	Hluboká- riverbank	0.10	0.755	0.04	0.845	1.23	0.300 decrease	2.80	0.133 decrease
	Prague- railway station	0.16	0.697	0.31	0.591	0.11	0.744	0.72	0.421 decrease
	Zliv- railway station	0.40	0.545	0.15	0.713	0.01	0.916	1.51	0.254 increase
<i>O. erythrosepala</i>	Kladno- abandoned garden	0.60	0.462 increase	0.95	0.359 increase	0.07	0.802	0.38	0.554
	Č. Budejovice- Stromovka	0.14	0.716	0.02	0.886	0.03	0.866	0.38	0.556
<i>O. rubricaulis</i>	Kladno- railroad	7.34	0.027 increase	2.00	0.195 increase	1.20	0.306 increase	0.08	0.784
<i>O. pycnocarpa</i>	Prague, Pruhonic- garden	0.09	0.776	0.40	0.544	0.01	0.938	1.13	0.318 decrease
<i>O. fallax</i>	Prague, Pruhonic- garden	0.07	0.801	0.06	0.810	0.21	0.662	2.13	0.182 decrease
	Horazdovice- riverbank	0.09	0.777	0.42	0.533	0.01	0.918	0.08	0.787
<i>O. ammophila</i>	Prague, Pruhonic- garden	0.02	0.879	0.03	0.871	0.21	0.658	0.58	0.468 decrease
<i>O. rosea</i>	Leipzig(Germany)	0.42	0.533	0.09	0.776	0.10	0.762	0.04	0.838
<i>O. tetragona</i>	Prague, Troja	0.12	0.737	0.01	0.940	0.00	0.998	0.27	0.616
<i>O. moravica</i>	Prague, Pruhonic- garden	0.30	0.601	0.02	0.886	0.04	0.851	0.52	0.490 decrease
<i>O. scabra</i>	Č. Budejovice, Sádka garden	0.06	0.809	0.05	0.836	0.06	0.818	0.57	0.472 decrease
<i>O. perennis</i>	Prague, Troja- botanic garden	1.78	0.231 decrease	1.24	0.307 decrease	1.35	0.290 decrease	4.18	0.087 decrease
<i>O. coronifera</i>	Berlin- railroad (Germany)	0.33	0.589	0.32	0.590	0.09	0.772	0.00	0.963
<i>O. stuccii</i>	Livorno- motorway (Italy)	1.99	0.196 increase	2.47	0.155 increase	1.48	0.258 increase	0.84	0.385 increase
<i>O. b. subsp. sulphurea</i>	Č. Budejovice, Sádka garden	0.23	0.643	1.01	0.345 increase	0.26	0.622	0.00	0.963
<i>Verbascum thapsus</i>	Č. Budějovice- Sádka garden	1.15	0.320 increase	0.00	0.989	0.00	0.976	0.16	0.700

Table 6.

Variability in leaf number, rosette diameter, above- and underground biomass.

Whenever the $p < 0.5$ the direction of response is shown.

Significant responses are in lighted **bold**.

For comparison *Verbascum thapsus*, *O. biennis subsp. sulphurea* and *O. stuccii* are added.

Comparative study of variously invasive *Oenothera* species with special ephasis on phenotypic plasticity of their seedling traits

□ **Species level**

Four major responses could be seen among species (See **Figure 4**): Response 1 (virtually no response of a given trait to nutrient adding), Response 2 (with increased nutrient availability the trait increases, but the dosage of fertiliser does not affect the performance of trait), Response 3 (with increasing nutrient availability the trait increases) and Response 4 (with even more nutrients added the trait decreases, though not significantly).

Results from the one-way ANOVA with treatment as a main effect are compressed in the **Table 8** displaying the variability of chosen traits and also the achieved levels of significance. To every characteristics a type of response is added.

The least plastic character was the root biomass (**Table9**) (which did not vary in majority of the species except *O. rosea*, *O. scabra* and *O. coronifera*).

Character	%plastic responses of the traits found among chosen species of the genus <i>Oenothera</i>
leaf number	61
rosette diameter	50
shoot biomass	67
root biomass	17

Table 9. Plasticities of chosen characteristics, computed from Table 8.

Variability of chosen characteristics in response to nutrient enhancement

Species	Locality	leaf number		rosette diameter		shoot biomass		root biomass					
		F	p	Response	F	p	Response	F	p	Response			
<i>O. biennis</i>	Hluboká- riverbank	0.25	0.7863	1	0.52	0.6084	1	0.68	0.5239	1	0.52	0.6049	1
	Prague- railway station	2.72	0.1059	1	1.98	0.1805	1	8.99	0.0041	2	0.67	0.5306	1
	Zliv- railway station	0.76	0.4902	1	0.69	0.5190	1	0.83	0.4580	1	1.00	0.3978	1
<i>O. erythrosepala</i>	Kladno- abandoned garden	9.77	0.0030	2	11.83	0.0015	2	10.03	0.0027	2	1.69	0.2261	1
	České Budejovice- Střemovka	15.93	0.0004	2	5.27	0.0227	3	20.13	0.0001	2	2.18	0.1555	1
<i>O. rubricaulis</i>	Kladno- railroad	1.09	0.3684	1	2.30	0.1424	1	1.22	0.3302	1	0.33	0.7229	1
<i>O. pycnocarpa</i>	Prague, Pruhonice- garden	0.63	0.5488	1	0.35	0.7141	1	0.60	0.5683	1	0.57	0.5808	1
<i>O. fallax</i>	Prague, Pruhonice- garden	10.28	0.0025	2	3.36	0.0695	1	7.95	0.0063	2	1.68	0.2278	1
	Horázdovice- riverbank	23.93	0.0001	2	9.46	0.0034	3	35.47	0.0000	2	2.45	0.1284	1
<i>O. ammophila</i>	Prague, Pruhonice- garden	4.25	0.0403	4	2.64	0.1121	1	4.37	0.0374	4	2.10	0.1652	1
<i>O. rosea</i>	Leipzig(Germany)	37.21	0.0000	2	30.23	0.0000	2	37.95	0.0000	2	7.53	0.0076	2
<i>O. tetragona</i>	Prague, Troja	7.36	0.0093	3	8.89	0.0051	2	16.59	0.0005	2	3.26	0.0775	1
<i>O. moravica</i>	Prague, Pruhonice- garden	8.12	0.0059	2	11.52	0.0016	3	15.65	0.0005	2	1.04	0.3826	1
<i>O. scabra</i>	České Budejovice, Sádka garden	24.66	0.0001	2	9.57	0.0033	2	10.66	0.0022	2	8.02	0.0061	2
<i>O. perennis</i>	Prague, Troja- botanic garden	0.55	0.5921	1	0.66	0.5346	1	0.57	0.5798	1	0.99	0.4022	1
<i>O. coronifera</i>	Berlin- railroad (Germany)	18.50	0.0004	2	22.69	0.0002	2	18.63	0.0004	2	8.83	0.0062	4
<i>O. stuechlii</i>	Livorno- motorway (Italy)	4.15	0.0426	3	4.04	0.0456	1	4.23	0.0408	1	1.64	0.2341	1
<i>O. b. subsp. sulphurea</i>	České Budejovice, Sádka garden	1.90	0.1951	1	2.28	0.1487	1	2.49	0.1284	1	1.38	0.2930	1
<i>Verbascum thapsus</i>	České Budejovice- Sádka	12.47	0.0015	2	11.93	0.0018	2	13.09	0.0012	2	1.46	0.2748	1

Table 8.

Variability in leaf number, rosette diameter, above- and underground biomass.

For each character and species a pattern of response is shown (Response 1-4, in Response 3* significant differences between all treatments were found).

Species are arranged with respect to their invasibility, from the most invasive one (*O. biennis*) to the unsuccessful ones.

Significant differences are typed in lighted bold.

For comparison *Verbascum thapsus*, *O. biennis subsp. sulphurea* and *O. stuechlii* are added.

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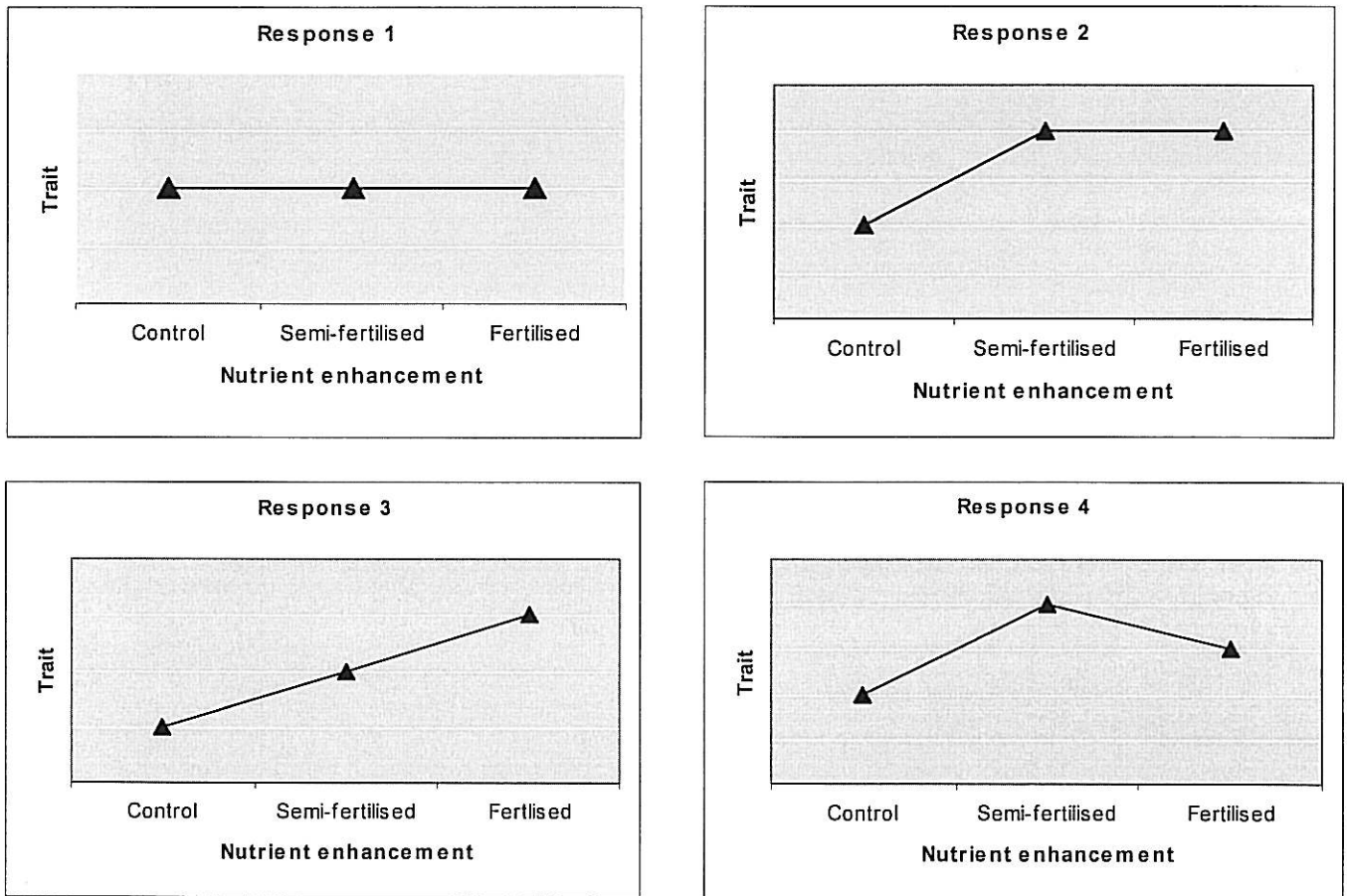


Figure 4. Schematic responses to the nutrient enhancement.

response relation body traits!

□ Group level

There could also be seen differences (see Table 10) between variously invasive groups in the pattern of their response. Among the most invasive

	Invasibility group		
	EXTREME	MEDIUM	UNSUCCESSFUL
Response 1 (%)	65	55	30
Response 2 (%)	30	33	55
Response 3 (%)	5	4	10
Response 4 (%)	0	8	5

Table 10. Representation of response in variously invasive groups.

species the Response 1 (no response) was the most propagated, while the

unsuccessful responded in such a manner the least of the groups and reacted variously.

The most uncommon Response 4 was found only in medium invader *O. ammophila* and in unsuccessful *O. coronifera*. *Verbascum thapsus* possesses

very different!

2
6

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all characters plastic except the root biomass. No characteristics of *O. biennis subsp. sulphurea* responded on the nutrient adding, it has responded in Response 1 style in all studied characters alike the most successful invaders and its relatives- *O. biennis*. *O. stuebelii* also did not show any plasticity in majority of characteristics except the leaf number, which number increased (R3).

3.1.3 Growth of chosen characteristics (leaf number and rosette diameter)

As the groups can differ not only in morphological characteristics but also in the physiological or developmental way, I also analysed the data available for the number of leaves and rosette diameter to find out if there are some differences in their growth in time (**Table 11**).

	Time		Treatment*time		Invasibility*time		Treatment*invasibility*time	
	F	p	F	p	F	p	F	p
leaf number	1178.02	<<0.001	26.45	<<0.001	7.02	<<0.001	1.82	<0.001
rosette diameter	644.39	<<0.001	38.07	<<0.001	5.85	<<0.001	2.33	<<0.001

Table 11. Results from the 2-way ANOVA with repeated measures, invasibility group, treatment and time as main factors.

All interaction terms were significant indicating differences in growth among the invasive groups (see **Figure 5**) and among treatments (**Figure 6**).

Investigating the main effect TIME, it verified our presumption about slowed down growth in the later phases of the experiment (last four measurements taken did not differ from each other in the number of leaves and rosette diameter).

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Figure 5³

Picture 7. Growth of the rosette diameter in variously invasive groups

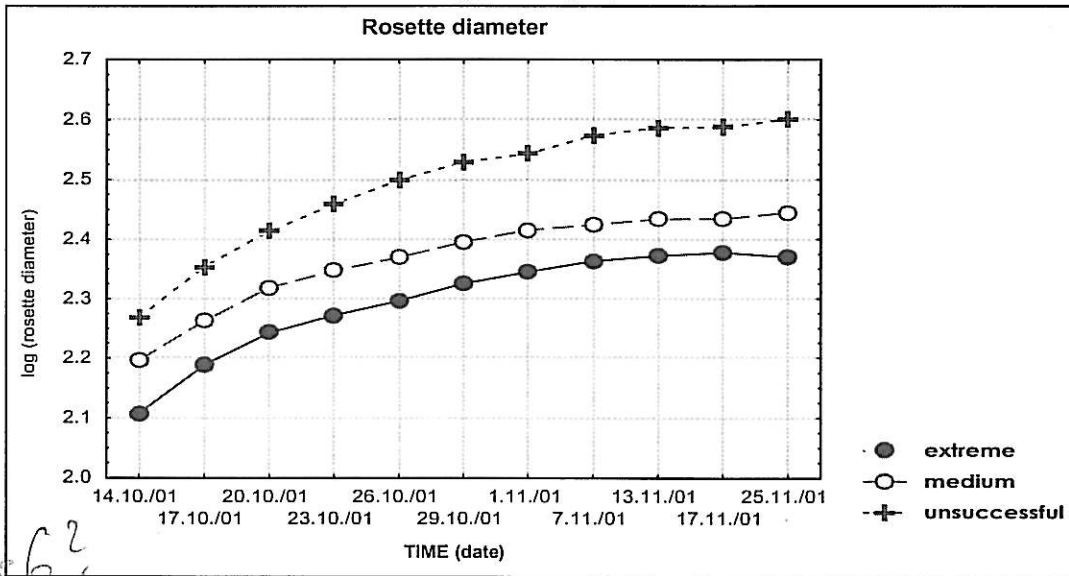
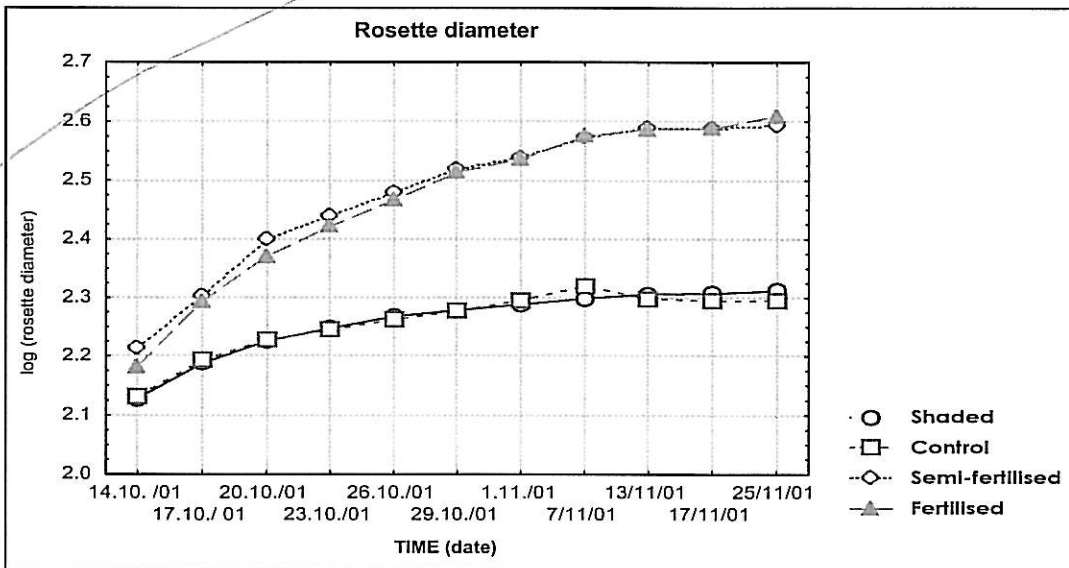


Figure 6²

Picture 9. Growth of rosette diameter under different treatments.



for dist?
max 9.7?

3.2 Coefficient PC

For each species four PC coefficients were computed (See Table).

Species	Locality	Leaf nr. PC	Rosette PC	Shoot b. PC	Root b. PC
<i>O. biennis</i>	Hluboká- riverbank	62.37	56.82	30.07	31.27
	Prague- railway station	18.33	21.07	14.21	39.57
	Zliv- railway station	17.96	14.58	17.04	12.67
<i>subsp. sulphurea</i>	České Budějovice, Sádka- garden	16.20	19.22	16.18	15.19
<i>O. erythrosepala</i>	Kladno- abandoned garden	17.04	13.63	11.37	18.50
	České Budějovice- Stromovka	14.60	16.73	11.72	32.09
<i>O. rubricaulis</i>	Kladno- railroad	23.13	18.38	21.98	28.80
<i>O. pycnocarpa</i>	Prague, Průhonice- garden	36.55	39.13	24.47	22.68
<i>O. fallax</i>	Prague, Průhonice- garden	13.18	12.52	10.22	18.66
	Horažďovice- riverbank	12.31	11.20	10.11	34.27
<i>O. ammophila</i>	Prague, Průhonice- garden	15.07	15.79	11.15	17.96
<i>O. rosea</i>	Leipzig (Germany)	5.20	10.53	7.39	15.66
<i>O. tetragona</i>	Prague, Troja- botanic garden	11.71	11.08	8.83	18.67
<i>O. moravica</i>	Prague, Průhonice- garden	14.00	14.58	11.44	27.97
<i>O. scabra</i>	České Budějovice, Sádka- garden	7.01	6.66	5.84	6.84
<i>O. perennis</i>	Prague, Troja- botanic garden	11.94	11.79	13.91	14.51
<i>O. coronifera</i>	Berlin- railroad (Germany)	9.40	7.09	6.44	6.86
<i>O. stucchii</i>	Livorno- motorway (Italy)	15.54	10.36	11.41	1.19
<i>Verbascum thapsus</i>	České Budejovice- Sádka garden	8.83	8.20	7.66	14.03

Table 12. Table of the species traits phenotypic canalizations.

3.2.1 Differences in phenotypic canalizations

□ Species level

The group of extremely successful invaders (*O. biennis* and *O. erythrosepala*) encompasses species with very similarly stabilised number of leaves and rosette diameter. Only exception is one population of *O. biennis*, namely the one from Hluboká, which leaf number PC and rosette diameter PC are very high compared to other species in the extreme group. The shoot biomass was globally more stabilised in *O. biennis*.

Within the group of medium invaders, species with the highest canalization of the leaf number, rosette diameter and shoot biomass were also the ones with the highest number of localities recorded: *O. pycnocarpa* (60 localities), *O. rubricaulis* (68 localities). These species traits varied even less than in the majority of extreme invaders in our study. The smallest PC of the leaf number and i.e. the smallest shoot biomass PC had *O. rosea*, which

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produces adventive rosettes when environment is fitting. The rosette diameter does not change so much in this species and the PC of the rosette diameter is similar to the rest (*O. fallax*, *O. rubricaulis* and *O. ammophila*).

In the group of unsuccessful invaders *O. moravica* is generally the one with the highest PCs, followed by *O. tetragona* and *O. perennis*, the most unstabilised ones are *O. coronifera* and *O. scabra*.

□ Group level

One- way ANOVA with invasibility as a main factor was performed to find out if the three group differ in the phenotypic canalization (**Table 13**). Again the three species (*Verbascum thapsus*, *O. biennis* subsp. *sulphurea* and *O. stucchii*) were excluded due to lack of knowledge about their invasive potential.

Main effect- invasibility group		
	F	p
leaf number PC	40.56	<< 0.001
rosette diameter PC	41.54	<< 0.001
shoot biomass PC	43.84	<< 0.001
root biomass PC	55.36	<< 0.001

Table 13. Results from the one-way ANOVA with invasibility group as a main factor

The group of extreme invaders was found to be the one with the highest stabilization (lowest phenotypic changes during the course of experiment) of all the traits (leaf number, rosette diameter,

shoot biomass, root biomass) measured. The groups differed from each other (Tukey).

The unsuccessful invaders possessed more environment- changeable traits, i.e. PCs of their traits were significantly smallest from the group studied (**Table14**).

	leaf number PC	rosette diameter PC	shoot biomass PC	root biomass PC
extreme	26.06	24.57	16.88	26.82
medium	17.57	17.92	14.22	23.01
unsuccessful	10.81	10.24	9.29	14.97
mean trait PC	17.86	17.29	13.54	20.19

Table 14. Mean PC of traits and of the invasibility groups.

3.2.2 Canoco

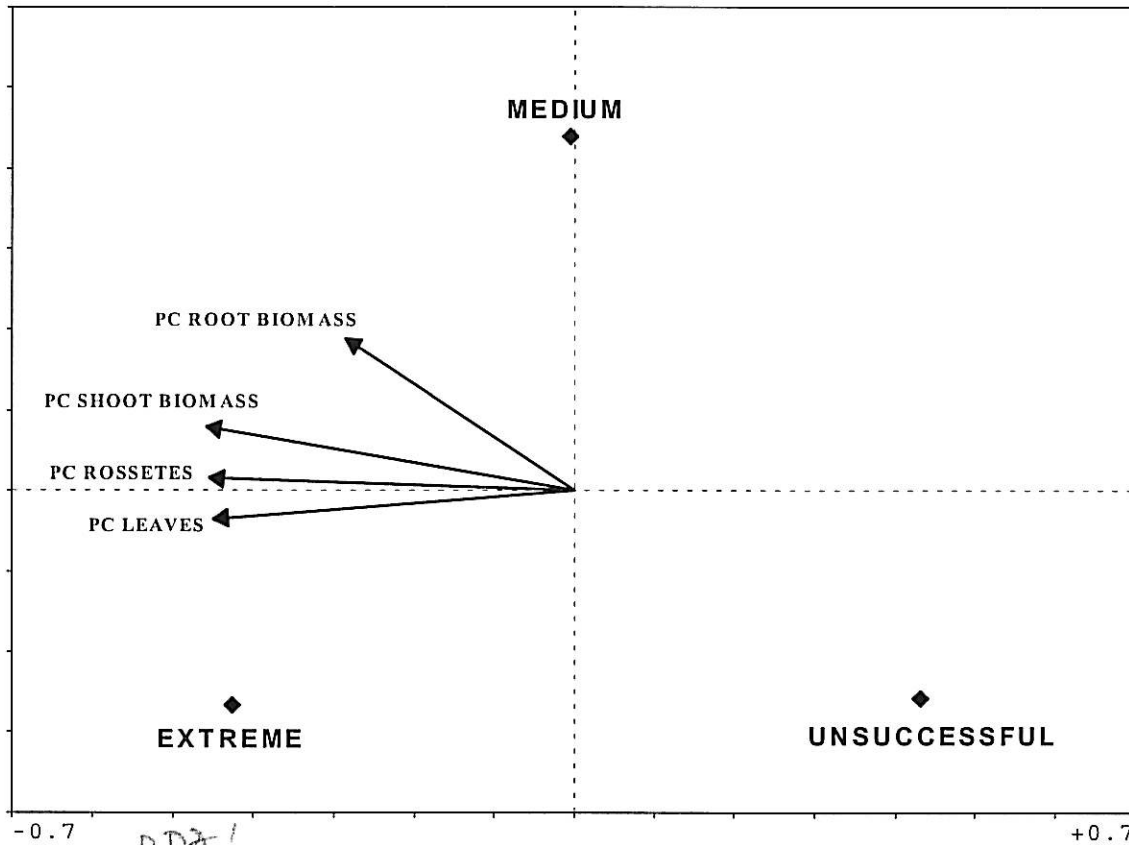


Figure 7. Arrows stand for PCs, centroids for invasibility status. Species data are not shown.

RDA diagram (Figure 7) shows the relation between the achieved phenotypic stability (PCs) and the invasive success of *Oenothera* species. First two axes explain 35% of variability. We may say that phenotypic canalizations of the studied traits are tightly correlated and in relation to invasive success. The phenomenon of phenotypic stabilisation is highly negatively correlated with invasive failure of *Oenothera* species in Central Europe.

3.3 Populational differentiation in morphological traits and in phenotypic canalizations

Species	Locality
<i>O. biennis</i>	Hluboká- riverbank Prague- railway station Zliv
<i>O. erythrosepala</i>	Kladno České Budejovice- Stromovka
<i>O. fallax</i>	Prague- Průhonice park Horažďovice- riverbank

Table 15. Investigated populations.

Populations of *O. biennis* significantly differed^{var} all measured characters (Table 16).

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	<i>O. biennis</i>		<i>O. erythrosepala</i>		<i>O. fallax</i>	
	F	p	F	p	F	p
number of leaves	21.83	<< 0.001	13.38	< 0.001	1.01	0.32
rosette diameter	24.86	<< 0.001	18.4	< 0.001	0.6	0.44
shoot biomass	25.49	<< 0.001	22.5	< 0.001	0.6	0.44
root biomass	23.82	<< 0.001	83.42	<< 0.001	0.2	0.66

Table 16. Results from the one-way ANOVA with population as the main effect.

The greatest mean trait values had the population from the Prague-railway station. Significantly smaller and similar (Tukey unsign.) number of leaves was found in the latter two populations: population from Zliv-railway station and Hluboká-riverbank. The diameter of the rosette, shoot biomass and root biomass differed among all populations (Tukey).

From the species *O. erythrosepala* two populations were analysed, one from Kladno and one from České Budějovice-Stromovka. All measured characteristics showed significant interpopulational differences and were bigger in the population from Kladno.

From the species *O. fallax* also just two populations were available, one from Prague, Průhonice- park and second from Horažďovice- riverbank. These two populations didn't differ in any of chosen traits.

As phenotypic plasticity has a genetic basis alike the morphological traits, we may assume, that similar differences between populations will be found in the achieved phenotypic plasticities.

Comparing the plasticities, which were computed for each population, we found that among the *O. biennis* populations, the Hluboká- population has the highest phenotypic canalization for number of leaves, rosette diameter and shoot biomass (these characteristics varied the least in this population). The latter two have similar and much smaller PC for these traits. The root biomass PC was highest in the population from Prague-railway station.

Among *O. erythrosepala* populations one with the stronger canalization of leaf number was the one from Kladno, whereas the rosette diameter was more canalised in the population from České Budějovice. The shoot biomass was stabilised more or less the same whereas the root biomass

fluctuates more among the population from Kladno (smaller PC root biomass).

In *O. fallax* all the traits are similarly canalised in both populations, except the root biomass, which was less fluctuating in the population from the Horažďovice- riverbank.

4. Discussion

➤ Comparison- resistant morphological characteristics

As the shoot biomass (trait tied more with the fitness than the morphometric characteristics) did not differ between the variously invasive groups, we may assume, that the greatest leaf number found in the medium invaders may be due to the presence of *O. rosea*, whose high leaf number tends to push the mean of the group higher. Similarly the significantly greatest rosette diameter found in unsuccessful invaders may be due to the presence of *O. tetragona*, which has very long narrow leaves in contrast to all other species.

As can be seen, comparison of morphological traits of variously invasive species remains generalisation resistant. On the other hand, with the use of relative traits – PCs, I found out interesting differences.

➤ High phenotypic canalizations of the more successful invaders seedling characteristics

Colonizers are frequently thought to have high phenotypic plasticity, permitting phenotypic variation of a particular genotype under different environmental challenges and providing tolerance over a range of environmental conditions (Bradshaw 1965, Scheiner and Goodnight 1984, Thompson 1991). Phenotypic plasticity is known to have contributed to invasiveness in several species, including *B. tectorum* (Rice and Mack 1991), *Avena* spp. (Marshall and Jain 1968), *Pennisetum setaceum* (Williams et al. 1995), *Polygonum persicaria* (Sultan and Bazzaz 1993) and *Melaleuca quinquenervia* (Kaufmann and Smouse 2001). In these cases the selection

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favoured phenotypic plasticity resulting in greater environment-induced variation, which, namely in those morphological characters related directly to growth rather than differentiation or morphogenesis, is certainly of great adaptive value in plants as discussed by Bradshaw (1965), Harper (1967) and others.

Unlike all these examples cited, where it was the high phenotypic variation typical of an invader, in *Oenothera* species, the most successful invaders possess the least environmental variability of their seedlings traits. What is the advantage?

There are some easily deducible disadvantages of high phenotypic differentiation and variation: 1) Expensive/dangerous information acquisition (possible harms or even deaths of such individuals), 2) Unreliable information (unpredictability of the environment and possible misunderstandings of the signals), 3) Too little too late (problems with the cost of tuning the right adjustment of the responses).

The phenotypic plasticity refers to the general effect of environment on phenotypic expression and as the phenotypic plasticity of a trait is a trait itself, that can be inherited (Scheiner 1993), we cannot see the small phenotypic variance (e.g. high PC) in the seedlings of extremely successful invaders of the genus *Oenothera* as a lack of phenotypic plasticity and our results can not be seen as simply counteractive. Moreover the plastic responses (variability caused by environment) early in the life history may occur at the cost of reduced plasticity later in the life history (Weinig and Delph 2001). While talking about a single trait or one correlated set of traits this may result from a structural feedback mechanism (Weinig and Delph 2001). Alternatively, when a cost of phenotypic plasticity¹ is introduced (Scheiner 1993), the trade-offs may be expected among plasticities for different traits and thus those *Oenothera* species with stabilised seedlings characteristics may trump the others lately with the greatest plasticity in other, maybe more important characters, e.g. seed numbers and so. Though usually the optimal

¹ The cost of maintaining the genetic and cellular machinery necessary to be plastic, e.g. regulatory genes and enzymes, which is always borne by an organism regardless of an environment in which it develops.

strategy for fitness traits is to be 'nonplastic' and maximal in all environments, for example study on *Danthonia spicata* (Scheiner 1991) recorded plastic responses of such traits and as the trade-off between survival and reproduction has long been recorded, the trade-off between plasticities tight up with these various challenges may be of evolutionary significance.

➤ **High level of environment induced variability in unsuccessful invaders**

Specialised genotypes (species) may perform well in a particular environment, but may have to pay a cost of relatively poor performance in other environments. As a consequence such species, which have above-average performance under favorable conditions but below average performance under unfavorable conditions, will display relatively high levels of environment-induced variation and this high level of phenotypic variance is not adaptive but simply a consequence of specialisation (Taylor and Aarssen 1988).

➤ **Differences among populations**

Many populations of introduced colonizers are started by small number of propagules and the resulting founder effect can lead to an absence of alleles or a shift of alleles frequencies (Nei et al 1975, Barton and Charlesworth 1984). The likelihood of a loss in genetic variation within populations and an increase in differentiation among populations in the new range would be compounded in a predominantly self-pollinating species (Brown and Marshall 1981, Barrett and Richardson 1986).

This allelic frequencies shift along with selection for new habitat conditions can result in substantial genetic and phenotypic differentiation among population. Such an effect has been documented, for example in *Echium plantagineum* (Brown and Burdon 1983), *Bromus tectorum* (Novak et al. 1991) and *Bryonia alba* (Novak and Mack 1995). Such a phenomenon can be to some degree found also in our study, namely applying to the morphological characters in *O. biennis* and *O. erythrosepala*. The differences in phenotypic canalization found among populations may arise from similar consequences

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(due to its genetic basis) and such a result was recorded also in other studies, in *Melaleuca quinquenervia*- an alien in Florida (Kaufmann and Smouse 2001) which phenotypic variation showed similar interpopulation differences.

Another fact which can not be omitted in the case of *Oenothera* genus is the peculiarity of their genetic system which in uncertain taxonomical status of every population (Mihulka and Pyšek 2001). — by way to captivity

In my study due to poor germination and low seedlings vigour some populations (2 *O.pycnocarpa* populations) and one whole species (*O. issleri*) had to be excluded. As a result I had the opportunity to analyse just three species with more than one population: *O. biennis* (3 populations), *O. erythrosepala* (2 populations) and *O. fallax* (2 populations).

The higher among-population variation of *O. biennis* may be presumably tight up with longer (e.g. 100 years) time period available for population differentiation including natural selection (Table 17) (Kaufmann & Smouse 2001). Similarly the absence of interpopulational variance in the morphological traits which was found among the populations of *O. fallax* may be likewise explained because it is a hybrid originated in Europe with relatively short history compared to other two species.

	Date of first record in Europe(UK)
<i>O. biennis</i>	1780
<i>O. erythrosepala</i>	1866
<i>O. fallax*</i>	1892

**O. fallax* is a hybrid of latter two
 Table 17.

On the other hand Kaufmann and Smouse (2001) suggest, that 50 generations is enough time for some adaptive population differentiation and every *Oenothera* species in Europe has roughly gone through such a number of generations.

➤ **Less successful invaders and new genotypes**

As the assignment to variously invasive groups was based on number of localities found up to now, we may presuppose, that some of the less successful invaders which arrived later and also the species which arose in Europe as new genotypes (medium successful *O. fallax*, unsuccessful *O. moravica* and *O. coronifera*) did not show their real invasive potential yet, just because the lack of time and in some cases we may expect future increase in occupied localities (e.g. *O. moravica* with relatively high PCs).

➤ ***Verbascum thapsus***

PCs of *Verbascum thapsus* are in general small and in this respect it could be most probably assigned to the group of unsuccessful invaders. Thus the superiority in invasibility of *O. biennis* may not only be based on ecological similarity to *Verbascum thapsus*.

How many!

5. Conclusions

Variouly invasive representatives of the genus *Oenothera* differ in their environmentally induced phenotypic plasticity, namely in the PC indexes of their seedling traits. The most successful invaders were found to possess the most stabilised seedling characteristics. Such a phenomenon may be serviceable ability to maintain biomass, i.e. also fitness, under a wider range of conditions occurring in their invaded habitats.

The invading species properties are of significance and their study may contribute to better understanding of the invasions.

trivial

6. Questions that remain

The low phenotypic variation (high phenotypic canalization) of the traits of more successful invaders populations could be a property of the initial germplasm that was introduced to Europe or a consequence of subsequent selection for such a stabilisation in novel environments (Kaufmann and Smouse 2001).

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Does the low phenotypic variation of seedlings characteristics correlate with higher plasticity in adult Oenothera plants traits, e.g. seed number?

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APENDIX

Seedlings of average appearance taken from "fertilised" and "control" treatment respectively.

O. biennis (extremely successful invader)



O. scabra (unsuccessful invader)

