RELATING INVASION SUCCESS TO PLANT TRAITS: AN ANALYSIS OF THE CZECH ALIEN FLORA

Petr Pyšek[1], Karel Prach[2] and Petr Šmilauer[2]
[1]*Institute of Applied Ecology, University of Agriculture Prague, CZ-281 63 Kostelec nad Černými lesy, Czech Republic;* [2]*Faculty of Biological Sciences, University of South Bohemia, Branišovská 31, CZ-370 01 České Budějovice, Czech Republic*

Abstract

Alien species introduced into the Czech Republic since 1492 (excluding rare and ephemeral introductions) are analysed and various species characteristics (geographical area of origin, taxonomic position, species height, life form, life strategy, pollination and dispersal agents, planting history, and ecological requirements expressed using the Ellenberg indicator values) are used to explain their invasion success. The species success in man-made and seminatural habitats was evaluated separately by using a semiquantitative three degree scale. Total success in both types of habitats was also assessed. The aliens were also compared with native flora for the particular characteristics. A total of 132 alien species were analysed of which about 20% may be considered successfully naturalized. Invasion success in seminatural habitats was found to be favoured by height, hemicryptophyte life form and C-strategy. The successful invaders into this habitat type also differed from unsuccessful ones in *(1)* requiring sites which are more moist and *(2)* more frequent planting in the past. Species successfully invading man-made habitats showed an increased representation of therophyte life form and of C- or CR-strategy. They were mostly introduced spontaneously and are able to grow successfully in drier sites. There is an increased representation of therophytes and members of *Asteraceae* family among the whole set of aliens when compared with the native flora. Further, species of North American and Asian origin and those confined to sites with higher nitrogen input were overrepresented. The study confirms the fact that there is no single characteristic which can reliably predict the success of any particular species as an invader. However, if a large data set is used, some differences between alien and native species and differences among the aliens invading contrasting habitat types can be revealed.

Introduction

Ecologists interested in biological invasions have consistently attempted to answer two main questions: *(a)* what are the traits of invasive species? and *(b)* what are the characteristics of those communities or ecosystems vulnerable to invasions? (Baker 1965, 1974; Barrett and Richardson 1986; Gray 1986; Hobbs 1989; Noble 1989; Rejmánek 1989; Roy 1990; Lodge 1993a).

So far, however, extensive sets of species or communities have only exceptionally been taken into account and analysed quantitatively with respect to species traits and invasion success (Newsome and Noble 1986). This is in part due to the fact that considering a large set of species, viewed at the landscape level, brings about inevitable limitations in the exactness and amount of detail of the analyses conducted.

The present study attempts to extend the usual coordinates of ecological studies (Pimm 1994) to an area of 72,000 km^2, for more than a hundred species, and over an historical time dimension. As there is an increasing agreement that it is probably impossible to identify simple, unequivocal plant traits with a high predictive power of invasion success (Lodge 1993a), it is becoming accepted that the performance of invading species should be assessed with respect to a particular ecological situation

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(Crawley 1987; Noble 1989; Mooney and Drake 1989; Lodge 1993a). To take this into account in the present study, invaders into seminatural vegetation and those successful in man-made habitats were treated separately. The following questions were addressed: *(a)* Are there any plant traits on the basis of which the alien species can be distinguished from native ones? *(b)* Are there any particular traits favouring invasion success of certain alien species, and if so, do these differ in contrasting (*i.e.*, seminatural *versus* man-made) habitats?

Materials and methods

Species selection

Alien species introduced into Europe after the discovery of America in 1492 (*i.e.*, those classified as neophytes in central European phytogeographical terminology, see *e.g.*, Kornas 1990) were identified from the database covering the territory of former East Germany compiled by Frank and Klotz (1990). The list was revised with respect to the territory of the Czech Republic using local floras (Dostál 1982; Hejný and Slavík 1988-1992). Those species whose spontaneous occurrence had not been reported from this territory were excluded and those missing from the list of Frank and Klotz were added. Additionally, information from archaeological research (Opravil 1980) was considered in order to exclude those species introduced before 1492 (*i.e.*, archaeophytes). Only permanently established aliens were considered, those with only ephemeral occurrence were also excluded. An overview of alien species is given in Table 1 and Appendix 1.

Traits considered

Each species was characterized using the following traits:

a. Area of origin (extracted from Dostál 1958; Hejný and Slavík 1988-1992; Frank and Klotz 1990; Lohmeyer and Sukopp 1992).
b. Taxonomic position at the family level.
c. Plant stature expressed as the maximum height reached by a species (from Dostál 1958; Hejný and Slavík 1988-1992).
d. Life form according to Raunkiaer's scheme (see *e.g.*, Mueller-Dombois and Ellenberg 1974; taken from Frank and Klotz 1990; Ellenberg *et al.* 1991).
e. Life strategy according to Grime (1979), taken from Frank and Klotz (1990).
f. Pollination agents (Frank and Klotz 1990).
g. Dispersal agents (Frank and Klotz 1990).
h. Mode of spread, *i.e.*, by seed or vegetatively. A species was considered to possess the latter only if vegetative propagation was important for its spread at a site (taken from Dostál 1958; Hejný and Slavík 1988-1992).
i. Planting history, *i.e.*, whether the species had been planted in the territory of the Czech Republic (Dostál 1958, 1982; Hejný and Slavík 1988-1992).
j. Ecological requirements expressed by using Ellenberg indicator values for light, moisture, temperature and nitrogen (Ellenberg *et al.* 1991; Frank and Klotz 1990).

Assessment of invasion success

Evaluation of species invasion success was made semiquantitatively, based on the authors' personal experiences from the territory of the Czech Republic. The invasion success of each species was assessed separately for seminatural and man-made habitats using the following scale: 0 - absent, 1 - rare, 2 - scattered over the whole territory or locally abundant, 3 - common, *i.e.*, abundant within the whole territory. Man-made habitats included settlements, dumps in open landscape, arable land and various other disturbed areas. Meadows and grasslands, wetlands, water courses, shrubs and forests were considered as seminatural habitats and include rare remnants of natural communities in the territory under study, *i.e.*, natural habitats were not distinguished as a separate category (see *e.g.*, Kornas 1990) because of the problems of distinguishing between natural and seminatural habitats in the central European landscape.

Data treatment

A two-step comparison was used to analyse the data:

1. Comparison of characteristics of the total set of alien species with those of native flora. Since comparable concise information is not available for the flora of the Czech Republic, the characteristics of native flora were taken from Frank and Klotz (1990). This database, covering the territory of former East Germany, comprises 1,669 native species. Even if the floristic differences between East Germany and Czech Republic are taken into account, the database used undoubtedly provides a highly representative sample, characteristics of which may be considered as very similar to those of the Czech native flora.
2. Comparison within aliens for which three categories were distinguished: *(a)* species successful in seminatural habitats, *(b)* species successful in man-made habitats, and *(c)* unsuccessful species, *i.e.*, those successful in neither *(a)* nor *(b)* (see Table 1 for the list of successful species and Appendix 1 for the list of unsuccessful species). Species reaching the value of 0 or 1 in the above scale are termed as 'unsuccessful', those with scores 2 or 3 as 'successful'.*

Data were analysed using standard methods (Sokal and Rohlf 1981).

The most successful invaders, *i.e.*, those that attained score of total success at least 3 (obtained by summing the scores for seminatural and man-made habitats), were subjected to ordination to analyse the relationships between species traits and their success as invaders. (The only woody species among the most successful invaders, *Robinia pseudoacacia*, was excluded from the evaluation.) The technique of Canonical Correspondence Analysis (CCA; Ter Braak 1987) was used with the program CANOCO 3.12. Input data used were: success in seminatural habitats, success in man-made habitats, and total invasion success scores together with selected species traits. To stress the life history characteristics, *i.e.*, those supposed to be functionally related to a species success, only those traits listed under (c)-(h) were considered (*i.e.*, excluding the area of origin, taxonomic position and Ellenberg indicator values). The Monte-Carlo permutation test was used to evaluate whether the relationship between species traits and invasion success was significant.

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*In the present paper, 'successful' and 'unsuccessful' are used as technical terms defined by a species' position at the 0-3 abundance scale.

Results

Overall characteristics of alien flora

In total 132 alien species appeared on the list, about 20% of which may be considere(to be successfully naturalized. The proportion of successful invaders was similar ir seminatural and man-made habitats (Table 2).

Table 1. Overview of successful aliens in the Czech flora. Species are divided according to their succes: in particular habitat categories: 0: absent; 1: rare; 2: scattered over the whole territory or locally abundant; 3: common. Total success is expressed as the sum of values in seminatural and man-made habitats. Origir is shown: N: north; E: east; W: west; S: south; C: central.

	Seminatural	Man-made	Total	Origin
Successful in both groups of habitats				
Epilobium adenocaulon	2	3	5	N America
Juncus tenuis	3	2	5	N America
Reynoutria japonica	2	3	5	E Asia
Solidago canadensis	2	3	5	N America
Bidens frondosa	2	2	4	N America
Heracleum mantegazzianum	2	2	4	W Asia
Robinia pseudoaccacia	2	2	4	N America
Trifolium hybridum	2	2	4	W Europe
Successful in seminatural habitats				
Elodea canadensis	3	0	3	N America
Impatiens parviflora	3	1	4	C Asia, Siberia
Solidago gigantea	3	1	4	N America
Acorus calamus	2	0	2	Asia
Impatiens glandulifera	2	1	3	S Asia
Lupinus polyphyllus	2	1	3	N America
Pinus nigra	2	0	2	S Europe
Pinus strobus	2	0	2	N America
Successful in man-made habitats				
Amaranthus retroflexus	0	3	3	N America
Cardaria draba	0	3	3	S Europe, C Asia
Chamomilla suaveolens	0	3	3	W Asia
Conyza canadensis	0	3	3	N America
Galinsoga ciliata	0	3	3	C,S America
Galinsoga parviflora	0	3	3	S America
Veronica persica	0	3	3	Asia
Amaranthus chlorostachys	0	2	2	tropical America
Bunias orientalis	0	2	2	S Europe
Lycium barbarum	0	2	2	S Europe
Medicago sativa	0	2	2	Asia

Table 2. Overall characteristics of the alien flora analysed. Only species introduced after 1492 are considered. Very rare, ephemeral and taxonomically problematic introductions were omitted.

	Number of species	Percentage
Aliens total	132	100.0
Successful in seminatural habitats	16	12.1
Successful in man-made habitats	19	14.4
Successful in both	8	6.1
Successful total	27	20.5
Unsuccessful total	105	79.5

Features distinguishing alien species from the others

Taxonomic position

The composition of the alien flora with respect to the proportion of species in particular families differed remarkably from that of the native flora (Fig. 1a). Among the families overrepresented in the alien flora were *Asteraceae* (20.5% in alien flora *vs.* 10.0% in native), *Brassicaceae* (8.3% *vs.* 4.0%), *Chenopodiaceae* (4.5% *vs.* 1.7%), *Onagraceae* (3.8% *vs.* 1.1%) and *Fabaceae* (7.6% *vs.* 3.9%). On the other hand, the proportion of *Poaceae* and *Rosaceae* was higher in the native flora (4.5%

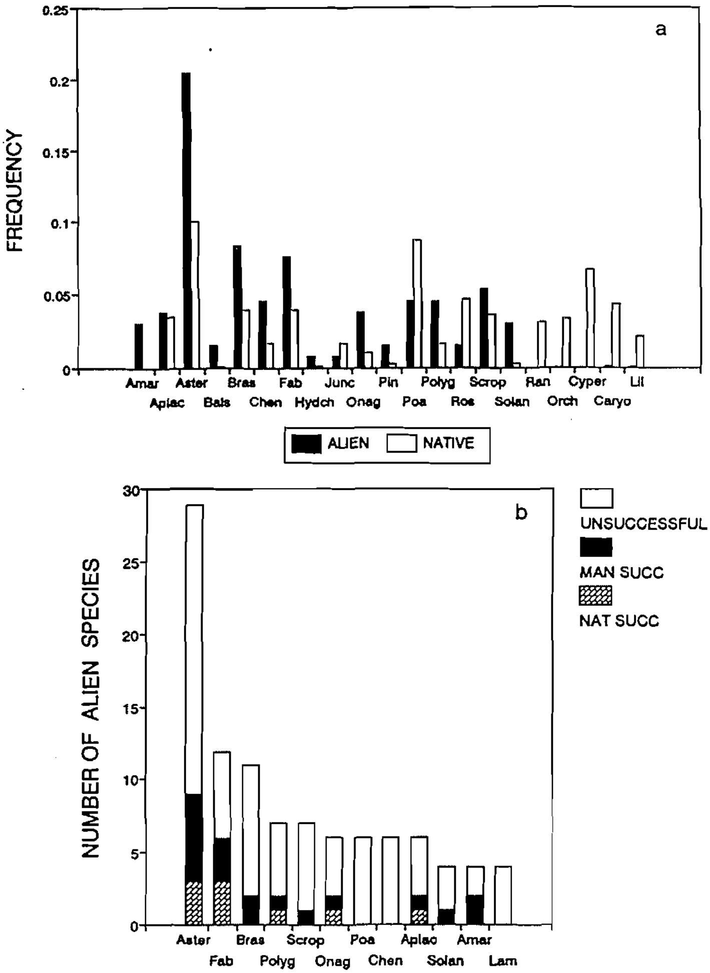


Fig. 1. Frequency of particular families among aliens in comparison with the native flora *(a)*, and differences in taxonomic position of alien species successful in man-made habitats (MAN SUCC), in seminatural habitats (NAT SUCC) and those relatively UNSUCCESSFUL *(b)*. Family codes: Amar: *Amaranthaceae*; Apiac: *Apiaceae*; Aster: *Asteraceae*; Bals: *Balsaminaceae*; Bras: *Brassicaceae*; Chen: *Chenopodiaceae*; Fab: *Fabaceae*; Hydch: *Hydrocharitaceae*; Junc: *Juncaceae*; Onag: *Onagraceae*; Pin: *Pinaceae*; Poa: *Poaceae*; Polyg: *Polygonaceae*; Ros: *Rosaceae*; Scrop: *Scrophulariaceae*; Solan: *Solanaceae*; Ran: *Ranunculaceae*; Orch: *Orchidaceae*; Cyper: *Cyperaceae*; Caryo: *Caryophyllaceae*; Lil: *Liliaceae*.

Table 3. Differences in plant traits between particular groups of aliens classified according to their success (I - successful in seminatural habitats, successful in man-made habitats, unsuccessful) and between the total set of alien species and native flora (II). The following null hypotheses were tested: I: Categories distinguished among aliens do not differ in the proportion of species with particular characters (chi^2 test on contingency tables); II: Alien species do not differ from native flora in the proportion of species with particular characters. Characteristics of native flora, if given (N.G.: not given), were extracted from Frank and Klotz (1990). N.T.: not tested as alien species differ in origin from others by definition. Test used was the chi^2 goodness-of-fit test, with expected value derived from the proportions of considered categories in the native flora. N.S. means that we cannot reject null hypothesis on significance level less than 0.05.

	I. Within aliens			II. Aliens *vs.* native flora		
	df	chi^2-value	*P*	df	chi^2-value	*P*
Origin	12	11.03	N.S.		N.T.	
Life form	10	25.56	<0.01	5	75.36	<0.001
Life strategy	12	14.11	N.S.	6	215.64	<0.001
Pollination	4	0.94	N.S.	2	2.42	N.S.
Dispersal	8	14.15	N.S.	4	163.47	<0.001
Mode of spread	4	1.50	N.S.		N.G.	
Planting	2	6.08	<0.05		N.G.	

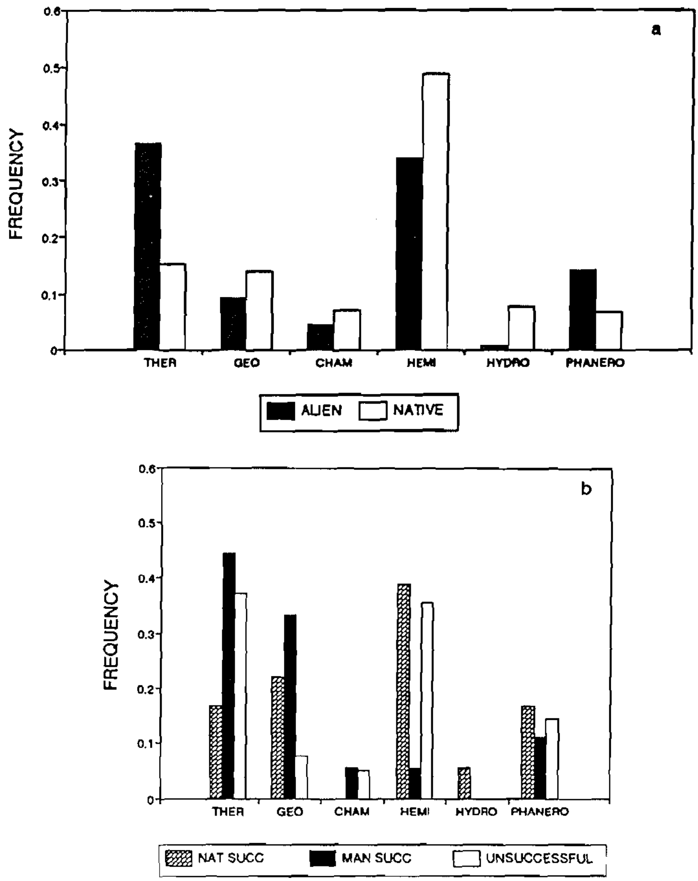


Fig. 2. Frequency of particular Raunkiaer's life forms among aliens and native flora *(a)*, and among the particular groups of alien species *(b)*. See Fig. 1 for codes of particular groups of aliens.

vs. 8.7% and 1.5% *vs.* 4.7%, respectively). No alien species occurred in the list among some of the families with relatively high representation in the native flora (*Ranunculaceae, Orchidaceae, Cyperaceae* and *Caryophyllaceae*, Fig. 1a).

Biological and ecological traits

The alien species differed significantly from the native flora in the frequency distribution of life forms and life strategies (Table 3). Therophytes and phanerophytes showed remarkably higher representation among aliens than among the native flora whereas hemicryptophytes and hydrophytes were underrepresented (Fig. 2a). There was a high representation of species with C- and CR-strategies among aliens. On the contrary, those species possessing a combination including S-strategy (CS, CSR, SR) contributed conspicuously more to the native flora (Fig. 3a).

No significant differences between aliens and native flora were found with respect to pollination (Fig. 4a). There was a significant difference in dispersal agents, with higher frequency of species dispersed by man among aliens (Fig. 5b, Table 3).

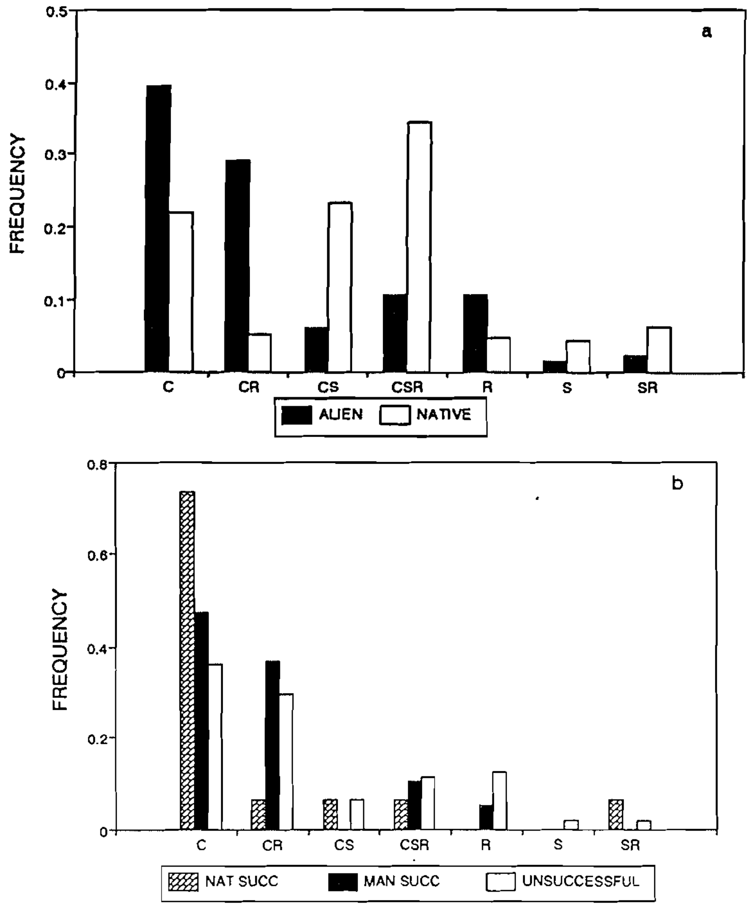


Fig. 3. Frequency of life strategies (Grime 1979) among aliens and native flora *(a)*, and among the particular groups of alien species *(b)*. See Fig. 1 for codes of particular groups of aliens.

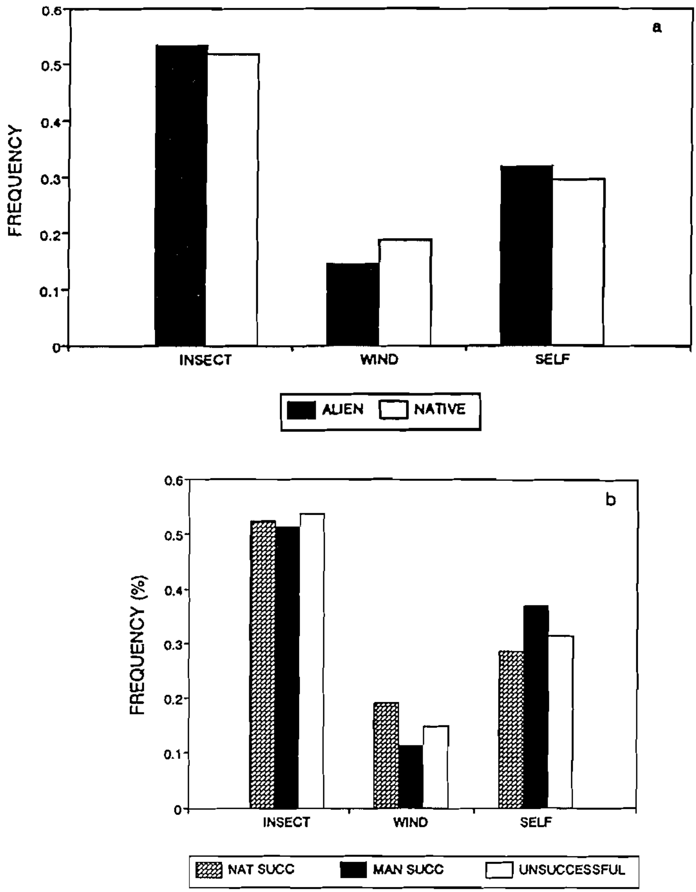


Fig. 4. Frequency of main pollination agents among aliens and native flora *(a)*, and among the particular groups of aliens *(b)*. See Fig. 1 for codes of particular groups of aliens.

Table 4. Comparison of ecological requirements of alien flora in the Czech Republic. Ellenberg indicator values are given (mean±S.D.) for each factor. Number of species for which the tabulated value was available is shown on the bottom line. Data characterizing native flora (n=1,669) were extracted from Frank and Klotz (1990). Kruskal-Wallis test was used to test for the differences. Means followed by the same letter row-wise were not significantly different. Level of significance of the difference in means for the comparison of aliens with native flora is indicated between the values (***: P<0.001).

	Successful in seminatural	Successful in man-made	Unsuccessful	Aliens		Native
Light	6.46±1.31^a 16	6.87±1.23^a 17	7.42±0.90^b 75	7.38±1.22 95	***	6.76±1.52 1313
Moisture	6.57±2.49^a 15	5.00±1.57^b 18	4.67±1.49^b 65	4.90±1.79 88	***	5.91±2.57 1239
Temperature	6.07±1.00^a 14	6.47±1.45^{ab} 16	6.98±1.38^b 57	6.84±1.37 77	***	5.51±1.19 916
Nitrogen	6.75±1.12^a 16	6.47±1.56^a 19	6.45±1.47^a 64	6.67±1.45 88	***	4.32±2.09 1311

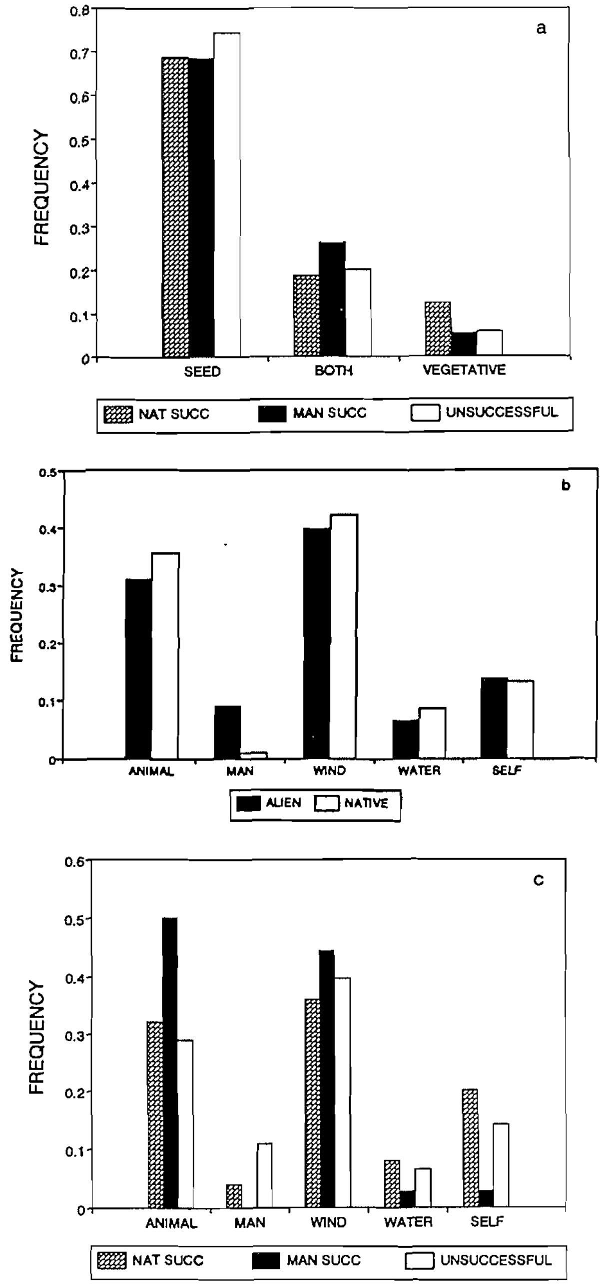


Fig. 5. Frequency of two main modes of spread (by seeds and vegetatively) among the particular groups of alien species *(a)*. Comparison of aliens with native flora is not given because the relevant data on native flora are not available in Frank and Klotz 1990. Frequency of main dispersal agents among aliens and native flora *(b)*, and among the particular groups of alien species *(c)*. See Fig. 1 for codes of particular groups of aliens.

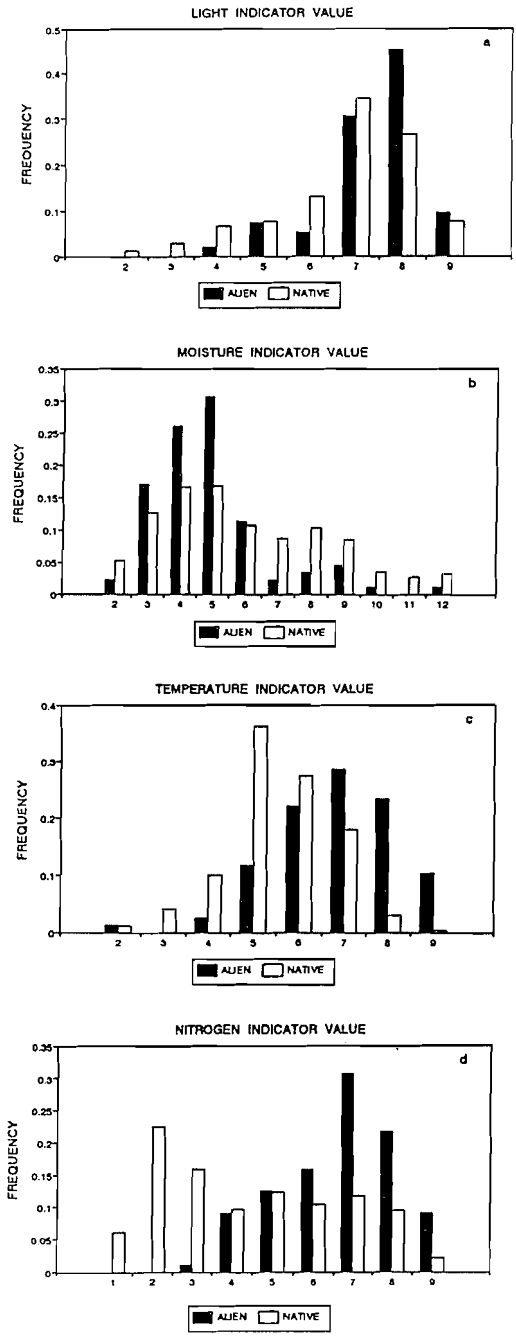


Fig. 6a-d. Frequency of Ellenberg's indicator values for light, moisture, temperature and nitrogen among aliens and native flora. See Fig. 1 for codes of particular groups of aliens.

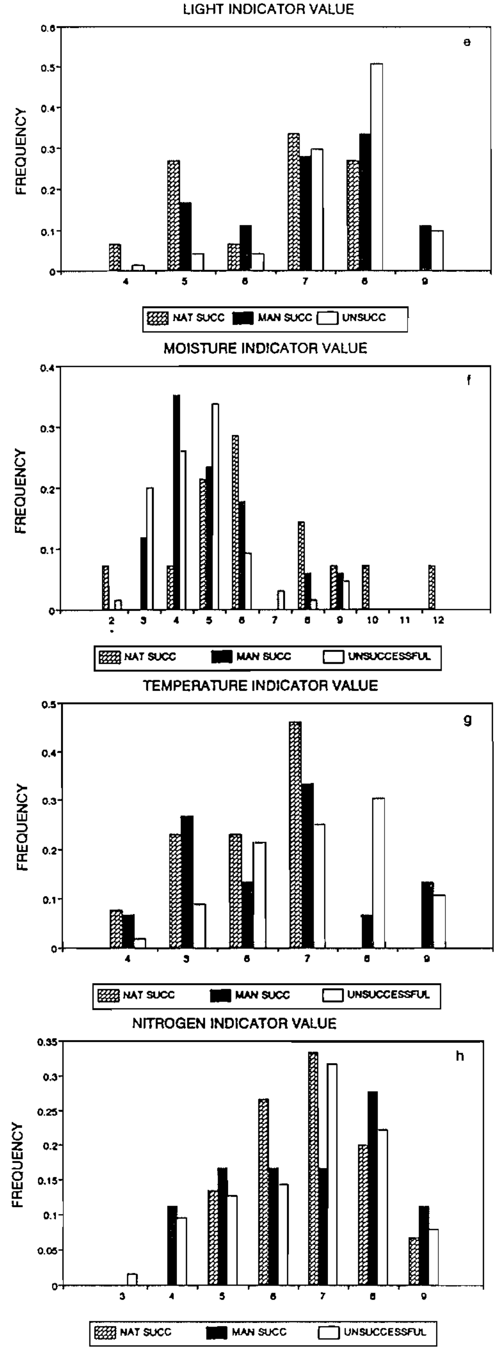


Fig. 6e-h. Frequency of Ellenberg's indicator values for light, moisture, temperature and nitrogen among the particular groups of alien species. See Fig. 1 for codes of particular groups of aliens.

Ecological requirements
Compared to the native flora, alien species showed higher mean indicator values for light, temperature and nitrogen (Fig. 6a, c,d) and these differences were highly significant (Kruskal-Wallis test, H=17.12, 66.18 and 95.19, respectively, $P<0.001$, Table 4). The native flora exhibited a significantly higher mean indicator value for moisture (H=11.73, $P<0.001$, Table 4, Fig. 6b).

Effect of plant traits on invasion success

Origin
There were apparent differences in the frequency distribution of areas of origin between particular groups of aliens classified according to invasion success, but these

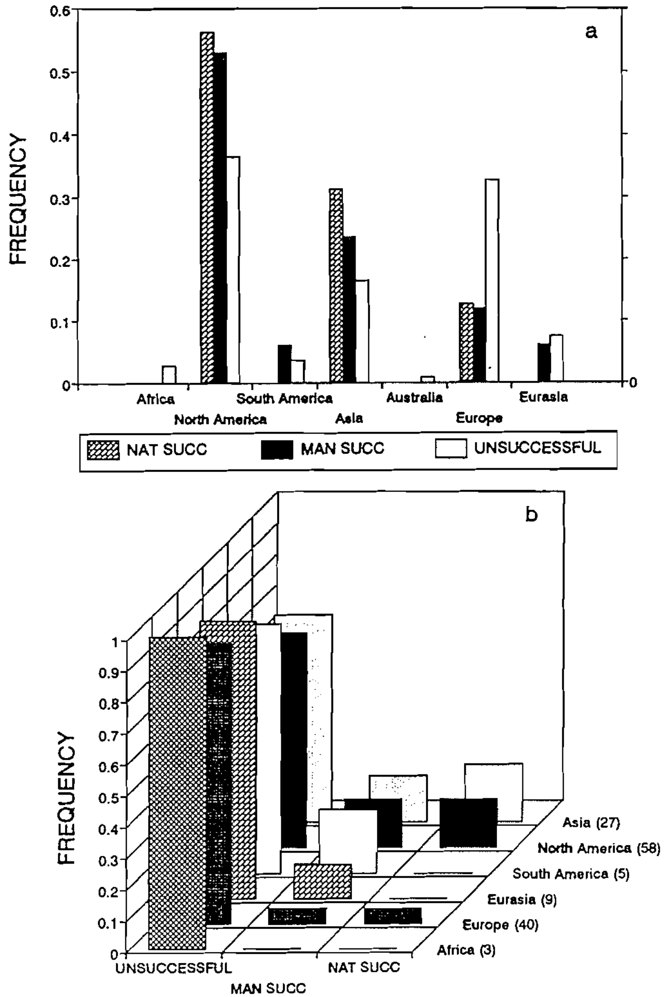


Fig. 7. Geographical origin of alien species distinguished according to their invasion success: frequency *(a)*, and relative frequency *(b)*. The numbers of species of respective origin are given with the names of the continents in *(b)*.

differences were not statistically significant (Table 3). The proportion of North American and Asian species was higher in aliens successful in both seminatural and man-made habitats than in those considered unsuccessful. In the latter, European species made a greater contribution (Fig. 7a). The relative contribution of successful and unsuccessful species for particular areas of origin is shown in Fig. 7b. In seminatural habitats, only North American, Asian and European species were among those successfully naturalized whereas in man-made habitats, naturalization also occurred in some species of South American and Eurasian origin. The percentage of successful invaders (for both seminatural and man-made habitats) decreased in the following order: Asia 33.3, North America 31.0, South America 20.0, Eurasia 11.1, Europe 10.0, Australia 0, Africa 0.

Taxonomic position

Asteraceae and *Fabaceae* contributed most to the number of successful aliens in both seminatural and man-made habitats. Species successful in both habitat groups were also found among *Polygonaceae, Onagraceae* and *Apiaceae.* The representatives of *Brassicaceae, Scrophulariaceae, Solanaceae* and *Amaranthaceae* were only successful in man-made habitats and the proportion of successful invaders was remarkably high in the latter family. No successful invaders were present among, *e.g., Poaceae, Chenopodiaceae* and *Lamiaceae* (Fig. 1b).

Biological and ecological traits

There was a significant effect on species invasion success of plant stature (expressed as its maximum height) (ANOVA, $P<0.01$), those considered successful in seminatural habitats were taller. The effect was still significant ($P<0.05$) when shrubs and trees were excluded from the analysis. There was no difference in height between successful and unsuccessful species in man-made habitats (Table 5).

Table 5. Summary of ANOVAs showing an effect of plant height on invasion success of a species. Heights are given (m). Log-transformation of the data was used to achieve normality.

	Seminatural habitats				Man-made habitats			
	Mean±S.E.	df	F	*P*	Mean±S.E.	df	F	*P*
Aliens total								
Successful	5.82±2.38	1,129	11.18	0.0011	2.31±1.01	1,129	0.019	0.8910
Unsuccessful	1.84±0.37				2.33±0.49			
Forbs only								
Successful	1.78±0.31	1,121	4.73	0.036	1.32±0.27	1,121	0.063	0.8045
Unsuccessful	1.18±0.09				1.23±0.09			

Particular categories of invasion success differed in the frequency distribution of life forms and in planting history (Table 3).

Therophytes and geophytes were conspicuously overrepresented among aliens successful in man-made habitats compared to those successfully invading seminatural vegetation. The reverse was the situation in hemicryptophytes. Unsuccessful species were mostly classified as therophytes or hemicryptophytes (Fig. 2b).

The proportion of species which had been planted in the territory of the Czech Republic was remarkably lower among the aliens successful in man-made habitats

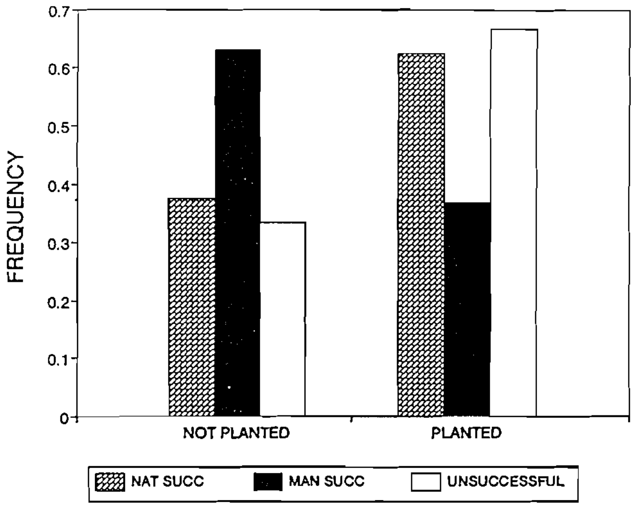


Fig. 8. Planting history, *i.e.*, whether or not species had been planted in the territory of the Czech Republic, distinguished according to invasion success.

than in those successfully invading seminatural sites (Fig. 8).

Only species possessing C-strategy were successful in seminatural habitats (the representation of other strategies was very low) whereas in man-made sites, CR-strategists were equally important (Fig. 3b). These differences, however, were not significant (Table 3).

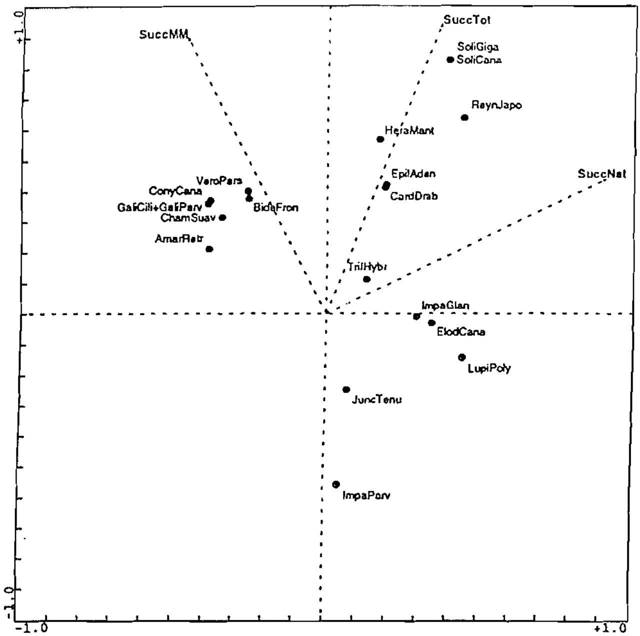
Similarly, no significant differences between particular categories of invasion success were found with respect to pollination (Fig. 4b), dispersal agents (Fig. 5c), and mode of spread (Fig. 5a, Table 3).

Ecological requirements

Successful invaders showed lower requirements for light than unsuccessful species (Table 4). Species successfully invading vegetation of man-made sites had a higher mean indicator value for light than those in seminatural habitats. This difference was, however, not significant (Kruskal-Wallis test; Fig. 6e).

Invaders into seminatural vegetation exhibited a higher mean indicator value for moisture than either unsuccessful species or those successful in man-made habitats (Table 4, Fig. 6f).

Fig. 9. (a) CCA ordination biplot representing the relationship of alien species to scores describing their invasion success in man-made habitats (SuccMM), seminatural habitats (SuccNat), and total success as a sum of both values (SuccTot). Abbreviations of species names are composed from the first four letters of genera and species names which are listed in Table 1. Only the most successful species, *i.e.*, those which attained the score of total success at least 3 were considered. *(b)* CCA ordination biplot of species traits (full arrows) related to species invasion success (dashed arrows). Explanations of species traits - Life forms according to Raunkiaer: therophytes (Ther), geophytes (Geoph), hemicryptophytes (Hemicr), chamaephytes (Cham) (phanerophytes were excluded from this evaluation); Life strategies according to Grime: C,S,R; Maximum height reached by a species (Height); Pollination agents: wind (windP), insect (insectP), self-pollinated (selfP); Dispersal agents: wind (Dwind), animals (Danim), water (Dwater), man (Dman), and self-dispersed mechanisms (Dself), vegetatively dispersed species (Veget), and seed dispersed species (Seeds); Planted species (Planted).


SuccTot
SuccMM
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SoliGiga
SoliCana
ReynJapo
HeraMant
EpilAden
CardDrab
VeroPars
ConyCana
GaliCili+GaliParv
ChamSuav
BideFron
AmarRetr
TrifHybr
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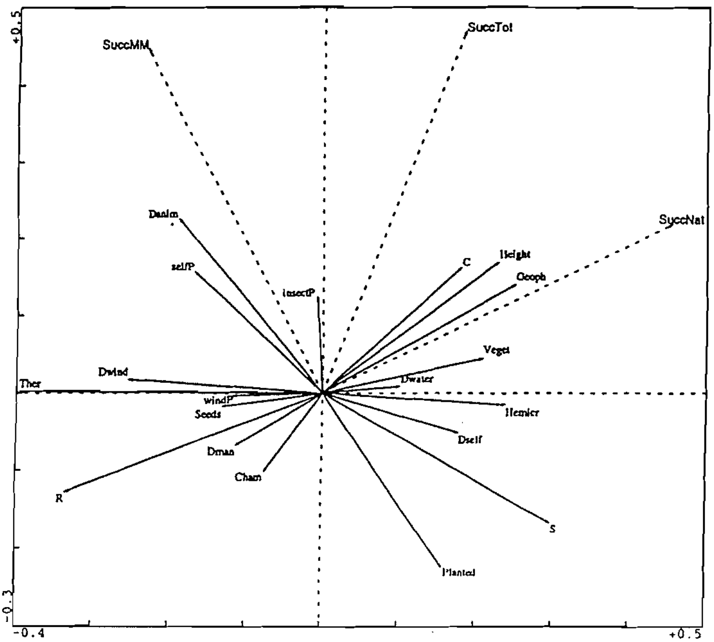
Fig. 9a.


SuccMM
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selfP
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C
Height
Geoph
Veget
Dwater
Dwind
Ther
windP
Seeds
Dman
Cham
R
Hemicr
Dself
S
Planted
+0.5
-0.3
-0.4
+0.5

Fig. 9b.

Requirements for temperature increased from the invaders of seminatural habitats category through those invading man-made sites to the unsuccessful aliens category (Table 4, Fig. 6g).

No differences between invasion success categories were found with respect to nitrogen indicator values (Table 4, Fig. 6h).

Relations between species traits and species success evaluated by CCA

The distribution of species in the ordination biplot reveals several groups of species distinguishable in relation to their success in various habitats (Fig. 9a). Arable weeds are clustered along the arrow symbolizing success in man-made habitats; strong competitors such as both *Solidago* species, *Reynoutria japonica*, and *Heracleum mantegazzianum* were distinquished as the most successful in both types of habitats. The group of species more successful in seminatural habitats is less compact. The position of an outlier *Impatiens parviflora* reflects the fact that it is the only SR-strategist.

The core information obtained by the ordination is displayed in Fig. 9b in which the species traits are related to the invasion success. Remember that the longer the arrow the higher the importance of a trait and the more acute the angle between a 'trait' arrow and a 'success' arrow the closer the positive relation between both (see Jongman *et al.* 1987). The height of a species, vegetative spreading, geophyte life form and C-strategy as a general characteristic appear to favour the species success in seminatural habitats, whereas zoochory as well as self- and insect pollination are the traits best related to its success in man-made habitats. On the other hand, R-strategy, therophyte life form, and anemochory are negatively correlated with success in seminatural habitats. Further, those species that were introduced intentionally *via* cultivation and those possessing S-strategy are not successful as invaders in man-made habitats. The Monte-Carlo permutation test showed a significant correspondence ($P<0.01$) between species traits and their success as invaders.

Discussion

The results of the present study indicate that there are *(1)* some significant differences between alien and native flora and *(2)* some plant traits which can favour the invasion success of a species (Table 6). Among the main features distinguishing the alien species from the others is an increased proportion of therophytes, especially those adopting CR-strategy (*sensu* Grime 1979). The C-strategy is also overrepresented in aliens which, further, appear to be very weak stress-tolerators (see Noble 1989). Ecological requirements of alien species are noticeably different from those of the local central European flora. They have higher demands for light, nitrogen and temperature and are confined to drier sites than local species. These conclusions correspond to the areas of origin which are, in the vast majority of cases, warmer compared to central European conditions. The correspondence between the performance of aliens in the territory under study and climatic conditions in the areas of their native distribution indicates the importance of homoclimatic analysis for understanding the pattern of plant invasions (Kruger *et al.* 1989; Lodge 1993b). Capability of growing in nitrogen-rich sites seems to support successful performance in many habitats of nutrient-overdosed Czech landscape.

Table 6. A simplified generalized scheme of the features of 'an average successful invader' and comparison of 'an average alien' with native flora. Traits in which the successful invader of seminatural habitats differs unambiguously from that of man-made sites are in bold font. N.A.: not analysed.

	Alien compared to native flora	Successful invader	
		Seminatural habitats	Man-made habitats
Taxonomy	prev. *Asteraceae*, some families not represented	*Asteraceae*, *Fabaceae*	*Asteraceae*, *Fabaceae*, *Brassicaceae*, *Amaranthaceae*
Origin	outside central Europe	prev. N America, Asia (3 areas in total)	prev. N America, Asia (5 areas in total)
Stature	N.A.	tall	normal
Life form	therophytes overrepresented	hemicryptophyte	therophyte, geophyte
Life strategy	more C, CR, less S	C	C, CR
Dispersal	no difference	wind, animal, self	animal, wind
Pollination	no difference	insect	insect
Planting	N.A.	escaped from cultivation	introduced spontaneously
Mode of spread	N.A.	seed	seed
Ecology	drier, warmer, nutrient-rich open sites	moister sites with higher nitrogen input	drier, warmer sites with higher nitrogen input

The traits conditioning successful invasion differ with respect to habitat type. An 'ideal' successful invader into seminatural vegetation appears to be a geophyte or hemicryptophyte, perennial forb or woody plant, with C-strategy, the spread of which has been assisted by cultivation as an ornamental plant. These features are associated with a high competitive ability which allows the species to compete successfully with native flora even in moist sites. Given that the plant size is related to competitive ability (Grime 1979; Keddy 1989), the taller stature of aliens successful in seminatural habitats may be taken as another fact supporting this view.

On the other hand, a species successfully naturalized in man-made sites is likely to be a therophyte (annual) using CR-strategy (note that R-strategy itself is not sufficient - see Kornas 1990) or a geophyte using C-strategy, introduced unintentionally rather than *via* escape from cultivation. The difference in planting history can reflect the fact that *(a)* species introduced unintentionally by humans are more confined to man-made habitats even in the area of their origin (so that they have a better chance to be transported by activities linked with trade, traffic *etc.* - Sýkora 1990), and *(b)* their ability to spread in man-made habitats is higher (which is evidenced by the simple fact of them having been transported from the area of origin) than that of those escaped from cultivation (which were transported intentionally, often with less consideration of their ecological demands). Consequently the chance of naturalization in the disturbed vegetation of man-made sites is higher for those species unintentionally introduced than for those escaped from cultivation. Higher temperature requirements, capability of growing in drier sites and greater importance of spread by animals are among further features distinguishing the invader naturalized in man-made sites from the species successful in seminatural vegetation.

Invaders into both habitat types come mostly from North America and Asia and are concentrated in the *Asteraceae* family (Kornas 1990; Sýkora 1990). The high number of aliens among *Asteraceae* (and among other families rich in species and therefore contributing remarkably to local flora) in itself would not be surprising because many of the characteristics conditioning their evolutionary success has also contributed to their success as invaders (Heywood 1989). However, the relative representation of aliens among this family compared to that of native species reveals that the former is really noticeably high. Surprisingly, no clear difference was found with respect to the mode of spread, suggesting some kind of trade-off between *(a)* taking advantage of numerous seeds produced with good long-distance dispersal, and *(b)* efficient use of the space once occupied through vegetative spread (see Grime 1979; Noble 1989; Di Castri 1990; Roy 1990). Generally, there is no simple biological predictor of a successful invasion (Noble 1989; Lodge 1993a; *etc.*). However, promising results emerge from analyses using species' native geographical ranges as predictors of their invasiveness (Rejmánek 1995).

Community-centered interpretation of our results suggests that communities in nutrient-rich sites in warmer parts of the country appear to be more susceptible to invasions as the invaders often require such conditions. Higher requirement for light among invaders suggests that more open, *i.e.*, early successional stages or disturbed habitats also tend to be more vulnerable to invasions (see Rejmánek 1989). However, these hypotheses are not easy to verify and the data set analysed in the present study is insufficient to do that.

In searching for general characteristics conditiong invasion success, mutual comparison of a large set of species is the most promising and, in fact, the only possible method. However, when carrying out such an analysis, one meets a number of methodological problems among which incomplete data is the main one. These problems are faced at various stages of the research:

1. Compiling the list of aliens for a given territory is rather difficult. Sources differ in their approaches to the alien status of a species which is, to a certain extent, due to phytogeographical reasons. Species considered in more northern parts of central Europe as aliens can reach the southern part of the Czech Republic so that they are native in the territory covered by this study. Moreover, increasing knowledge arising from developments within the field changes the view and some species having been considered as aliens in the past may be proved to be native. Similarly, it may be revealed that those considered as neophytes have occurred in the territory before 1492. Furthermore, lists including species only temporarily introduced or rarely escaping from cultivation can hardly ever be complete. Similar problems to those associated with the alien status of a species concern the area of its origin; especially in widespread species, it is sometimes difficult to tell the range of their original distribution.

   For these reasons, the set of alien species analysed in the present paper was restricted to those permanently established. Based on our personal view, it certainly lacks some of the species which other workers would include. More precise information about both native and alien flora is needed to assess the proportion of invaders in the Czech flora and to evaluate the probability that, once introduced, an alien species will become successfully established (see Kowarik 1995).
2. Species traits for which data are available are necessarily selective and we do not have enough quantitative data for those attributes which are extremely important for the process of plant invasions (*i.e.*, seed set, germination conditions, growth rate, regeneration ability, competitive ability, physiological features, effect of pests and pathogens *etc.* - Noble 1989; Roy 1990). The present study shows that schemes summarizing biological and ecological traits (namely life forms and Grime's strategies) are among the characteristics best correlated with the species invasion success. The separate analysis of particular traits would provide us with

a more detailed understanding of the invasion process.
3. Data necessary to describe invasion success quantitatively are not available for large sets of species (Lodge 1993a). The simple semiquantitative assessment of species abundance in the landscape which was adopted in the present study must be considered as the first step to the detailed study of the issue. Certainly, lack of a detailed knowledge of species' invasion history makes the analysis more difficult. For example, the comparison of successful and unsuccessful invaders is necessarily biased by the unavailability of information about the date of species' introduction into the area. It is clear that not all the species have had the same historical chance to reach the invasion success simply because some of them were introduced later - hence their time still may come (consider the duration of lag phases reported in *e.g.*, Pyšek and Prach 1993; Kowarik 1995). However, studies on invasion dynamics based on historical reconstruction indicate that in central Europe, there is a great potential for describing the invasion process of particular species in detail (Pyšek 1991; Pyšek and Prach 1993).

Conclusions

The results obtained by our study confirm that there is no simple biological predictor of invasion success (see also Di Castri 1990; Roy 1990; Lodge 1993a). Nevertheless, some species traits appear to occur more frequently in either alien or native flora, and particular species characteristics also appear to determine a species' invasion success or failure in particular habitat types.

Despite a certain scepticism associated with the correlative approach used in the present study, we believe this is the first step which should precede any detailed analysis of functional relations between the species traits and their invasion success. Considering the knowledge accumulated so far in the field of plant invasions, it seems probable that the invasion success of any particular species can be predicted only if both the potential invader and its target community are intensively studied (Lodge 1993a).

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References

Baker, H.G. 1965. Characteristics and modes of origin of weeds. In: H.G. Baker and C.L. Stebbins (eds.), The Genetics of Colonizing Species, pp. 147-169. Academic Press, New York.

Baker, H.G. 1974. The evolution of weeds. Ann. Rev. Ecol. Syst. 5: 1-24.

Barrett, S.C.H. and Richardson, B.J. 1986. Genetic attributes of invading species. In: R.H. Groves and J.J. Burdon (eds.), Ecology of Biological Invasions: An Australian Perspective., pp. 21-33. Australian Academy of Sciences, Canberra.

Di Castri, F. 1990. On invading species and invaded ecosystems: the interplay of historical chance and biological necessity. In: F. di Castri, A.J. Hansen and M. Debussche (eds.), Biological Invasions in Europe and the Mediterranean Basin, pp. 3-16. Kluwer Academic Publ., Dordrecht.

Crawley, M.J. 1987. What makes a community invasible? In: A.J. Gray, M.J. Crawley and P.J. Edwards (eds.), Colonization, Succession and Stability, pp. 429-454. Blackwell Scientific Publ., Oxford.

Dostál, J. 1958. Key to the Flora of Czechoslovakia. 2nd Ed. Academia, Praha (in Czech).

Dostál, J. 1982. List of vascular plants of Czechoslovak flora. Trója Botanical Garden, Praha (in Czech).

Ellenberg, H. *et al.* 1991. Zeigerwerte von Pflanzen in Mitteleuropa. Scripta Geobot. 18: 1-248.

Frank, D. and Klotz, S. 1990. Biologish-ökologische Daten zur Flora der DDR. Wiss. Beitr. Martin Luther Univ. Halle-Wittenberg 32: 1-167.

Gray, A.J. 1986. Do invading species have definable genetic characteristics? Phil. Trans. Roy. Soc. Lond. B 314: 675-693.

Grime, J.P. 1979. Plant Strategies and Vegetation Processes. 222 pp. John Wiley and Sons, Chichester.

Hejný, S. and B. Slavík (eds.) 1988-1992. Flora of the Czech Republic. Vol. 1-3. Academia, Praha (in Czech).

Heywood, V.H. 1989. Patterns, extents and modes of invasions by terrestrial plants. In: J.A. Drake, H.A. Mooney, F. di Castri, R.H. Groves, F.J. Kruger, M. Rejmánek and M. Williamson (eds.), Biological Invasions: A Global Perspective, pp. 31-60. John Wiley and Sons, Chichester.

Jongman, R.H., Ter Braak, C.J.F. and Van Tongeren, O.F.R. 1987. Data Analysis in Community and Landscape Ecology. 299 pp. Pudoc, Wageningen.

Keddy, P.A. 1989. Competition. Chapman and Hall, London.

Kornas, J. 1990. Plant invasions in Central Europe: historical and ecological aspects. In: F. di Castri, A.J. Hansen and M. Debussche (eds.), Biological Invasions in Europe and the Mediterranean Basin, pp. 19-36. Kluwer Academic Publ., Dordrecht.

Kowarik, I. 1995. Time lags in biological invasions with regard to the success and failure of alien species. In: P. Pyšek, K. Prach, M. Rejmánek and M. Wade (eds.), Plant Invasions - General Aspects and Special Problems, pp. 15-38. SPB Academic Publ., Amsterdam.

Kruger, F.J., Breytenbach G.J., Macdonald, I.A.W. and Richardson, D.M. 1989. The characteristics of invaded mediterranean-climate regions. In: J.A. Drake, H.A. Mooney, F. di Castri, R.H. Groves, F.J. Kruger, M. Rejmánek and M. Williamson (eds.), Biological Invasions: A Global Perspective, pp. 181-213. John Wiley and Sons, Chichester.

Lodge, D.M. 1993a. Biological invasions: lessons for ecology. Trends Ecol. Evolut. 8: 133-137.

Lodge, D.M. 1993b. Species invasions and deletions - community effects and responses to climate and habitat change. In: P.M. Kareiva, J.G. Kingsolver and R.B. Huey (eds.), Biotic Interactions and Global Change, pp. 367-387. Sinauer Publ.

Lohmeyer, W. and Sukopp H. 1992. Agriophyten in der Vegetation Mitteleuropas. Schr. R. Vegetationskd. 25: 1-185.

Mooney, H.A. and Drake, J.A. 1989. Biological invasions: a SCOPE program overview. In: J.A. Drake, H.A. Mooney, F. di Castri, R.H. Groves, F.J. Kruger, M. Rejmánek and M. Williamson (eds.), Biological Invasions: A Global Perspective, pp. 491-506. John Wiley and Sons, Chichester.

Mueller-Dombois, D. and Ellenberg, H. 1974. Aims and Methods of Vegetation Ecology. John Wiley and Sons, Chichester.

Newsome, A.E. and Noble, I.R. 1986. Ecological and physiological characters of invading species. In: R.H. Groves and J.J. Burdon (eds.), Ecology of Biological Invasions: An Australian Perspective, pp. 1-20. Australian Academy of Sciences, Canberra.

Noble, I.R. 1989. Attributes of invaders and the invading process: terrestrial and vascular plants. In: J.A. Drake, H.A. Mooney, F. di Castri, R.H. Groves, F.J. Kruger, M. Rejmánek and M. Williamson (eds.), Biological Invasions: A Global Perspective, pp. 301-313. John Wiley and Sons, Chichester.

Opravil, E. 1980. On the history of synanthropic vegetation 1-3. Živa 28 (66): 4-5, 53-55, 88-90 (in Czech).

Pimm, S.L. 1994. Importance of watching birds from airplanes. Trends Ecol. Evolut. 9: 41-43.

Pyšek, P. 1991. *Heracleum mantegazzianum* in the Czech Republic: the dynamics of spreading from the historical perspective. Folia Geobot. Phytotax. 26: 439-454.

Pyšek, P. and Prach, K. 1993. Plant invasions and the role of riparian habitats: a comparison of four species alien to central Europe. J. Biogeogr. 20: 413-420.

Rejmánek, M. 1989. Invasibility of plant communities. In: J.A. Drake, H.A. Mooney, F. di Castri, R.H. Groves, F.J. Kruger, M. Rejmánek and M. Williamson (eds.), Biological Invasions: A Global Perspective, pp. 369-388. John Wiley and Sons, Chichester.

Rejmánek, M. 1995. What makes a species invasive? In: P. Pyšek, K. Prach, M. Rejmánek and M. Wade (eds.), Plant Invasions - General Aspects and Special Problems, pp. 3-13. SPB Academic Publ., Amsterdam.

Roy, J. 1990. In search of the characteristics of plant invaders. In: F. di Castri, A.J. Hansen and M. Debussche (eds.), Biological Invasions in Europe and the Mediterranean Basin, pp. 335-352. Kluwer Academic Publ., Dordrecht.

Sokal, R.P. and Rohlf, F.J. 1981. Biometry. W.H. Freeman, San Francisco.

Sýkora, K.V. 1990. History of the impact of man on the distribution of plant species. In: F. di Castri, A.J. Hansen and M. Debussche (eds.), Biological Invasions in Europe and the Mediterranean Basin, pp. 37-50. Kluwer Academic Publ., Dordreeht.

Ter Braak, C.J.F. 1987. CANOCO - a Fortran program for canonical community ordination by (partial) (detrended) (canonical) correspondence analysis, principal components analysis and redundancy analysis. 90 pp. ITI-TNO, Wageningen.

Appendix 1

List of unsuccessful invaders, *i.e.*, those receiving a higher score than 1 in neither seminatural nor man-made habitats. For a complete picture of the alien flora analysed in this paper, see also Table 1.

Acer negundo, Ailanthus altissima, Allium paradoxum, Amaranthus albus, Amaranthus blitoides, Ambrosia artemisüfolia, Ambrosia trifida, Amorpha fruticosa, Anethum graveolens, Angelica archangelica, Antirrhinum majus, Artemisia annua, Artemisia verlottorum, Asclepias syriaca, Aster lanceolatus, Aster novi-belgii, Atriplex hortensis, Bryonia alba, Calystegia pulchra, Cannabis sativa, Centaurea solstitialis, Cerastium tomentosum, Chenopodium botrys, Chenopodium foliosum, Chenopodium pumilio, Consolida orientalis, Cornus alba, Coronopus didymus, Corydalis lutea, Cymbalaria muralis, Digitalis purpurea, Echinocystis lobata, Elaeagnus angustifolia, Elsholtzia ciliata, Erigeron annuus, Erigeron strigosus, Fallopia aubertii, Galega officinalis, Geranium pyrenaicum, Guizotia abyssinica, Helianthus tuberosus, Hirschfeldia incana, Hordeum jubatum, Inula helenium, Isatis tinctoria, Iva xanthiifolia, Kochia densiflora, Kochia scoparia, Laburnum anagyroides, Lactuca tatarica, Lepidium densiflorum, Lepidium virginicum, Lolium multiflorum, Lonicera tatarica, Lycopersicon esculentum, Mahonia aquifolium, Malva mauritiana, Malva verticillata, Mentha spicata, Mimulus guttatus, Mimulus moschatus, Myrrhis odorata, Nicandra physalodes, Oenothera biennis, Oenothera erythrosepala, Oenothera parviflora, Oenothera renneri, Ornithogalum nutans, Oxalis corniculata, Oxalis dillenii, Panicum capillare, Parthenocissus inserta, Phacelia tanacetifolia, Phalaris canariensis, Physocarpus opulifolius, Potentilla norvegica, Quercus rubra, Reynoutria sachalinensis, Rhus typhina, Rudbeckia laciniata, Rumex patientia, Rumex scutatus, Rumex triangulivalvis, Salvia officinalis, Salvia verticillata, Sedum spurium, Sempervivum tectorum, Senecio vernalis, Silybum marianum, Sinapis alba, Sisymbrium irio, Sisymbrium volgense, Sisyrinchium angustifolium, Smyrnium perfoliatum, Solanum tuberosum, Sorghum halepense, Syringa vulgaris, Tanacetum parthenium, Telekia speciosa, Trifolium resupinatum, Veronica filiformis, Vicia lutea, Vicia sativa, Xanthium spinosum, Zea mays.