Compositae as invaders: better than the others?

Jsou složnokvěté úspěšné jako invazní druhy?

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Records of alien species in 26 local floras all over the globe were analysed. The representation of *Compositae* in these floras was assessed and compared with that of other families contributing most to the alien floras. The *Compositae* were present in all alien floras and by contributing 13.5 % on average represent the second most represented family (after *Gramineae*). Comparison of their performance in alien floras (13.5 %) with their proportion of the world flora (8.4 %) indicates that they are over-represented among aliens. When using a relative measure, i.e. relating species numbers to the global species pool in a family, *Compositae* rank about average. However, the family is remarkably successful in terms of dispersal and establishment.

Keywords: Alien species, regional floras, global pattern, *Compositae*, dispersal, mode of introduction, establishment, pollination, life strategies

Introduction

Compositae are probably the largest family of flowering plants; estimates of the species number it contains vary between 21,000 (e.g. Mabberley 1987) and 25,000 species (Heywood 1978). The family constitutes almost 10 % of the world flora which is evidence of their enormous success in the present-day plant kingdom. As an evolutionarily advanced family of dicotyledons, *Compositae* possess a number of correlated morphological features (Cronquist 1970, 1981) of undoubted ecological relevance. It is not surprising that the *Compositae* play an important role in alien floras worldwide; this phenomenon has been noted before (Heywood 1989). However, analysis of a proper data set is still needed to assess whether the representation of the family in alien floras reflects its superior ability to invade adventive areas or is simply a consequence of its abundance.

The present paper (1) summarizes available data on this point, (2) compares their performance as invaders with that of other families, (3) takes into account some other factors that may be expected to affect the outcome of invasions such as the mean of introduction, (4) evaluates not only the presence of *Compositae* in alien floras but also their ability to establish and create problems for and interference with human management objectives.

Data

The lists of alien species from 26 global regions were gathered (Table 1). These data sets represent complete records of aliens of given areas and cover various geographical locations, climates and ecological situations, thus providing a considerable insight into the variety of alien floras all over the world.

In each data set, the number of *Compositae* representatives was calculated (or taken directly from the original paper, if given) and the percentage contribution of the family to

Table 1. – Data sets used in the present paper. S – South, N – North, W – West, E – East, C – central. The minus sign indicates southern latitude. Habitat types to which the particular lists are related: c – complete data (all habitats considered), u – urban only, n – natural only. Total number of aliens recorded, number of families containing alien species, number of alien species of *Compositae*, their percentage contribution to the alien flora of the region and ranking among families according to the latter are shown. ? impossible to infer from the original data source.

						Alien flora		*Compositae*			
	Locality	Region	Climate	Latitude	Habitat	Number of spec.	Number of fam.	No.	%	Rank	Source
1	California (state)	North America	subtrop	28.00	c	975	?	142	14.6	2	Rejmánek et al. 1991
2	Hastings Reserve, Calif.	North America	subtrop	36.23	n	143	28	18	12.6	2	Knops et al. 1995
3	St Louis, Missouri	North America	temp	38.38	u-city	393	58	52	13.2	2	Muehlenbach 1979
4	SE Florida	North America	trop	25.40	c	169	60	12	7.1	3	Austin 1978
5	Chile	South America	subtrop	–31.00	c	128	30	25	19.5	1	Montenegro et al. 1991
6	Buenos Aires (province)	South America	temp	–34.37	c	483	60	75	15.5	2	Söyrinki 1991
7	Crozet Archipelago & oth.	Subantarctic Isl	polar	–46.20	c	112	24	22	19.6	1	Carcaillet 1993, Walton 1975
8	Galapagos	Pacific Isl	trop	–0.30	c	126	51	11	8.7	1	Macdonald et al. 1988
9	Hawaii	Pacific Isl	temp	22.00	c	813	113	95	11.7	2	Wester 1992
10	Northern Line Isl	Pacific Isl	trop	3.73	c	90	28	13	14.4	2	Wester 1985
11	South Australia (state)	Australia	trop	–29.00	c	904	?	123	13.6	2	Kloot 1991
12	SW South Island	New Zealand	temp	–44.00	c	140	40	19	13.6	2	Johnson 1982
13	Auckland	New Zealand	temp	–36.51	u-city	615	103	67	10.9	2	Esler 1987
14	Singapore (state)	Asia SE	trop	1.19	c	136	45	15	11.0	2	Corlett 1988
15	Hongkong (state)	Asia SE	subtrop	22.20	c	144	44	26	18.1	1	Corlett 1992
16	Israel (state)	Asia W	subtrop	31.30	c	122	25	21	17.2	2	Dafni et Heller 1990
17	Cape of Good Hope Res.	Africa S	subtrop	–34.12	n	77	28	3	3.9	7	Macdonald et al. 1987
18	Kruger National Park	Africa S	subtrop	–24.00	n	113	43	17	15.0	1	Macdonald et Gertenbach 1988
19	SW Africa/Namibia	Africa S	trop	–28.00	n-desert	164	37	28	17.1	1	Brown et Gubb 1986
20	Region N of Sahara	Africa N	subtrop	37.00	c	86	35	9	10.5	2	Lefloch et al. 1990
21	Germany (state)	Europe C	temp	51.00	c	595	73	81	13.6	1	Frank et Klotz 1990
22	Brno, Czech Republic	Europe C	temp	48.13	u-city	424	45	71	16.7	1	Grüll 1973
23	Leipzig, Germany	Europe C	temp	51.20	u-city	583	68	88	15.1	1	Gutte 1989
24	Riga, Lithuania	Europe N	temp	56.58	u-city	172	30	31	18.0	1	Schultz 1978
25	Kärsö-Högholmen Isl, Sweden	Europe N	temp	59.20	c	57	27	3	5.3	7	Holmberg 1975
26	NE Finland	Europe N	temp	65.58	c	239	35	33	13.8	1	Ahti & Hämet-Ahti 1971

the total of the respective alien flora was expressed. The average value from the 26 data sets considered was then calculated and taken as a quantitative measure of the family representation in the world alien floras. The information on species immigration status followed the original source (Table 1). 'Alien' is understood to mean a species that has reached a given area as a consequence of neolithic or post–neolithic human activities (Webb 1985, Pyšek 1995).

Representation of *Compositae* in the world flora was calculated on the basis of the species number given by Mabberley (1987). The results obtained for *Compositae* are compared with the other five families most represented in alien floras (Pyšek, in preparation).

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

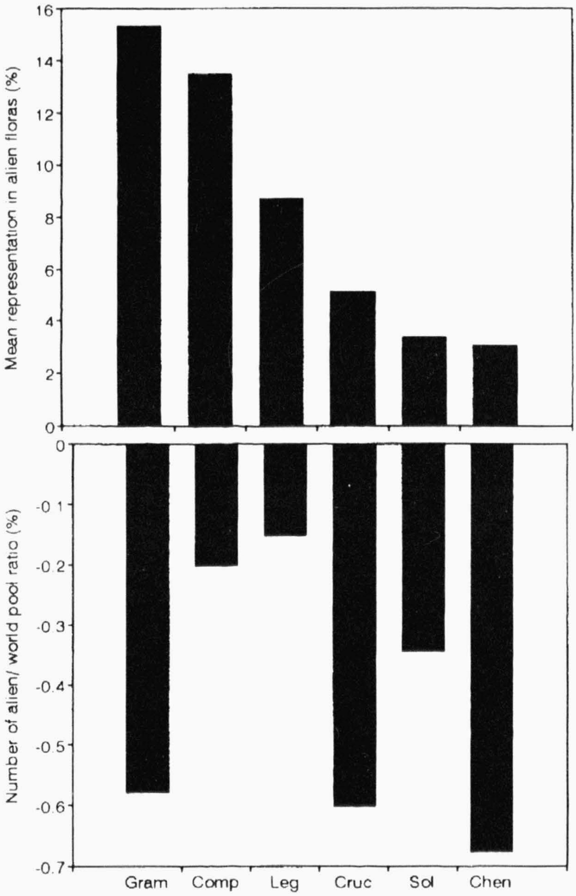


Fig. 1. – Position of *Compositae* among families supplying alien floras worldwide with most of their members. Mean percentage contribution to the alien floras (n = 26, see Table 1) is shown in the upper part of the diagram. Relative measure expressed as a ratio of aliens to the total number of species in the family, i.e. the percentage of its representatives in the world flora which were introduced into given regions, is shown at the bottom. The mean value for the 26 regions analysed is shown. Gram – *Gramineae*, Comp – *Compositae*, Leg – *Leguminosae*, Cruc – *Cruciferae*, Sol – *Solanaceae*, Chen – *Chenopodiaceae*.

Results

Representation of Compositae in alien floras: a global view

The performance of *Compositae* in particular alien floras is summarized in Table 1. Their proportion ranges from 3.9 % (Cape of Good Hope Nature Reserve, South Africa) to 19.6 % (Crozet Archipelago, Subantarctic Islands) with an average value of 13.47 %. Comparison of this value with the representation of the family in the world flora (8.4 %, Mabberley 1987) indicates that the family is over-represented among aliens. Numbers of *Compositae* species in particular floras are also shown in Table 1, though these are not comparable among regions because of different sizes of sample areas. Compared with other familes, *Compositae* rank 1 or 2 in most particular floras and are the second highest represented family (after *Gramineae*) if the average percentage contribution to the alien floras is taken as a measure.

Different species numbers in particular families make it necessary to take a relative measure of occurrence among aliens, if the families are being compared with each other. If a ratio of aliens introduced to a given region to the total number of species in the family is used (Fig. 1b), the value obtained for *Compositae* is remarkably lower (0.2 %) than for other leading invasive families, namely *Chenopodiaceae* (0.68 %), *Cruciferae* (0.60 %) and *Gramineae* (0.58 %).

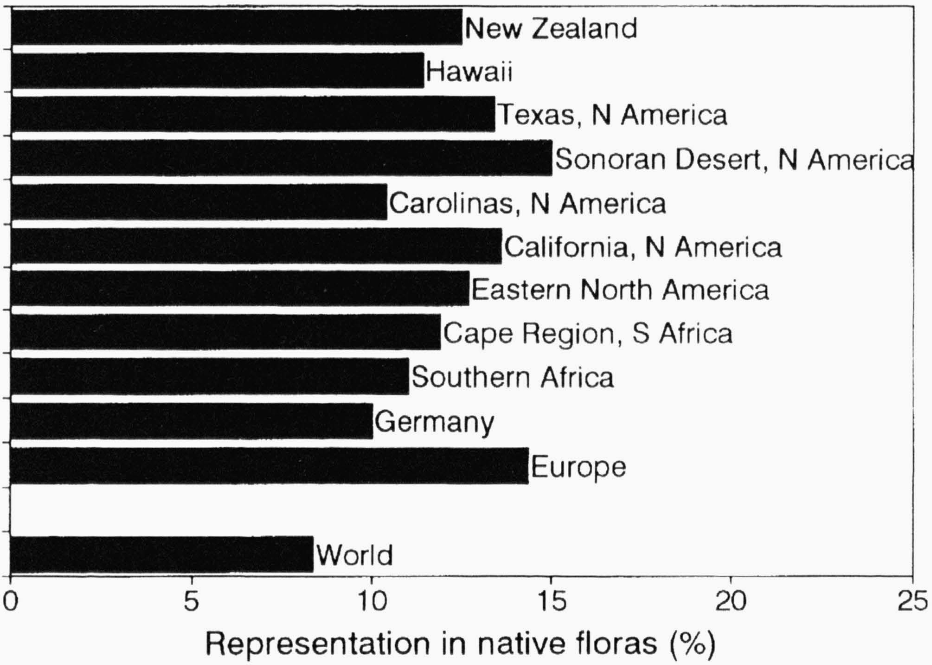


Fig. 2. – Representation of *Compositae* in selected native floras. Data for Europe were calculated from Flora Europaea (Tutin et al. 1964–1980), those for Germany from Frank et Klotz (1990), other data were taken from Goldblatt (1978). Contribution of the family to the world flora was calculated on the basis of the species number given in Mabberley (1987).

Comparison of the representation of *Compositae* in alien floras (13.5 %, Table 1) with that in native floras (12.4 %, Fig. 2) reveals similar average values. However, the data have only exploratory value since the performance of the family in native floras is not a convenient reference measure for evaluating the family representation among aliens. Moreover, the data set concerning native floras comes from a rather limited selection of areas.

Comparison of spontaneous and deliberate introductions

When spontaneous alien flora of particular regions (i.e. that resulting from unintentional introductions by humans) is analysed separately, quite a consistent pattern emerges in *Compositae* (Fig. 3). Unfortunately, there are only three data sets among those analysed in the present study which give carefully evaluated information on the mean of introduction, and hence allow the distinction between accidental introductions and deliberate translocations of crops and ornamentals by humans to be made. In all three data sets, the role of *Compositae*, in terms of their contribution to the alien flora, is much higher (as much as 5 times in the case of Hawaii) when spontaneous introductions are treated separately (Fig. 3).

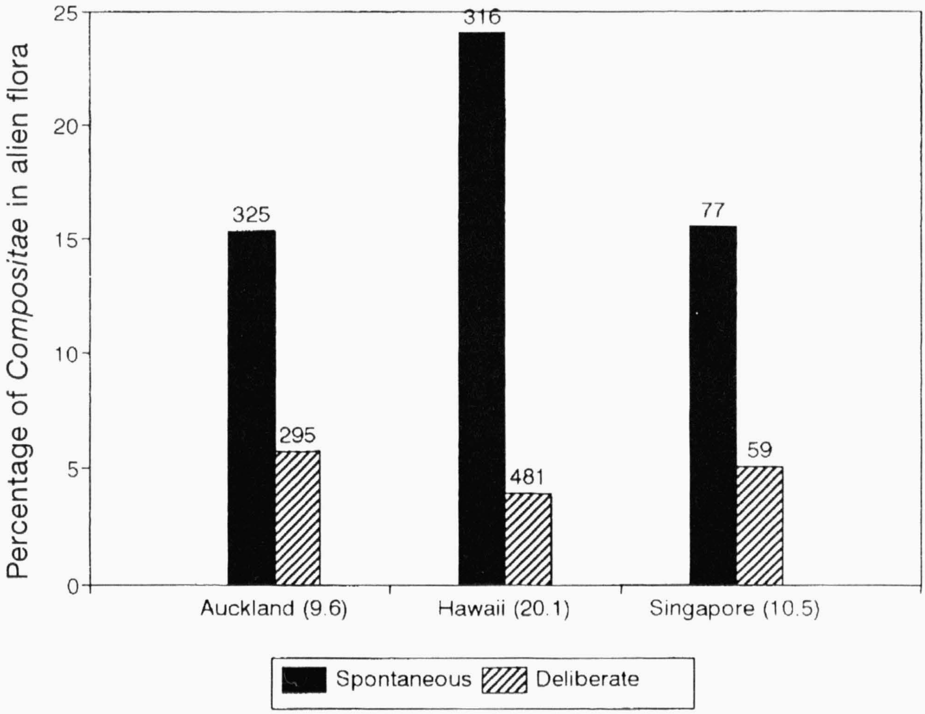


Fig. 3. – Effect of the mode of introduction on the representation of *Compositae* in selected alien floras. Percentage contribution of the family to spontaneously introduced alien flora and to that introduced deliberately are compared and the difference is shown in brackets following the name of the region. See Table 1 for details on the regions analysed. Species numbers are above the bars.

Establishment success of Compositae compared to other families

Eleven of the data sets listed in Table 1 include some measures of the degree of naturalization; these were used to evaluate the ability of *Compositae* to become permanently established in alien floras (Fig. 4). In the majority of cases (Table 2), *Compositae* were more represented in the data subsets consisting of established (or more abundant or frequent, see Fig. 4) species, compared to the complete list of aliens. This is indicative of their potential to invade. Compared to other families, *Compositae* not only exhibit the highest mean ratio of established species (Fig. 4b) but also is the only family whose representation is increased among successful species in most cases (Table 2).

Do alien Compositae differ from others in species traits?

Data available on German flora (Frank et Klotz 1990) made it possible to analyse in detail whether the alien representatives of *Compositae* differ in particular traits from other aliens and from native species (Fig. 5, Table 3). Despite the results being concerned with one particular region, they may be taken as indicative of Central Europe as a whole, because the latter's species pool is fairly similar to that covered by the work of Frank and Klotz.

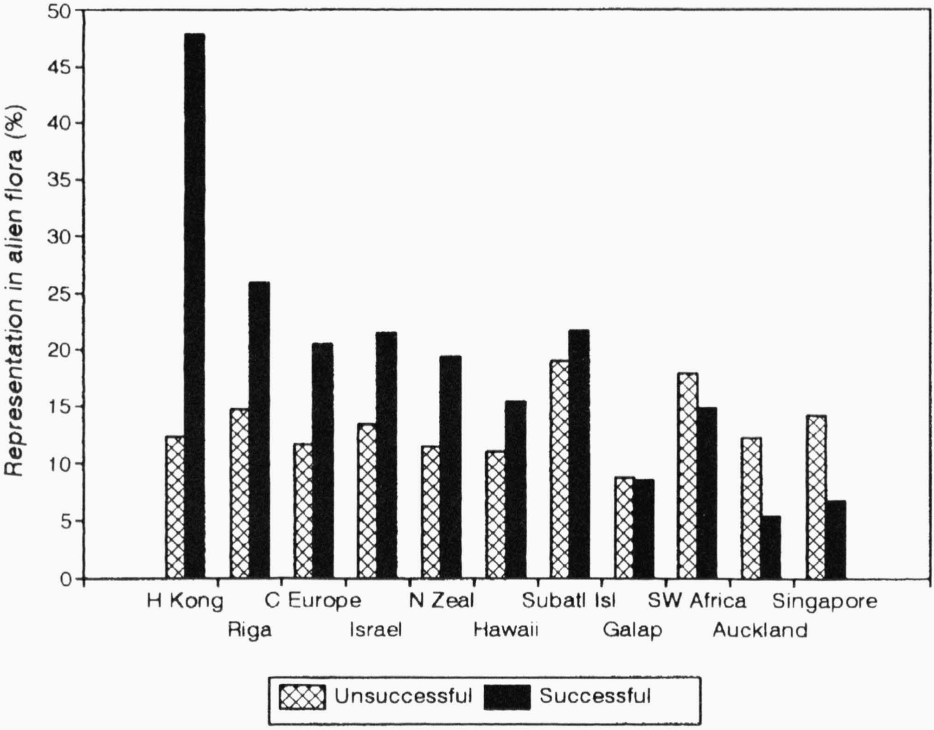
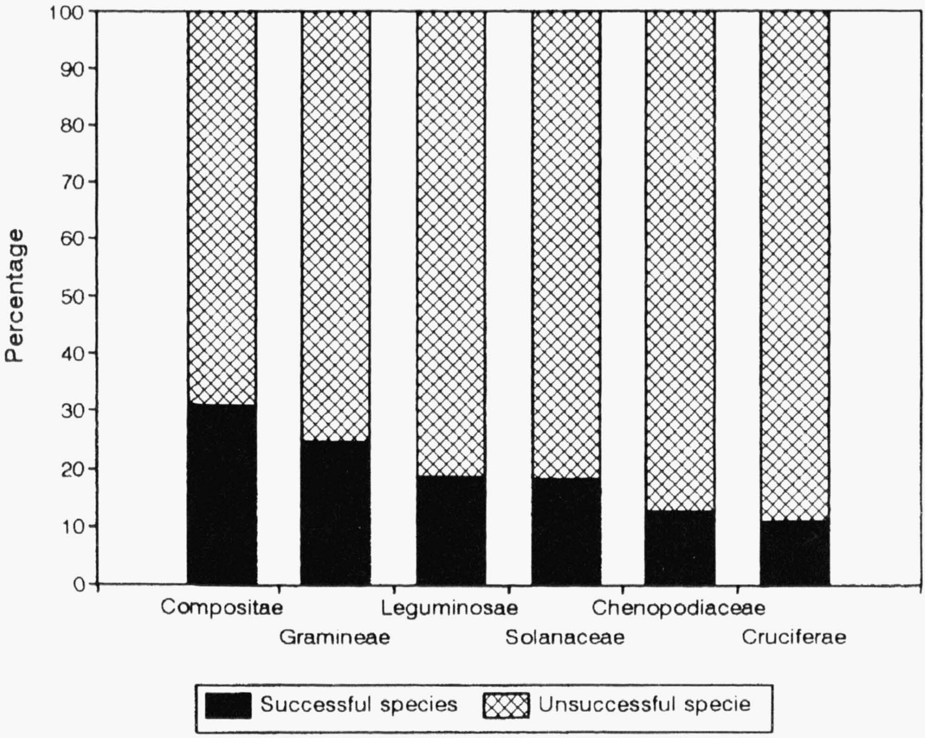


Fig. 4. – (a) Establishment success of *Compositae* in alien floras. Where some measure of success was available in the original source, the representation of the family among the "successful" species was compared with that among the others, i.e. relatively "unsuccessful". The following data sets were used, with the criterion for a species being considered successful mentioned and the rest taken as unsuccessful: Hongkong (Corlett 1992; common species); Riga (Schultz 1978; established neophytes); Central Europe (Frank et Klotz 1990; established neophytes listed by Pyšek et al. 1995); Israel (Dafni et Heller 1990; common and expanding species); New Zealand, SW South Island (Johnson 1982; species present in more than 11 localities, i.e. 20 %); Hawaii (Wester 1992; species present on at least 5 islands); Subantarctic Islands (Carcaillet 1993, Walton 1975; naturalized

Table 2. – Comparison of *Compositae* with other families according to establishment success. Where some measure of success was available in the original source (n = 11, see caption to Fig. 4) the representation of the family among the "successful" species was compared with that among those "unsuccessful". Number of cases (out of 11) in which the family was more represented among successful aliens (A) and vice versa (B) is shown, and families are ranked according to the difference between "over-represented" and "under-represented", i.e. the most successful appear on top.

Family	A	B	A–B
Compositae	7	4	3
Gramineae	5	6	–1
Solanaceae	4	6	–2
Chenopodiaceae	3	7	–4
Leguminosae	3	8	–5
Cruciferae	2	8	–6



and persisting species); Galapagos (Macdonald et al. 1988; species present on at least 3 islands); SW Africa/Namibia (Brown et Gubb 1986; species occurring in more than 4 habitats); Singapore (Corlett 1988; common species); Auckland, New Zealand (Esler 1987; increasing species). (b) Comparison of families. Proportion of successful species is expressed in each data set and the mean value is shown.

Some general features of *Compositae*, regardless of immigration status, are illustrated, i.e. large proportion of self-pollinated species (by about 20 % compared to the rest of central European vascular plants), increased dispersal by special structures such as hooks, adhesive mechanisms etc., as well as by ants, and relatively less importance of water, self-dispersal and vegetative spread. Alien *Compositae* differ from native members of the family in their higher proportion of therophytes. The most remarkable difference between both groups concerns life strategies (sensu Grime et al. 1988): 76.5 % of aliens from the *Compositae* family are classified as having C- or CR-strategy whereas combinations of S-strategy are strongly under-represented, being however rather important in the native flora (Fig. 5).

Differences in pollination and dispersal modes between alien species of *Compositae* and aliens from other families were also highly significant (Table 3), with namely self-pollination and special dispersal structures over-represented in the former (Fig. 5). These groups did not differ in life forms and also the difference in life strategies was less significant ($P < 0.05$, Table 3), alien *Compositae* being slightly more frequent among C- and CR-strategists than aliens from other families.

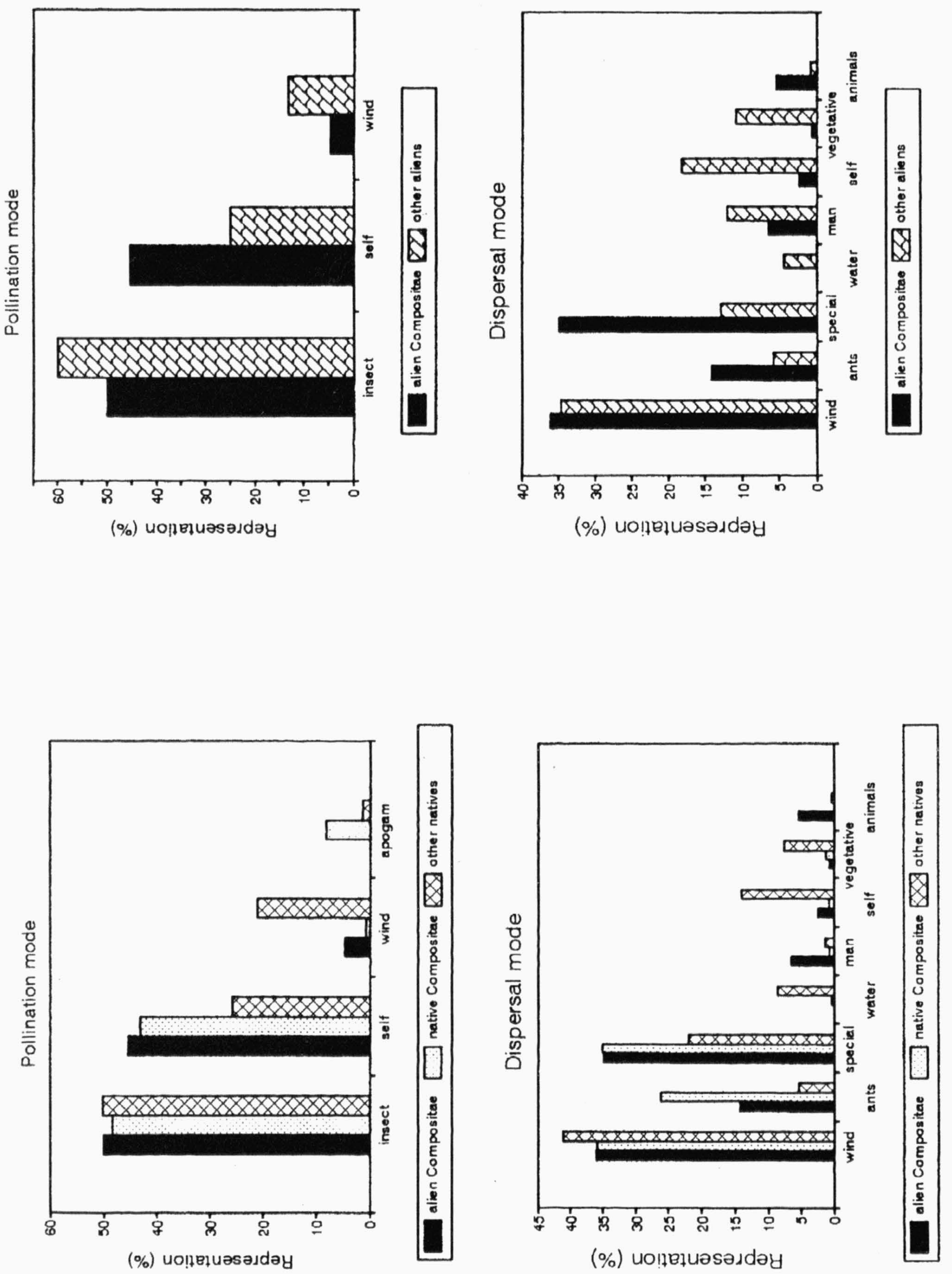
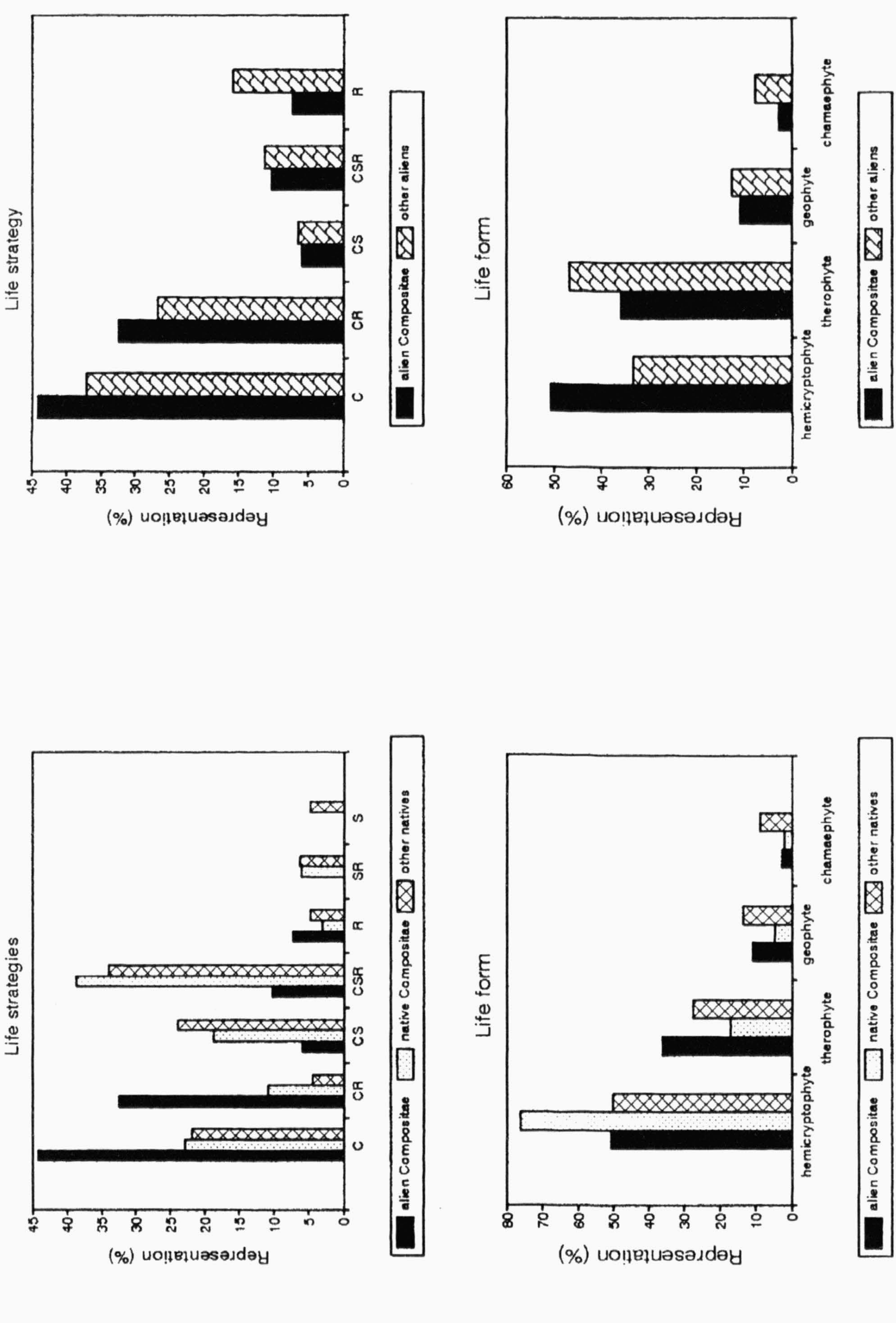


Fig. 5. – Comparison of (a) alien (n = 68) *Compositae* with both native *Compositae* (n = 167) and other native species (n = 1502), and (b) alien *Compositae* with other alien species (n = 378) of the German flora with



respect to the mode of pollination, dispersal, life forms and strategies (Grime's scheme). See Table 3 for the statistics. Data from Frank & Klotz (1990), only neophytes considered as aliens, archaeophytes excluded.

Table 3. – Difference in selected traits between (a) alien and native *Compositae*, and (b) alien *Compositae* and other alien species. Comparison was carried out on German flora (Frank et Klotz 1990). The null hypothesis was tested (chi^2 test on contingency tables) that the groups distinguished with respect to the systematic position and immigration status do not differ in particular traits. Information on traits was taken from Frank et Klotz (1990); life forms follow the Raunkiaer's scheme, life strategies that of Grime (Grime et al. 1988). NS means that we cannot reject null hypothesis on significance level less than 0.05.

		Alien vs. native *Compositae*		Alien *Compositae* vs. other aliens	
	df	chi^2-value	P	chi^2-value	P
Fertilization	2	8.29	0.0157	23.13	<0.0001
Dispersal	7	53.2	<0.0001	114.2	0.0001
Life strategy	3	16.78	0.0008	8.95	0.0298
Life form	5	44.74	<0.0001	5.61	NS

Discussion

Compositae as aliens on a global scale: a quantitative pattern

From the present paper it appears that *Compositae* play an important role among world invaders by being present in alien floras virtually worldwide and contributing to these principally. The reasons can be seen in that *Compositae* are one of the evolutionarily most advanced families (Cronquist 1981, Raven et al. 1992, Frohne et Jensen 1992) and possess a number of features that may represent an advantage in the course of the invasion process, e.g. high reproductive rate, specialized dispersal structures, diversity of metabolic products providing protection from grazing, high level of apomixis etc. (Heywood 1989). When alien floras are analysed with respect to their geographical location, climate and habitat type (Pyšek, in preparation), it appears that the distribution of *Compositae* among aliens is not determined by any of the factors mentioned, showing rather even, steadily high status in alien floras.

To overcome the fact that particular families differ in species numbers, i.e. there are species pools of different size serving as sources of potential invaders, a relative measure is better for comparative purposes. The most straightforward measure is the ratio of aliens introduced to a given region to the total number of species in the family (Rejmánek et al. 1991), i.e. the percentage of the global species pool in a family invading the given region. In such relative terms, however, *Compositae* appears to be a family with only an average ranking among those that are over-represented as invaders (the most successful being *Papaveraceae*, *Chenopodiaceae*, *Amaranthaceae*, *Cruciferae*, *Polygonaceae* and *Gramineae* – Pyšek, in preparation).

The role of *Compositae* among invasive families becomes more remarkable when only spontaneous introductions are taken into account. If complete floristic lists of aliens are used to assess how biological and ecological properties of particular species (and analogously, those of higher systematical units) affect their invasive potential, one must face an important bias related to the crucial step of invasion process, i.e. dispersal. Being translocated deliberately by humans undoubtedly constitutes a major advantage for a species which is usually, if planted as crop or ornamental, given also more time to adapt to climate, habitats or herbivore load before becoming a casual garden escape. For an inadvertedly introduced species, the situtation is more risky and demanding in terms of reproductive potential, effective dispersal and competitive ability. For that reason, excluding plants introduced on purpose and analysing only the lists of those arriving without direct human intervention, seems to be a convenient step to assess the real invasive potential of the species, and consequently of the family. Adopting this measure shows that *Compositae* are doing much better as spontaneous invaders and their success is favoured more than that of any other family (Pyšek 1997). Unfortunately, there is only a limited number of data sets providing carefully assessed information on the means of introduction (Esler 1987, Corlett 1988, Wester 1992). It is probable, that specialized dispersal structures (pappus, hooked fruits) provide the members of the family with a considerable dispersal potential and advantage. It is therefore not surprising that *Compositae* are successful as spontaneous invaders ever to the extremely isolated Hawaii archipelago, located 3000 km from the nearest mainland.

Complete lists of alien species reflect only species presence or absence and are thus the result of their ability to reach the area of adventive distribution and persist at least as long as to be recorded. Although different measures of naturalization and/or abundance were used in particular data sets analysed in the present paper, preventing therefore direct comparison, it is clear that *Compositae* are disproportionally successful in the phase of establishment. This fact may be, at least in part, related to their prevailing strategy (C and CR); the spectrum of life strategies is remarkably different from native flora indicating ability to exploit vacant niches in the landscape. Self-pollination and a high level of apomixis are also considered an advantage in establishment since species capable of uniparental reproduction are likely to be more effective colonizers because of their capability to start reproduction following long-distance dispersal of a single individual (Barrett et Richardson 1986, Michalakis et al. 1993) and maintain reproduction throughout the initial phase of the invading process, during which periods of low population density are inevitable (Roy 1990).

Compositae as noxious invaders

Even though in strictly relative terms *Compositae* show only an average success as invaders, there are many of them in terms of numbers and quite a few seriously interfere with human objectives in many areas of the world (Table 4). The list of Cronk et Fuller (1995), containing the world most noxious invaders, includes 15 species of *Compositae* (Table 4), i.e. 7.4 %. However, as for any such list it must be treated with caution to a certain extent. Lower representation of *Compositae* (which is still well on the level of their proportion in the world flora) may be due to the focus on natural habitats. High reproductive rate and R- or CR-strategy frequently occurring in *Compositae* indicates their being at least equally successful in disturbed sites (Timmins et Williams 1987). Some members of the family perceived as serious pests elsewhere are missing from the list, e.g. *Centaurea* species constituting serious problems in North America (Roché et Roché 1988). Moreover, a high proportion of *Compositae* was recorded in some local lists of noxious aliens (Groves 1986, Newsome et Noble 1986).

Attempts to eradicate a species can certainly be taken as a measure of how serious a pest it is perceived to be. Up to the mid eighties, there were 101 attempts at biological control of which the highest number of cases (25) concerned *Compositae* (Julien et al. 1984). This may be taken as another indication of the family success in practical terms.

Table 4. – Representatives of *Compositae* included in the list of the world's most noxious invaders compiled by Cronk et Fuller (1995). LF = life form: s – shrub, t – tree, h – herb, cl – climber. Origin: N – North, S – South, E – East, W – West, C – Central. IC = invasive category used by Cronk et Fuller (1995, see the definition therein); the higher the value, the more invasive the species is considered to be.

Species	LF	IC	Origin	Region invaded
Chrysanthemoides monilifera	s,t	3.5	Africa S	Australia, New Zealand, Europe
Mikania micrantha	cl	2.5	America S,C	India, Malaysia, Pacific Islands
Ageratina adenophora	h	2.5	America C	Asia, Australia, New Zealand, Hawaii, Africa, America N
Chromolaena odorata	s	2.5	America N,C,S	Africa S, Asia
Hieracium pilosella	h	2	Europe	New Zealand
Hypochoeris radicata	h	2	Europe	Hawaii
Hieracium praealtum	h	1	Europe	New Zealand
Rudbeckia laciniata	h	1	America N	Japan, Europe
Mikania scandens	cl	1	America N	Asia SE
Carduus nutans	h	1	Europe	Canada, New Zealand
Aster subulatus	h	1	America N	Asia W
Ageratina riparia	h	1	America C	Australia, New Zealand, Hawaii
Solidago canadensis	h	1	America N	Europe C
Helianthus tuberosus	h	1	USA	Europe C
Baccharis halimifolia	s	1	America N	Australia

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Souhrn

Práce analyzuje výskyt zástupců čeledi *Compositae* v invazních flórách. Data pocházejí z 26 floristických seznamů zavlečených druhů z nejrůznějších lokalit po celém světě, z různých zeměpisných a klimatických oblastí i typů stanovišť, takže poskytují poměrně ucelenou představu o zastoupení jednotlivých čeledí. *Compositae* se na invazních flórách podílejí v průměru 13,5 %. Srovnání této hodnoty s podílem čeledi na světové flóře (8,4 %) ukazuje, že *Compositae* patří mezi čeledi se zvýšeným zsatoupením v invazních flórách a že je tudíž nutno je považovat za úspěšné ve vztahu k invaznímu potenciálu. Protože počty druhů v jednotlivých čeledích se liší a každá má tudíž k dispozici odlišně velkou zásobu potenciálních invazních druhů, bylo použito ke srovnání skutečného invazního potenciálu relativní měřítko – procento druhů z celkového druhového bohatství čeledi, jež invadovalo do dané oblasti. Průměrnou hodnotou 0,2 % se *Compositae* řadí mezi průměrně úspěšné čeledi. Mimořádně úspěšné jsou druhy čeledi *Compositae*, vyloučíme-li z analýzy druhy introdukované člověkem úmyslně jako plodiny či okrasné rostliny; tento fakt svědčí o dobré schopnosti šíření. Také pokud jde o schopnost naturalizace, zdají se na základě dostupných dat zástupci čeledi úspěšnější než kterákoli jiná, z hlediska invazí významná čeleď. Na otázku, zda jsou *Compositae*, pokud jde o invaze, nadprůměrně úspěšnou čeledí, je třeba odpovědět spíše kladně. Tento závěr lze dát do souvislosti s řadou biologických vlastností typických pro tuto čeleď, jež mohou být výhodné v jednotlivých fázích invazního procesu, jako např. specializované struktury usnadňující rozšiřování, častý výskyt apomixe, přítomnost sekundárních metabolitů apod.

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