Reproductive characteristics of neophytes in the Czech Republic: traits of invasive and non-invasive species

Reprodukční vlastnosti českých neofytů: rozdíly mezi invazními a neinvazními druhy

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This paper describes the reproductive characteristics of 93 neophytes (alien species introduced after 1500 A.D.) of the flora of the Czech Republic and compares trait values between naturalized invasive and naturalized non-invasive neophytes. Species were sampled and seed collected in the field from multiple localities in the Czech Republic. Traits related to seed production (propagule number per plant and per population), dispersal (propagule size, length/width ratio and weight; buoyancy; epizoochory; terminal velocity) and establishment (germination; seedling relative growth rate; seedling establishment) were measured for each species either in the field, in a common garden experiment or in the laboratory. Invasive species significantly differ from naturalized non-invasive species in propagule length/width ratio (by having lower ratio, i.e. more rounded propagules) and fecundity (invasive species are more fecund, both per individual plant and in terms of the population propagule production). Invasive species have proportionally fewer seedlings establishing in the autumn and better capacity for dispersal by wind than non-invasive species. The results for several traits differ depending on whether or not the effect of phylogeny is included in analytical models. Considering species relatedness expressed as a taxonomic hierarchy, invasive species have lighter propagules and higher population propagule numbers, and marginally significantly differ in producing more propagules per plant and having higher capacity for dispersal by water. We found that most variation in invasiveness is linked to variation among species within genera. This distribution of relatedness means that predictions of whether a species will become invasive cannot be based on traits of the relatives of the given species at higher taxonomic levels. The distinction made in this paper, i.e. invasive species vs. naturalized but non-invasive species, can potentially contribute to a deeper understanding of the role of traits associated with invasiveness because the crucial transition from the naturalized to invasion stage is rarely addressed in invasion ecology.

K e y w o r d s: alien plant invasion, anemochory, buoyancy, dispersal, Central Europe, diaspore size and weight, epizoochory, fecundity, germination, neophyte, relative growth rate, seed production, seedling establishment, terminal velocity

Introduction

Biological invasions are among the most dynamically developing fields of ecology and recent intensive research has yielded continental to global syntheses over a wide range of topics, including dynamics of introductions, patterns and mechanisms of invasion, impact of invaders and management of invaded ecosystems (Millennium Ecosystem Assessment 2005, Hulme et al. 2008, 2009b, Blackburn et al. 2009, Davis 2009, McGeoch et al. 2010,

Pyšek et al. 2010a, Pyšek & Richardson 2010, Vilà et al. 2010). Predicting which species will become invasive is an important part of research in biological invasions and still represents an ultimate goal of invasion ecologists (Daehler & Carino 2000, Rejmánek 2000, Kolar & Lodge 2002, Richardson & Pyšek 2006, Pyšek & Richardson 2007). Our ability to predict, with reasonable precision, the outcome of invasion by a particular species depends on knowledge of its invasiveness in a given geographical area and the habitats it invades.

Biological and ecological determinants of invasive success can be studied in two ways. Detailed studies of invasion pattern in both secondary and native areas, including the population ecology of an invader and studies of its genetic make up and variation, and performed on groups of taxonomically related species or genera have proved to be a promising tool and have yielded robust information about determinants of species invasiveness (Rejmánek 1996, Rejmánek & Richardson 1996, Grotkopp et al. 2002, Van Kleunen et al. 2007, 2010). However, such detailed studies cannot be performed for tens or hundreds of species differing in their characteristics. Another research venue, making use of large species sets, are therefore analyses of regional inventories of alien plants that have the potential to produce invasion generalizations over a wide range of taxa, usually over vascular plants as a whole (e.g. Thompson et al. 1995, Crawley et al. 1996, Hamilton et al. 2005, Cadotte et al. 2006b; see Cadotte et al. 2006b and Pyšek & Richardson 2007 for reviews). A major constraint of such multispecies analyses includes, however, rather limited detail in terms of information on plant characteristics used as predictors of invasive behaviour. Most comparative papers use data available in databases in which the information on complete floras must be necessarily rather superficial and of limited comparability as it was collected by using various methods. Among data that are most urgently missing is information on reproductive characteristics that are generally considered as crucial determinants of invasion success (Pyšek & Richardson 2007).

The alien flora of the Czech Republic has been thoroughly investigated recently and this country belongs among those with the best information available in Europe on their alien flora (Pyšek et al. 2002, Lambdon et al. 2008). There is detailed information on the structure of the alien flora of the Czech Republic and its introduction dynamics (Pyšek et al. 2003b, c), habitat affinities (Chytrý et al. 2005, Sádlo et al. 2007, Hejda et al. 2009b) and spatial pattern of the level of invasion of plant communities in the country (Chytrý et al. 2009a). This knowledge has been used for analyses of habitat invasibility (Pyšek et al. 2005, Chytrý et al. 2008b), determinants of invasiveness of alien plant species (Křivánek et al. 2006, Křivánek & Pyšek 2006, Chytrý et al. 2008a, Pyšek et al. 2009b, Kubešová et al. 2010), including the effect of residence time (Pyšek & Jarošík 2005) and mutualistic interactions (Štajerová et al. 2009), dynamics of filling potential ranges (Williamson et al. 2009) and impact of invasive alien species on species diversity of invaded communities (Hejda & Pyšek 2006, 2008, Hejda et al. 2009a). Case studies of particular alien species complete the picture (see Pyšek et al. 2002 for overview up to then; Mihulka et al. 2003, Pyšek et al. 2003a, 2007, 2008a, Krinke et al. 2005, Moravcová et al. 2005, 2006, Pergl et al. 2006, Perglová et al. 2006, 2009, Mácová 2008, Skálová & Pyšek 2009). Last but not least, the data on the Czech alien flora have been used in pan-European analyses of invasion patterns and policy recommendations resulting from European framework-programmes projects on biological invasions (e.g. Chytrý et al. 2008b, 2009b, 2011, Hulme et al. 2008, 2009a, b, Pyšek et al. 2008b, 2010a, b, DAISIE 2009, Winter et al. 2009, Vilà et al. 2010). The information on alien species of the Czech Republic is stored in

the CzechFlor database held at the Institute of Botany, Academy of Sciences of the Czech Republic, Průhonice. The depth of information available makes the alien flora of the Czech Republic a convenient dataset for exploring determinants of plant invasions in a temperate region, including species invasiveness. However, for most alien floras and species, little is known about reproductive traits, the absence of which in databases constrains our ability to identify correct predictors of species invasiveness in comparative studies of alien floras (Pyšek & Richardson 2007).

The present paper uses a comparative ecological approach (Grime et al. 1988) with the aim of diminishing the gap between the two approaches mentioned above, ecological studies of individual invasive species and multispecies analyses of alien plants. It brings a general overview of reproductive characteristics of neophytes in the Czech Republic and compares trait values of invasive neophytes with those that occur as naturalized but are not invasive. The focus on these two stages of invasion was stimulated by the fact that the determinants of the transition from the stage of naturalization to that of invasion (in the sense of Richardson et al. 2000) are still poorly understood, yet crucial for our understanding of invasion mechanisms (Pyšek et al. 2008b, Murray & Phillips 2010, Phillips et al. 2010), and that determinants of invasion success differ between the stages of invasion process (Williamson 2006, Pyšek et al. 2008b, 2009a, b, Kubešová et al. 2010).

Methods

Species in the dataset

The species set included 93 neophytes (alien species introduced after 1500 A.D.; see Pyšek et al. 2002, 2004) occurring in the flora of the Czech Republic (Tables 1, 2). Species invasion status in the Czech Republic (casual; naturalized; invasive) was taken from Pyšek et al. (2002). The vast majority of species were naturalized and only three (*Ambrosia trifida*, *Bidens connata* and *Panicum miliaceum*) were classified as casual. Of the species set analysed, 41 neophytes were invasive and 52 were not invasive; since all but three species in the latter group were naturalized, this subset is further referred to as 'naturalized', meaning naturalized but not invasive (sensu Richardson et al. 2000, Pyšek et al. 2004). These two groups, invasive vs. naturalized but not invasive (including the three casuals), are compared for the traits investigated in the present paper.

The 93 species analysed are a highly representative sample, making up 40.6% of the total number of 229 naturalized neophytes in the Czech Republic (Pyšek et al. 2002). The species studied belonged to 70 genera and 32 families according to the Angiosperm Phylogeny Group classification (Stevens 2001), with *Asteraceae* most represented. The three life-history categories covered were all well represented among the species studied, but polycarpic perennial species were over-represented and monocarpic species under-represented among invasive aliens, compared to naturalized but non-invasive species (Table 1). Invasive species have on average longer residence times in the Czech Republic than naturalized non-invasive aliens (one-way ANOVA on square root transformed data: $F = 7.518$; $df = 1, 74$; $P = 0.008$), occupy more grid cells ($F = 28.636$; $df = 1, 89$; $P < 0.0001$ on ln transformed data) but do not differ in cover in plant communities invaded ($F = 0.639$; $df = 1, 65$; NS on arcsin√proportion transformed data) (Table 1).

Table 1. – Summary characteristics of the neophytes in the Czech flora shown separately for the two groups compared in the present paper, invasive vs naturalized but non-invasive alien species. Data taken from Pyšek et al. (2002) and CzechFlor database (see text for details); cover in plant communities from the TURBOVEG database (Chytrý & Rafajová 2003, Schaminée et al. 2009). Values for cover are based on 30 naturalized and 37 invasive species, for the minimum residence time on 40 and 36, respectively. Minimum residence time is the number of years elapsed since the first record of occurrence in the Czech Republic.

	Naturalized	Invasive	All species
Number of species	52	41	93
Most represented families (n)	*Asteraceae* (8), *Brassicaceae* (7), *Poaceae* (4)	*Asteraceae* (14), *Apiaceae* (4), *Polygonaceae*, *Scrophulariaceae* (3)	
Life history: Annual (%)	40.4	36.6	38.7
Monocarpic perennial (%)	25.0	19.5	22.6
Polycarpic perennial (%)	34.6	43.9	38.7
Minimum residence time (mean±S.D.)	130±49	165±70	147±62
Mean cover (%, min, max)	14.1 (1.5–48.0)	15.6 (1.8–42.9)	15.1 (1.5–48.0)
Number of grid cells (mean±S.D.)	92.2±127.3	260.6±192.0	167.5±179.6

Traits measured

Species were sampled and seed collected in the field from localities in the Czech Republic for each species during 2005–2007 (see Kubešová et al. 2010, their Electronic Appendix 1: http://www.preslia.cz/appendix.html#kubesova). Most species were sampled from three localities (range 1–6, mean 3.1; Table 2). The traits measured were selected so as to include those that play an important role in plant reproductive behaviour and may be therefore assumed to affect invasion success of the species studied. Further, they were selected with an aim to encompass the whole reproductive cycle, from seed production to dispersal potential to establishment, the latter consisting of germination, seedling growth and survival.

Seed production traits

Two measures were used to describe the number of generative propagules produced, relating to individual plants (or shoots) and to their populations. Depending on what is the basic reproductive unit entering the dispersal processes, numbers of propagules presented in the paper refer to those of seeds or fruits (Table 2).

Plant propagule number is the average number of propagules per single plant, or single shoot of a clonal species (hereafter termed plant). The number of propagules was based on measurements of 10 plants wherever possible (lower numbers were used where not enough fruiting/flowering individuals were available at the locality). The method of estimating propagule numbers was adjusted according to plant features (for this reason the measure of variation is not given in Table 2). The estimates were obtained by (i) counting all diaspores on the plant (in less productive species); (ii) collecting diaspores from the plant, obtaining their total weight and calculating the number based on the weight of an individual diaspore (in species with a high production of tiny diaspores, e.g. *Amaranthus* spp.); (iii) calculating the number of fruits per plant and average number of seed per fruit (10 replicates), and estimating the propagule (seed) number per plant based on multiplying

these two variables. For species bearing fruits and flowers at the same time (e.g. *Impatiens* spp., *Oxalis* spp.) the number of developed fruits and flowers was taken as the number of fruits.

Population propagule number is an average number of propagules per m^2 of maximum population density found in the locality. This density was estimated by calculating the number of shoots (plants) in 10 plots of 1 m^2, selected in dense stands of the species, to obtain a measure of maximum reproductive capacity of the population.

Dispersal traits

Propagule size (length and width, mm) was measured on propagules collected from the localities as the longest and widest dimensions. The third measure, diaspores length with pappus was obtained where applicable (in 14 species only, hence this measure was not subject to statistical analysis). Large propagules (> 1.5 mm) were measured by using rule calliper to the nearest 0.05 mm. In each of the species with bigger propagules, 100 propagules from each locality were measured. Small propagules (< 1.5 mm) and propagules with pappus were measured using Olympus SZX12 stereomicroscope associated with Quick Photo Micro 2.3 software. Fifty propagules from each locality were measured in each species with this propagule size. In species with a pappus easily detachable from the achene, only 25 propagules were measured, since it was difficult to obtain enough propagules with a pappus attached. Propagule size is presented in Table 2 but was not included in any statistical analysis since propagule weight is a more informative measure of the dispersal capability (see Römermann et al. 2005).

Propagule length/width ratio was calculated. This index describes the two-dimensional "shape" of the propagule, with low values characterizing rounded propagules. Pappus was not included in calculation of propagule length/width ratio .

Propagule weight (g) was obtained by weighing four sets of 25 propagules from each locality and calculating the average weight of one set. Weighing was performed using two analytical scales, Sartorius 4503 MP6 and Scaltec SBC 32, with six (for small diaspores) or four (for large diaspores) decimal places, respectively.

Water dispersal (buoyancy) was measured for each species, with 100 propagules from each locality randomly selected and placed (4 replicates of 25 propagules) in beakers filled with distilled water. The number of floating propagules was counted, following a thorough stirring of the water, after 0.5, 1, 2, 4, 6, 8, 24, 32, 48, 56, 72, 80, 96 and 104 hours, and then after each 24 hours until all propagules sank (Lhotská 1968). The time when all propagules sank (Ft_{100}, in hours) is used as a measure of buoyancy.

Table 2. – Seed production and dispersal traits of alien neophytes in the Czech flora. Whether a species was considered invasive or not was taken from Pyšek et al. (2002) with modifications reported in Kubešová et al. (2010). Propagule refers to the part of plant involved in dispersal; accordingly the measures reported refer to either seed or fruit. The figures are average values per species (mean±S.D. if not stated otherwise) based on samples from several localities (given in Loc no column), the number of measurements on which the mean value is based is given (n) where appropriate. See text for details on individual measurements. ▶▶

Species	Family	Life history	Invasive	Propagule	Loc no	Plant propagule number (per shoot)	Population propagule number (per m²)	n (propagule measures)	Propagule length (mm)
Abutilon theophrasti	*Malvaceae*	an	no	seed	3	1812	3473	300	3.15±0.13
Amaranthus albus	*Amaranthaceae*	an	no	seed	4	7775	12357	150	0.92±0.05
Amaranthus blitoides	*Amaranthaceae*	an	no	seed	1	11375	11375	50	1.45±0.09
Amaranthus powellii	*Amaranthaceae*	an	yes	seed	3	21144	75984	200	1.25±0.09
Amaranthus retroflexus	*Amaranthaceae*	an	yes	seed	6	23005	96477	200	1.11±0.09
Ambrosia artemisiifolia	*Asteraceae*	an	yes	fruit	3	1213	2468	300	4.02±0.57
Ambrosia trifida	*Asteraceae*	an	no	fruit	1	2176	2176	100	7.56±0.63
Angelica archangelica	*Apiaceae*	mono	yes	fruit	5	19289	19289	300	5.70±0.65
Antirrhinum majus	*Scrophulariaceae*	mono	no	seed	2	4327	5318	100	0.89±0.11
Arabis alpina	*Brassicaceae*	per	no	seed	2	238	15331	200	1.48±0.18
Asclepias syriaca	*Asclepiadaceae*	per	no	seed	3	385	1514	230	7.18±0.69
Aster lanceolatus	*Asteraceae*	per	yes	friut	3	4551	580067	150	2.14±0.53
Bidens connata	*Asteraceae*	an	no	fruit	2	1803	8169	200	10.16±1.49
Bidens frondosa	*Asteraceae*	an	yes	fruit	6	7198	12867	300	8.41±1.39
Bunias orientalis	*Brassicaceae*	mono	yes	fruit	3	603	10891	300	6.35±0.83
Cannabis ruderalis	*Cannabaceae*	an	no	fruit	2	1144	1650	200	3.59±0.31
Cardamine chelidonia	*Brassicaceae*	mono	no	seed	4	130	1130	250	2.71±0.21
Chenopodium pumilio	*Chenopodiaceae*	an	no	fruit	1	5359	229890	50	0.79±0.09
Chenopodium strictum	*Chenopodiaceae*	an	no	fruit	3	42704	102068	150	1.93±0.35
Claytonia alsinoides	*Portulacaceae*	an	no	seed	1	86	10617	100	1.58±0.14
Collomia grandiflora	*Polemoniaceae*	an	no	seed	1	1212	3637	100	3.04±0.19
Consolida orientalis	*Ranunculaceae*	an	no	seed	5	1526	10769	250	1.99±0.25
Conyza canadensis	*Asteraceae*	an	yes	fruit	4	37721	167998	150	1.12±0.11
Corydalis lutea	*Fumariaceae*	per	no	seed	3	235	3157	300	1.82±0.10
Cuscuta campestris	*Convolvulaceae*	an	yes	seed	3	2806	2806	150	1.36±0.17
Datura stramonium	*Solanaceae*	an	no	seed	4	10771	17835	300	3.32±0.20
Digitalis purpurea	*Scrophulariaceae*	mono	yes	seed	4	35225	141708	200	0.80±0.09
Duchesnea indica	*Rosaceae*	per	no	fruit	3	169	13265	150	1.16±0.08
Echinocystis lobata	*Cucurbitaceae*	an	yes	seed	4	159	159	300	18.42±1.97
Echinops sphaerocephalus	*Asteraceae*	per	yes	fruit	4	1400	5075	300	18.50±1.48
Epilobium ciliatum	*Onagraceae*	per	yes	seed	3	9653	41596	76	0.92±0.17
Epilobium dodonaei	*Onagraceae*	per	no	seed	3	1235	12020	75	1.76±0.20
Erigeron annuus	*Asteraceae*	mono	yes	fruit	5	12188	117199	152	1.01±0.16
Erucastrum gallicum	*Brassicaceae*	mono	no	seed	1	4239	4239	100	1.24±0.09
Galega officinalis	*Fabaceae*	per	no	seed	4	1652	10225	300	3.53±0.36
Galinsoga quadriradiata	*Asteraceae*	an	yes	fruit	5	1818	8071	150	1.38±0.13
Galinsoga parviflora	*Asteraceae*	an	yes	fruit	4	1738	18078	150	1.43±0.14
Geranium pyrenaicum	*Geraniaceae*	per	yes	fruit	4	235	563	300	2.74±0.18
Helianthus tuberosus	*Asteraceae*	per	yes	fruit	3	102	1840	200	5.04±0.48
Heracleum mantegazzianum	*Apiaceae*	mono	yes	fruit	5	20000	20000	300	11.22±1.48
Hesperis matronalis	*Brassicaceae*	per	no	seed	3	646	2330	200	2.36±0.36
Hordeum jubatum	*Poaceae*	an	no	fruit	3	44	1903	200	6.48±0.58
Impatiens glandulifera	*Balsaminaceae*	an	yes	seed	4	3635	18560	300	3.97±0.47
Impatiens parviflora	*Balsaminaceae*	an	yes	seed	5	279	2689	300	4.01±0.34
Imperatoria ostruthium	*Apiaceae*	per	yes	fruit	5	776	4228	300	4.17±0.70
Inula helenium	*Asteraceae*	mono	no	fruit	1	156	290	100	5.36±0.35
Iva xanthiifolia	*Asteraceae*	an	no	fruit	2	5306	26029	200	2.42±0.20

Propagule width (mm)	Propagule length/width ratio	n (weight)	Weight of 25 propagules (g)	n (buoyancy)	Buoyancy (Ft_{100}, hrs)	n (epizoochory)	Epizoochory (%, range)	n (terminal velocity)	Anemochory: terminal velocity (m/s)
2.83±0.13	1.11±0.04	12	0.2462±0.0213	12	0.0±0.0	12	67.0 (56–80)	150	2.732±0.023
0.87±0.06	1.05±0.04	12	0.0080±0.0009	12	7.8±16.6	12	23.0 (12–40)	150	2.280±0.106
1.34±0.09	1.08±0.05	4	0.0269±0.0010	4	36.0±41.6	4	39.0 (32–44)	50	2.558±0.034
1.04±0.06	1.20±0.06	12	0.0133±0.0013	12	0.8±1.1	12	49.3 (32–72)	150	2.405±0.058
1.02±0.07	1.09±0.05	12	0.0112±0.0011	12	0.5±0.1	12	14.3 (8–32)	150	2.396±0.047
2.01±0.24	2.02±0.30	12	0.1218±0.0128	12	61.3±40.8	12	78.0 (60–92)	150	2.642±0.097
3.98±0.53	1.92±0.24	4	0.3993±0.0407	4	100.0±4.6	4	61.0 (52–72)	50	2.496±0.186
4.01±0.53	1.43±0.14	12	0.1136±0.0176	12	1202.0±554.3	12	59.0 (40–72)	150	2.018±0.161
0.71±0.07	1.26±0.14	8	0.0032±0.0003	8	10.3±11.4	8	55.5 (44–76)	100	1.828±0.068
1.12±0.13	1.34±0.17	8	0.0075±0.0005	8	0.3±0.4	8	54.0 (40–68)	100	1.926±0.161
4.86±0.55	1.48±0.11	12	0.2562±0.0420	12	1404.0±913.4	12	24.0 (12–32)	150	0.353±0.069
0.48±0.08	4.48±1.09	12	0.0046±0.0007	12	97.8±75.0	12	75.3 (40–96)	150	0.534±0.125
2.38±0.31	4.39±1.10	8	0.1055±0.0057	8	9089.0±560.6	8	98.0 (92–100)	100	2.094±0.133
2.01±0.27	4.28±1.07	12	0.0537±0.0043	12	2497.5±610.6	12	87.3 (84–92)	150	1.752±0.135
4.02±0.50	1.59±0.19	12	0.8179±0.0755	12	106.7±88.5	12	34.7 (20–44)	150	2.758±0.030
2.67±0.21	1.35±0.09	8	0.2321±0.0140	8	52.0±60.8	8	60.0 (48–76)	100	2.728±0.027
1.13±0.15	2.42±0.31	12	0.0288±0.0036	12	1.3±1.1	12	46.7 (28–68)	150	2.361±0.097
0.72±0.08	1.10±0.10	4	0.0022±0.0000	4	52.0±4.6	4	50.0 (44–56)	50	1.515±0.069
1.55±0.26	1.25±0.18	12	0.0180±0.0037	12	54.7±20.7	12	64.3 (36–80)	150	2.405±0.061
1.29±0.13	1.24±0.13	4	0.0204±0.0012	4	50.0±20.0	4	48.0 (44–56)	50	2.383±0.107
1.53±0.12	1.99±0.16	4	0.0839±0.0085	4	0.0±0.0	4	49.0 (44–60)	50	2.616±0.035
1.46±0.26	1.39±0.23	12	0.0487±0.0026	12	0.1±0.2	12	70.7 (44–100)	150	2.506±0.095
0.33±0.05	3.45±0.47	12	0.0009±0.0003	12	14.4±13.1	12	76.3 (64–88)		
1.72±0.10	1.06±0.05	12	0.0359±0.0032	12	29.3±9.2	12	65.7 (44–84)	150	2.440±0.127
1.14±0.13	1.20±0.13	12	0.0201±0.0048	12	21.6±22.7	12	66.3 (40–84)	150	2.529±0.054
2.66±0.18	1.25±0.07	12	0.1907±0.0144	12	10.8±16.7	12	41.3 (28–56)	150	2.700±0.029
0.50±0.08	1.62±0.26	12	0.0016±0.0001	12	0.8±0.5	12	45.3 (36–60)	100	1.584±0.585
0.82±0.09	1.43±0.13	12	0.0070±0.0008	12	26.5±15.1	12	54.3 (40–68)	150	2.167±0.127
8.62±0.89	2.14±0.17	12	6.1790±0.2868	12	47.3±22.0	12	0.0 (0–0)	150	2.760±0.036
2.10±0.33	8.97±1.25	12	0.5973±0.0784	12	51.3±24.7	12	82.7 (68–92)	150	2.113±0.109
0.33±0.05	2.80±0.52	12	0.0016±0.0003	12	38.7±34.3	12	46.7 (28–68)	150	0.160±0.036
0.60±0.08	2.96±0.38	12	0.0086±0.0013	12	18.7±28.7	12	63.0 (48–72)	200	0.265±0.079
0.31±0.06	3.34±0.52	12	0.0009±0.0002	12	25.8±22.5	12	35.7 (20–44)	150	1.071±0.102
0.82±0.05	1.51±0.11	4	0.0118±0.0005	4	1.6±2.9	4	52.0 (40–68)	50	2.316±0.084
1.88±0.16	1.89±0.24	12	0.1640±0.0242	12	0.4±1.2	12	51.3 (24–76)	150	2.717±0.024
0.56±0.06	2.47±0.28	12	0.0054±0.0003	12	8.0±9.7	12	92.3 (80–100)	150	1.624±0.158
0.51±0.06	2.80±0.35	12	0.0047±0.0007	12	14.7±15.3	12	90.7 (84–100)	150	1.240±0.229
1.23±0.07	2.23±0.16	12	0.0493±0.0054	12	16.5±20.1	12	60.3 (36–88)	150	2.524±0.047
2.12±0.20	2.40±0.29	8	0.1223±0.0148	8	40.0±11.3	8	50.5 (20–76)	100	2.476±0.132
7.20±0.78	1.56±0.14	12	0.3795±0.0504	12	5.2±2.0	12	47.0 (32–68)	150	1.921±0.178
1.15±0.13	2.08±0.38	12	0.0421±0.0057	12	8.9±11.2	12	70.0 (48–96)	150	2.532±0.056
1.22±0.17	5.41±0.86	12	0.0590±0.0165	12	37.3±26.3	12	92.0 (84–100)	150	0.766±0.159
2.82±0.38	1.42±0.19	12	0.2385±0.0287	12	13.3±15.1	12	46.0 (28–64)	150	2.700±0.048
1.97±0.29	2.06±0.26	12	0.1422±0.0135	12	1.3±1.1	12	47.7 (28–68)	150	2.639±0.051
3.35±0.50	1.25±0.15	12	0.0310±0.0022	12	309.3±179.4	16	49.5 (32–68)	150	1.459±0.225
0.95±0.11	5.73±0.76	4	0.0598±0.0028	4	52.0±4.6	4	89.0 (80–96)	50	1.613±0.528
1.42±0.18	1.72±0.16	8	0.0242±0.0040	8	16.5±10.5	8	73.0 (64–80)	100	2.239±0.170

Species	Family	Life history	Invasive	Propagule	Loc no	Plant propagule number (per shoot)	Population propagule number (per m²)	n (propagule measures)	Propagule length (mm)
Juncus tenuis	*Juncaceae*	per	yes	seed	4	2343	184557	150	0.41±0.05
Kochia scoparia	*Chenopodiaceae*	an	yes	fruit	3	6080	41902	150	2.70±0.60
Lepidium densiflorum	*Brassicaceae*	mono	no	seed	3	2141	34362	250	1.47±0.17
Lupinus polyphyllus	*Fabaceae*	per	yes	seed	6	150	1291	300	4.30±0.33
Lychnis coronaria	*Caryophyllaceae*	mono	no	seed	3	833	4463	300	1.14±0.07
Lysimachia punctata	*Primulaceae*	per	no	seed	3	24	320	200	1.45±0.13
Matricaria discoidea	*Asteraceae*	an	yes	fruit	4	6186	156249	150	1.32±0.11
Medicago sativa	*Fabaceae*	per	no	fruit	2	329	3417	150	4.92±0.60
Mimulus guttatus	*Scrophulariaceae*	per	yes	seed	3	11094	281453	300	0.50±0.06
Myrrhis odorata	*Apiaceae*	per	yes	fruit	3	433	5265	300	20.32±1.70
Oenothera biennis	*Onagraceae*	mono	yes	seed	2	4555	4555	100	1.72±0.17
Oenothera glazoviana	*Onagraceae*	mono	no	seed	1	55841	55841	50	1.65±0.17
Oxalis corniculata subsp. *repens*	*Oxalidaceae*	mono	no	seed	5	508		300	1.39±0.07
Oxalis dillenii	*Oxalidaceae*	mono	no	seed	4	689	10849	300	1.18±0.07
Oxalis fontana	*Oxalidaceae*	mono	no	seed	4	729	4767	300	1.21±0.07
Oxybaphus nyctagineus	*Nyctaginaceae*	per	no	fruit	1	368	1472	100	3.81±0.33
Panicum capillare	*Poaceae*	an	no	friut	3	1608	22185	250	1.65±0.31
Panicum miliaceum	*Poaceae*	an	no	fruit	3	357	2460	300	3.01±0.16
Phytolacca esculenta	*Phytolaccaceae*	per	no	fruit	3	2784	22272	150	3.72±0.31
Potentilla intermedia	*Rosaceae*	mono	no	seed	2	4141	33631	100	0.95±0.11
Rudbeckia hirta	*Asteraceae*	per	no	fruit	1	899	2698	100	2.31±0.10
Rudbeckia laciniata	*Asteraceae*	per	yes	fruit	4	926	6473	300	4.56±0.37
Rumex alpinus	*Polygonaceae*	per	yes	fruit	3	5579	13353	200	4.70±0.64
Rumex longifolius	*Polygonaceae*	per	yes	fruit	2	5009	8866	150	4.12±0.56
Rumex patientia	*Polygonaceae*	per	no	fruit	3	5181	19256	200	6.08±0.99
Rumex thyrsiflorus	*Polygonaceae*	per	yes	fruit	5	846	3372	300	3.89±0.44
Scutellaria altissima	*Lamiaceae*	per	no	fruit	3	152	2497	200	1.40±0.10
Sedum hispanicum	*Crassulaceae*	per	yes	seed	2	12234	160340	100	0.61±0.04
Sedum rupestre	*Crassulaceae*	per	no	seed	2	418	4179	100	1.16±0.22
Sedum spurium	*Crassulaceae*	per	no	seed	1	400	10274	50	0.92±0.06
Senecio inaequidens	*Asteraceae*	per	no	fruit	2	22038	32488	100	2.36±0.20
Senecio vernalis	*Asteraceae*	an	no	fruit	3	3866	18849	100	2.51±0.19
Setaria faberii	*Poaceae*	an	no	fruit	1	656	16398	100	2.54±0.09
Silene dichotoma	*Caryophyllaceae*	mono	no	seed	2	2409	15183	200	1.20±0.14
Sisymbrium altissimum	*Brassicaceae*	an	no	seed	5	11243	32687	300	1.06±0.14
Sisymbrium loeselii	*Brassicaceae*	an	yes	seed	4	29164	84245	250	0.81±0.09
Sisymbrium strictissimum	*Brassicaceae*	per	no	seed	4	6706	50757	300	1.82±0.26
Smyrnium perfoliatum	*Apiaceae*	mono	no	fruit	3	309	3092	300	2.76±0.36
Solidago canadensis	*Asteraceae*	per	yes	fruit	5	27749	243341	150	1.14±0.13
Solidago gigantea	*Asteraceae*	per	yes	fruit	4	1094	7563	150	1.59±0.20
Telekia speciosa	*Asteraceae*	per	yes	fruit	2	3310	7233	200	3.19±0.28
Trifolium hybridum	*Fabaceae*	mono	yes	fruit	3	396	2875	200	4.18±0.46
Veronica persica	*Scrophulariaceae*	an	yes	seed	3	102	821	200	1.60±0.19
Vicia grandiflora	*Fabaceae*	an	no	seed	1	37	347	100	3.97±0.30
Virga strigosa	*Dipsacaceae*	mono	yes	fruit	3	2688	40948	300	4.12±0.21
Xanthium albinum	*Asteraceae*	an	no	fruit	4	568	1260	300	20.86±1.93

Propagule width (mm)	Propagule length/width ratio	n (weight)	Weight of 25 propagules (g)	n (buoyancy)	Buoyancy (Ft_{100}, hrs)	n (epizoochory)	Epizoochory (%, range)	n (terminal velocity)	Anemochory: terminal velocity (m/s)
0.22±0.03	1.89±0.23	12	0.0003±0.0001	12	1.4±1.3	12	12.3 (4–28)		
2.12±0.53	1.29±0.19	12	0.0305±0.0029	12	13.5±9.3	12	62.3 (44–76)	150	2.242±0.193
0.88±0.10	1.67±0.10	12	0.0075±0.0023	12	0.4±0.4	12	41.3 (20–72)	150	2.038±0.107
3.09±0.31	1.40±0.13	12	0.5649±0.0462	12	0.3±0.6	12	39.7 (16–60)	150	2.792±0.021
0.93±0.05	1.23±0.08	12	0.0149±0.0009	12	0.0±0.0	12	61.0 (48–72)	150	2.441±0.039
1.10±0.15	1.37±0.61	8	0.0122±0.0006	8	5.3±1.0	8	62.0 (52–68)	100	2.247±0.093
0.49±0.06	2.70±0.32	12	0.0033±0.0005	12	5.3±2.1	16	34.5 (12–60)	150	1.710±0.129
		8	0.3230±0.0674	8	24.0±0.0	8	94 (88–100)	100	2.460±0.191
0.30±0.04	1.70±0.20	12	0.0005±0.0000	12	0.5±0.4	12	22.3 (12–36)		
2.69±0.28	7.62±1.02	12	0.9669±0.0947	12	22.7±4.6	12	56.7 (48–68)	150	2.559±0.063
1.26±0.20	1.39±0.24	8	0.0160±0.0017	8	491.0±99.7	8	73.5 (60–84)	100	2.152±0.104
1.01±0.16	1.67±0.30	4	0.0070±0.0004	4	118.0±38.9	4	59.0 (52–68)	50	1.903±0.208
0.93±0.05	1.50±0.09	12	0.0054±0.0006	12	0.1±0.3	12	52.7 (28–76)	150	1.883±0.145
0.83±0.05	1.42±0.07	12	0.0045±0.0007	12	0.0±0.0	12	32.3 (24–40)	150	1.829±0.114
0.79±0.05	1.55±0.09	12	0.0048±0.0003	12	0.0±0.1	12	43.0 (28–60)	150	1.847±0.125
1.95±0.18	1.96±0.17	4	0.1553±0.0052	4	4.5±1.0	4	72.0 (64–80)	50	2.662±0.040
0.88±0.07	1.88±0.36	12	0.0138±0.0021	12	13.4±19.3	12	60.7 (40–88)	150	2.246±0.130
2.07±0.09	1.46±0.11	12	0.1357±0.0055	12	6.3±10.7	12	59.7 (40–76)	150	2.712±0.027
3.04±0.21	1.22±0.09	12	0.2698±0.0793	8	10.5±13.7	8	79.7 (48–100)	150	2.699±0.098
0.72±0.11	1.33±0.13	8	0.0032±0.0007	8	58.0±20.4	8	47.5 (32–64)	100	1.897±0.166
0.75±0.04	3.09±0.20	4	0.0131±0.0019	4	106.0±50.3	4	44.0 (28–60)	50	1.933±0.299
1.52±0.15	3.02±0.28	12	0.0726±0.0070	12	4.3±6.5	12	64.0 (40–80)	150	2.399±0.070
3.95±0.60	1.20±0.14	12	0.0536±0.0116	12	43.3±12.0	12	92.7 (80–100)	150	1.588±0.192
3.78±0.50	1.09±0.08	8	0.0610±0.0085	8	60.0±12.8	8	94.0 (88–100)	100	1.653±0.171
5.49±0.85	1.11±0.10	12	0.1160±0.0202	12	44.7±13.0	12	92.0 (84–100)	150	1.694±0.117
2.71±0.41	1.45±0.16	12	0.0198±0.0030	12	57.3±18.3	12	80.3 (68–92)	150	1.214±0.226
1.09±0.08	1.29±0.08	12	0.0355±0.0019	12	30.7±8.9	12	71.3 (60–84)	150	2.549±0.042
0.28±0.02	2.23±0.22	8	0.0005±0.0000	8	2.3±2.2	8	23.5 (12–40)	35	1.243±0.120
0.37±0.05	3.19±0.57	8	0.0012±0.0003	8	29.9±30.8	8	34.5 (24–40)	50	1.112±0.300
0.41±0.06	2.28±0.32	4	0.0015±0.0001	4	10.5±9.1	4	42.0 (32–56)	50	1.557±0.197
0.43±0.04	5.54±0.60	8	0.0055±0.0005	8	43.0±25.3	8	48.0 (40–60)	100	0.589±0.791
0.42±0.04	6.06±0.77	8	0.0055±0.0003	8	2.3±2.4	8	63.0 (40–80)		
1.42±0.06	1.79±0.09	4	0.0464±0.0026	4	5.0±2.0	4	60.0 (48–68)	50	2.505±0.086
0.81±0.13	1.50±0.26	8	0.0206±0.0007	8	0.0±0.0	8	62.5 (52–76)	100	2.417±0.153
0.65±0.10	1.65±0.29	12	0.0053±0.0007	12	6.9±10.6	12	48.0 (24–68)	150	2.090±0.074
0.51±0.05	1.60±0.23	12	0.0022±0.0001	12	4.4±6.7	12	40.0 (20–56)	150	1.778±0.154
0.58±0.07	3.19±0.63	12	0.0101±0.0014	12	6.7±8.4	12	44.0 (28–60)	150	2.080±0.112
2.27±0.29	1.22±0.13	12	0.2105±0.0437	12	9.2±12.7	12	83.3 (76–92)	150	2.710±0.027
0.36±0.04	3.20±0.53	12	0.0018±0.0002	11	21.2±20.4	12	83.3 (68–96)	150	0.532±0.117
0.44±0.06	3.72±0.63	12	0.0046±0.0008	12	27.5±18.9	12	96.7 (88–100)	150	0.802±0.123
0.67±0.09	4.87±0.77	8	0.0140±0.0007	8	1.4±1.1	8	46.5 (28–60)	100	1.902±0.114
2.08±0.19	2.02±0.25	8	0.0599±0.0035	8	86.0±11.1	8	89 (84–96)	100	2.026±0.240
1.04±0.15	1.55±0.19	12	0.0133±0.0016	12	0.6±0.2	12	77.0 (60–88)	150	2.276±0.085
3.47±0.25	1.15±0.06	4	0.5951±0.0296	4	0.0±0.0	4	39.0 (36–44)	50	2.795±0.019
1.54±0.10	2.69±0.16	12	0.1499±0.0145	12	0.0±0.1	12	51.7 (36–68)	150	2.662±0.034
13.52±1.32	1.55±0.11	12	8.6231±1.3908	12	130.0±42.3	12	100.0 (100–100)	150	2.658±0.052

Animal dispersal (epizoochory) was tested as the ability of propagules to attach to wild boar fur. Wild boar was selected because most plant species' propagules easily attach to its fur, and it can be assumed, due to its migration potential, to spread propagules over a large distance (Couvreur et al. 2004). A wooden frame 40×15 cm, with a handle, was covered with the fur and pressed to a sheet of paper with propagules spread over it. The number of attached propagules was counted after three circular movements of the frame pressed to the paper. For each species, 100 propagules from each locality were randomly selected and used to make four replicates of 25 propagules.

Wind dispersal (terminal velocity) was used to express the potential for anemochory. Terminal velocity was measured by using special equipment constructed according to Askew et al. (1997). Propagules were released from 85 cm within a tube with a cross-section of 25×25 cm and the time of propagule fall was electronically measured between two laser detectors 50 cm apart. Terminal velocity in m/s was calculated based on these values (Askew et al. 1997). For each species 50 randomly selected diaspores from each locality were used. Seeds of *Conyza canadensis*, *Juncus tenuis* and *Mimulus guttatus* were too small to be detected and the pappus in *Senecio vernalis* breaks off from the achene when touched; for these reasons terminal velocity of these species could not be measured. The low values of terminal velocity suggest better capacity for wind dispersal, reflecting lower speed of seed fall.

Establishment traits

Germination was investigated using seeds that were freshly harvested, dry-stored for one month or cold-stratified and then germinated under different temperature regimes. Germination of freshly harvested seeds (at most five days from the harvest) was tested at 25/10, 20/5 and 15/5 °C, while germination of dry-stored and cold-stratified seed was tested at 25/10 °C (12 h in light under the higher temperature/12 h in dark at the lower temperature). Seed stratification was performed in the dark at temperature of 1–4 °C in plastic Petri dishes filled with heat sterilized river sand for a period of 3 or 5 months. The seeds in stratification were watered once a week and monitored for germination. Germination of fresh and one-month stored seed was performed in plastic Petri dishes filled with filter paper, which was watered and monitored three times a week; all germinated seeds were recorded. Each treatment consisted of four replicates of 25 seeds, only in exceptional cases were less seeds per replicate used in case of small amounts of seeds. **Total maximal germination** (TG_{max}, %) is the highest germination percentage achieved by the species under all the treatments used.

Seedling relative growth rate (RGR, $g \cdot g^{-1} \cdot day^{-1}$**)** was measured following Grime & Hunt (1975) and calculated following Hunt et al. (2002). For each species, 21 seedlings proportionally representing the localities sampled were used (e.g. 7 seedlings from each locality were measured if the species was sampled at three localities).

Seedling establishment was measured in a common garden at the Institute of Botany Academy of Sciences of the Czech Republic. Twenty five propagules were sown in a plastic container 10×10 cm in size and for each species, three replicates from each locality were used. Emerging seedlings were counted in the autumn following sowing and in the spring of the next year. This yielded two measures: **total seedling establishment** is the percentage of seed that appeared until spring, **autumn seedling establishment** the percentage recorded in the autumn following sowing, of all established seedlings.

Statistical analysis

Except seedling relative growth rate, for which the data from the individual localities were averaged before the analysis, variability of each trait within localities was evaluated by mixed effect nested ANOVA (e.g. Sokal & Rohlf 1995), with invasion status (naturalized/invasive) as a fixed effect, and localities nested within individual species as a random factor. The individual localities are considered as a random factor because the individual species are collected at different localities, and the localities can be therefore treated as statistical plots (see Underwood 1997).

The effect of invasion status, simultaneously taking into account species relatedness, was evaluated separately for each trait as the response variable by linear mixed effect models (LMMs) following Blackburn & Duncan (2001). Invasion status was a fixed effect, and the levels of the taxonomical hierarchy (genera, families, orders and classes) were considered as random effects. Significance of the random effects was evaluated by likelihood ratio tests, except classes which could not be tested statistically due to singular convergence. The treatment of taxonomical hierarchy as a random effect means that the inference on taxonomy can be applied to a wider population from which the species are derived, i.e. to any species belonging to that genus, family, order and class.

Random effects of taxonomic hierarchy were also evaluated by nested analyses of variance (Harvey & Pagel 1991), separately for each trait as the response variable, using variance components analyses with restricted maximum likelihood method (Pyšek et al. 2009a). Similar to LMMs, these analyses are able to show how much variation in the response variable is due to variation among species within genera, genera within families, families within orders and orders within classes, for a wider population from which the species are derived than are the particular species analyzed. However, nested ANOVA is not a rigorous test of statistical independence below a particular level of taxonomic hierarchy (Harvey & Pagel 1991), and unlike LMMs, it does not take simultaneously into account the fixed effect of invasion status. The method thus can illustrate how the total variation of the individual traits is distributed among taxonomic levels, but cannot give consistent results with LMMs which simultaneously take into account the effect of invasion status.

Because the effects of plots nested within species always appeared insignificant, all LMMs were applied on trait data including their plot replications. Except the data on seedling relative growth rate, for which the replications were not available, the LMM analyses were then repeated on mean values for each species from the individual plots. Both results were consistent and only those on data including plot replications are presented.

Before each analysis, for each trait transformation that maximizes the likelihood for the set of explanatory variables was chosen from a series of Box-Cox transformations (e.g. Crawley 2002), and the data then checked for normality by the Shapiro-Wilk test (Shapiro & Wilk 1965). All calculations were done in TIBCO Spotifire® S+ v. 8.

Table 3. – Establishment traits of alien neophytes in the Czech flora. See Table 2 and text for details.

Species	n (germination)	Total germination (%, mean, range)	Seedling RGR (g·g⁻¹·day⁻¹, mean±95% c.i.)	n (seedling establishment)	Seedling establishment: Total (%, mean, range)	Seedling establishment: Autumn (% of total seedling establishment, mean, range)
Abutilon theophrasti	12	72.7 (48–100)	0.1510±0.088	9	35.1 (8–60)	29.6 (0–56)
Amaranthus albus	12	98.7 (96–100)	0.2591±0.093	12	37.3 (0–96)	0.0 (0–0)
Amaranthus blitoides	4	77.5 (60–90)	0.1901±0.112	3	15.6 (13–20)	0.0 (0–0)
Amaranthus powellii	8	78.5 (60–100)	0.1706±0.158	9	44.0 (16–84)	0.0 (0–0)
Amaranthus retroflexus	12	97.3 (88–100)	0.2182±0.088	9	29.3 (8–76)	0.0 (0–0)
Ambrosia artemisiifolia	12	89.9 (68–100)	0.2192±0.093	12	32.7 (0–92)	0.0 (0–0)
Ambrosia trifida	4	78.0 (64–84)	0.2071±0.138	3	29.3 (12–40)	0.0 (0–0)
Angelica archangelica	16	86.0 (76–96)	0.1583±0.112	12	52.7 (32–80)	7.3 (0–40)
Antirrhinum majus	8	91.0 (88–96)	0.2405±0.107	3	37.3 (28–48)	2.8 (0–8)
Arabis alpina	8	98.0 (92–100)	0.1915±0.081	6	44.0 (16–64)	83.7 (50–100)
Asclepias syriaca	12	99.0 (96–100)	0.1536±0.063	9	46.2 (36–68)	0.0 (0–0)
Aster lanceolatus	12	100.0 (100–100)	0.2277±0.099	9	39.6 (16–64)	0.0 (0–0)
Bidens connata	8	98.5 (96–100)	0.2370±0.057	6	42.0 (28–52)	0.0 (0–0)
Bidens frondosa	12	96.3 (88–100)	0.2271±0.145	12	33.0 (0–68)	0.0 (0–0)
Bunias orientalis	12	12.0 (4–24)		12	11.0 (0–36)	14.8 (0–100)
Cannabis ruderalis	8	99.0 (96–100)	0.1773±0.096	6	24.7 (16–40)	0.0 (0–0)
Cardamine chelidonia	12	100.0 (100–100)	0.1848±0.062	9	51.1 (12–84)	40.2 (0–93)
Chenopodium pumilio	4	100.0 (100–100)	0.2817±0.215	6	8.0 (0–28)	35.1(0–100)
Chenopodium strictum	12	73.3 (20–100)	0.1896±0.146	9	25.3 (0–56)	0.0 (0–0)
Claytonia alsinoides	4	94.0 (92–96)	0.1262±0.135	3	48.0 (28–64)	86.3 (71–100)
Collomia grandiflora	4	100.0 (100–100)	0.1141±0.114	6	63.3 (24–92)	41.1 (0–85)
Consolida orientalis	12	62.0 (24–88)		6	2.7 (0–8)	16.7 (0–100)
Conyza canadensis	12	99.3 (96–100)	0.2099±0.139	12	49.7 (0–84)	62.4 (0–100)
Corydalis lutea	12	22.9 (0–56)		12	9.0 (0–40)	9.0 (0–0)
Cuscuta campestris	8	57.5 (30–80)		9	40.0 (10–90)	11.1 (0–100)
Datura stramonium	4	68.0 (52–84)	0.1876±0.111	12	0.0 (0–0)	0.0 (0–0)
Digitalis purpurea	8	98.0 (92–100)	0.2039±0.138	12	45.7 (24–68)	74.5 (50–100)
Duchesnea indica	12	87.7 (80–96)	0.1836±0.139	3	8.0 (0–16)	58.3 (0–100)
Echinocystis lobata	12	97.5 (80–100)	0.1374±0.058	9	58.2 (32–80)	2.2 (0–20)
Echinops sphaerocephalus	8	62.0 (48–76)	0.1746±0.095	12	53.7 (16–100)	56.0 (0–91)
Epilobium ciliatum	8	98.0 (92–100)	0.2234±0.174	12	43.7 (16–76)	38.6 (0–94)
Epilobium dodonaei	8	92.0 (72–100)	0.2265±0.066	9	48.0 (24–100)	0.0 (0–0)
Erigeron annuus	12	92.0 (84–96)	0.2746±0.136	9	29.3 (12–64)	25.6 (0–100)
Erucastrum gallicum	4	100.0 (100–100)	0.1910±0.129	3	64.0 (40–76)	32.6 (21–40)
Galega officinalis	12	29.3 (12–56)	0.1604±0.097	12	12.3 (0–28)	52.5(0–100)
Galinsoga quadriradiata	12	99.7 (96–100)	0.3222±0.077	9	20.9 (4–44)	0.0 (0–0)
Galinsoga parviflora	8	93.5 (76–100)	0.2895±0.125	9	0.4 (0–4)	0.0 (0–0)
Geranium pyrenaicum	12	93.7 (76–100)	0.1612±0.096	9	5.3 (0–20)	34.8 (0–100)
Helianthus tuberosus	8	99.5 (96–100)	0.1868±0.068	6	60.0 (30–80)	0.0 (0–0)
Heracleum mantegazzianum	16	85.3 (68–100)	0.1789±0.085	12	31.0 (4–68)	0.0 (0–0)
Hesperis matronalis	12	96.7 (84–100)	0.1624±0.112	3	36.0 (24–44)	25.5 (0–40)
Hordeum jubatum	12	99.3 (92–100)	0.2580±0.093	3	66.7 (52–76)	100.0 (100–100)
Impatiens glandulifera	12	96.3 (84–100)	0.1508±0.095	15	36.8 (0–68)	0.0 (0–0)
Impatiens parviflora	12	99.0 (96–100)	0.1684±0.069	12	40.0 (4–96)	0.0 (0–0)
Imperatoria ostruthium	12	41.0 (12–80)	0.1240±0.120	12	26.7 (8–52)	0.0 (0–0)
Inula helenium	4	100.0 (100–100)	0.2156±0.069	6	32.7 (0–80)	0.0 (0–0)
Iva xanthiifolia	8	93.0 (84–100)	0.2585±0.082	9	40.9 (0–72)	0.0 (0–0)

Species	n (germination)	Total germination (%, mean, range)	Seedling RGR (g·g⁻¹·day⁻¹, mean±95% c.i.)	n (seedling establishment)	Seedling establishment: Total (%, mean, range)	Seedling establishment: Autumn (% of total seedling establishment, mean, range)
Juncus tenuis	12	91.8 (80–100)		12	19.3 (0–80)	0.0 (0–0)
Kochia scoparia	12	97.3 (92–100)	0.2087±0.119	9	70.2 (36–96)	0.0 (0–0)
Lepidium densiflorum	12	100.0 (100–100)	0.2070±0.103	9	73.8 (40–100)	99.1 (92–100)
Lupinus polyphyllus	12	62.0 (28–96)	0.1270±0.054	15	57.9 (24–76)	2.7 (0–11)
Lychnis coronaria	12	100.0 (100–100)	0.1927±0.061	9	56.4 (32–92)	59.7 (0–100)
Lysimachia punctata	8	77.0 (60–100)	0.1801±0.131	6	27.7 (12–50)	0.0 (0–0)
Matricaria discoidea	16	99.0 (84–100)	0.2165±0.162	6	27.3 (4–44)	55.1 (0–100)
Medicago sativa	8	48.0 (40–60)	0.1712±0.104	6	19.3 (4–36)	26.8 (0–78)
Mimulus guttatus	8	100.0 (100–100)	0.2837±0.180	9	28.4 (12–68)	17.7 (0–67)
Myrrhis odorata	12	97.7 (92–100)	0.1131±0.102	9	9.3 (0–16)	0.0 (0–0)
Oenothera biennis	8	98.0 (96–100)		6	30.0 (4–40)	0.0 (0–0)
Oenothera glazoviana	4	59.0 (56–68)		3	13.3 (12–16)	0.0 (0–0)
Oxalis corniculata subsp. *repens*	12	98.7 (92–100)	0.1735±0.147	12	40.8 (8–100)	41.5 (0–95)
Oxalis dillenii	12	97.7 (88–100)	0.2033±0.162	9	51.1 (28–72)	47.1 (0–100)
Oxalis fontana	12	91.0 (72–100)	0.1912±0.226	9	37.8 (4–88)	21.3 (0–100)
Oxybaphus nyctagineus	4	100.0 (100–100)	0.1768±0.066	3	54.7 (52–60)	0.0 (0–0)
Panicum capillare	12	47.3 (8–96)	0.2206±0.103	9	42.2 (12–72)	0.0 (0–0)
Panicum miliaceum	8	77.3 (60–96)	0.2231±0.106	6	14.7 (0–40)	0.0 (0–0)
Phytolacca esculenta	12	61.6 (36–75)	0.1303±0.064	6	14.0 (0–20)	0.0 (0–0)
Potentilla intermedia	8	92.6 (60–100)	0.2627±0.077	6	35.7 (8–60)	41.8 (0–100)
Rudbeckia hirta	4	65.0 (52–72)	0.2004±0.145	3	28.0 (20–40)	0.0 (0–0)
Rudbeckia laciniata	12	98.0 (92–100)	0.1825±0.059	9	41.3 (16–84)	0.0 (0–0)
Rumex alpinus	12	86.0 (60–100)	0.2369±0.126	9	64.0 (28–84)	61.4 (38–89)
Rumex longifolius	8	91.5 (84–100)	0.2613±0.143	6	62.7 (40–80)	44.5 (11–90)
Rumex patientia	12	96.7 (92–100)	0.2562±0.060	9	59.6 (8–100)	75.2 (33–100)
Rumex thyrsiflorus	12	85.3 (60–100)	0.2230±0.115	12	57.7 (48–80)	77.8 (53–100)
Scutellaria altissima	12	98.7 (92–100)	0.1977±0.110	9	39.1 (8–100)	0.0 (0–0)
Sedum hispanicum	4	96.0 (92–100)	0.2136±0.131	6	12.7 (4–24)	53.9 (0–100)
Sedum rupestre	4	100.0 (100–100)		3	24.0 (0–40)	4.2(0–13)
Sedum spurium	4	65.0 (56–80)	0.1808±0.152	6	9.3 (0–16)	0.0 (0–0)
Senecio inaequidens	8	96.5 (92–100)	0.3160±0.093	6	62.0 (24–100)	37.7 (9–75)
Senecio vernalis	8	95.5 (88–100)	0.2585±0.161	9	63.6 (36–88)	88.9 (50–100)
Setaria faberii	4	74.0 (64–84)	0.2073±0.070	3	56.0 (52–60)	0.0 (0–0)
Silene dichotoma	8	100.0 (100–100)	0.1551±0.074	6	78.7 (64–92)	99.1 (94–100)
Sisymbrium altissimum	12	97.7 (92–100)	0.1438±0.093	12	72.3 (36–92)	100.0 (100–100)
Sisymbrium loeselii	12	97.3 (88–100)	0.1983±0.098	12	46.3 (28–72)	97.9 (75–100)
Sisymbrium strictissimum	12	100.0 (100–100)	0.1694±0.075	9	58.7 (20–100)	39.9 (0–96)
Smyrnium perfoliatum	12	62.0 (40–92)	0.1194±0.088	12	29.7 (0–72)	0.0 (0–0)
Solidago canadensis	12	96.7 (88–100)	0.2564±0.121	12	36.7 (20–52)	0.0 (0–0)
Solidago gigantea	12	98.7 (92–100)	0.2060±0.088	6	21.3 (0–56)	0.0 (0–0)
Telekia speciosa	8	99.5 (96–100)	0.2173±0.051	6	40.0 (24–68)	21.5 (0–67)
Trifolium hybridum	4	84.0 (76–88)	0.1943±0.162	6	58.0 (36–84)	21.5 (7–64)
Veronica persica	8	97.3 (88–100)	0.1452±0.109	6	20.6 (7–40)	50.0 (0–100)
Vicia grandiflora	4	31.0 (25–35)	0.1459±0.065	6	19.3 (4–44)	21.7 (0–67)
Virga strigosa	12	96.3 (84–100)	0.2051±0.104	9	34.7 (16–56)	0.0 (0–0)
Xanthium albinum	12	59.3 (37.5–82.5)	0.1456±0.109	9	53.3 (40–78)	0.0 (0–0)

Results

Reproductive, dispersal and establishment traits of neophytes in the Czech flora

Seed production and dispersal traits of the species studied are summarized in Table 2, traits relating to establishment in Table 3. Many of the traits are significantly correlated with each other (bivariate correlations presented in Table 4). These correlations include well-known demographic correlations previously reported for native species, such as e.g. negative ones between seed size/weight and the number of seed produced or between RGR and seed size (Fig. 1). Not surprisingly there is a close correlation between both measures of fecundity, i.e. the number of propagules produced per plant and by population, or both measures of propagule size (i.e. length and width) and its weight (Table 4).

The data also indicate that there are positive correlations between dispersal by water (buoyancy) and dispersal by animals (epizoochory); propagules that spread well on animal fur also possess increased capability for floating (Fig. 1). Both modes of dispersal, by animals and water, are easier for species with larger propagules. Capacity for dispersal by wind (anemochory) is positively correlated with buoyancy as indicated by the negative correlation between terminal velocity and floating time (Fig. 1). In addition, the positive correlation between terminal velocity and propagule weight (Table 4) indicates that light propagules have better capacity for dispersal by wind. As for the establishment traits, good germination results in better seedling establishment (Fig. 1).

Differences between traits of invasive and non-invasive species

Without considering the effect of phylogeny, invasive species significantly differ from those that do not invade in propagule length/width ratio (invasive species have more rounded propagules as indicated by a lower ratio) and in being more fecund, both per individual plant (shoot) and in terms of the population propagule production. As far other traits are concerned, invasive species have proportionally less seedlings establishing in the autumn, better capability for anemochory (i.e. lower terminal velocity) and also marginally significantly differ from non-invasive species in higher total maximal germination and lower floating capability, i.e. buoyancy (Table 5).

In analyses that consider relatedness among species expressed as a taxonomic hierarchy, invasive species have lighter propagules and higher population propagule numbers. Invasive species also differ from non-invasive species in producing more propagules per plant and have higher capability of water dispersal, but the differences in these two traits were only marginally significant (Table 5).

Therefore, the results for several traits differ depending on whether or not the effect of phylogeny is included in the model. This concerns differences between invasive and non-invasive species in plant propagule number which becomes significant instead of marginally significant when phylogenetic relatedness is considered, while the differences in total maximal germination and capability for wind dispersal become non-significant in phylogenetically-informed analyses. Most importantly, the highly significant difference in propagule length/width ratio becomes non-significant, and the non-significant difference in propagule weight becomes highly significant with phylogenies included. In this model, invasive species differ from naturalized but non-invasive species in having lighter propagules and this difference is the most pronounced of all traits measured. Finally, the
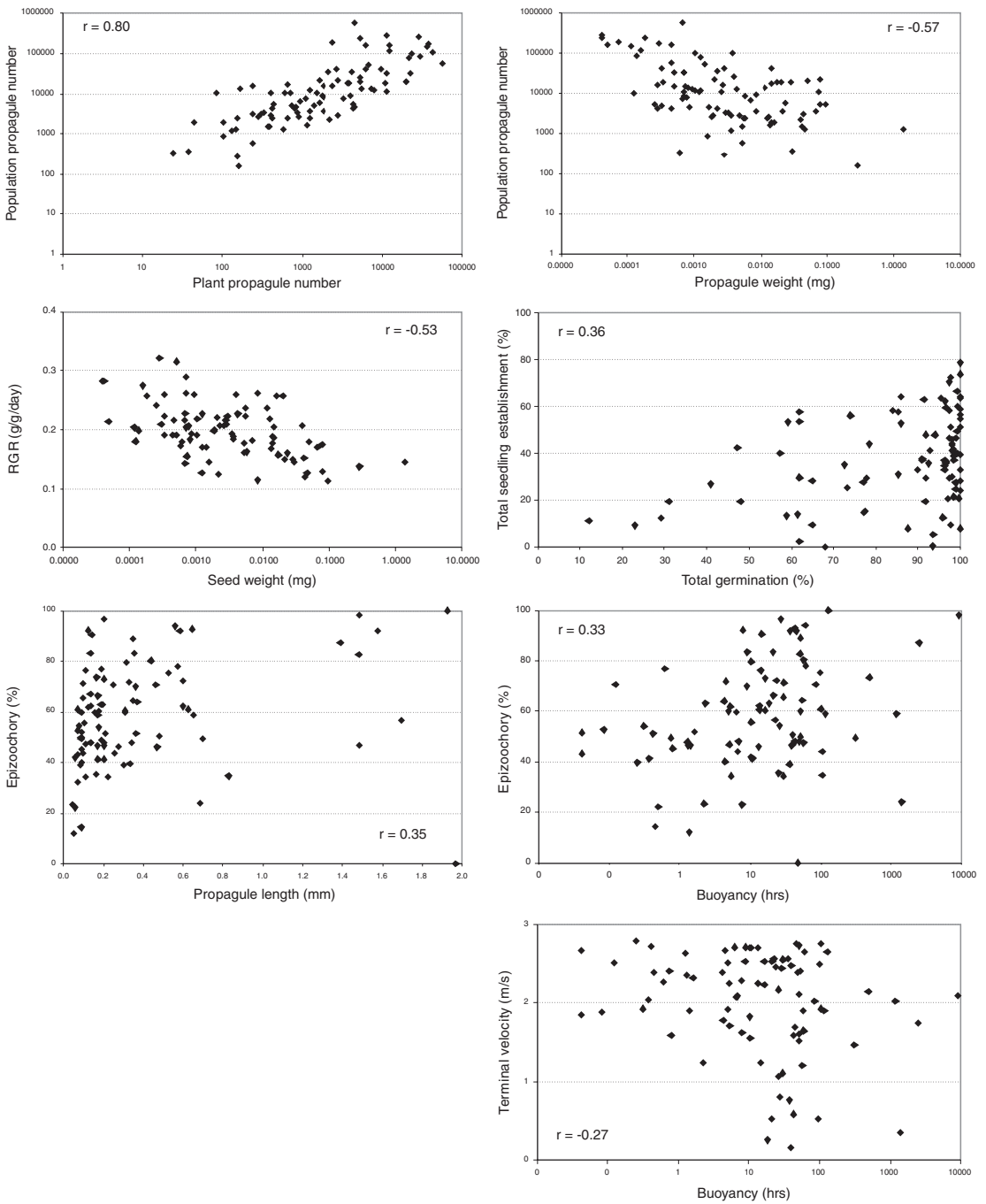
Fig. 1. – Correlation between selected traits studied (correlation coefficients are given, otherwise see Table 4 for statistics). Note (semi)log scale in some plots.

Table 4. Correlation between pairs of traits of alien neophytes in the Czech flora. Values are Spearman rank correlation, n = 85–93, depending on data availability (see Table 2). Correlations significant at the 0.01 (**) and 0.05 (*) level (2-tailed) are shown in bold.

	Plant propagule number	Population propagule number	Propagule length	Propagule width	Propagule length/width ratio
Plant propagule number	–				
Population propagule number	**0.804****	–			
Propagule length	**–0.346****	**–0.499****	–		
Propagule width	**–0.302****	**–0.479****	0.832**	–	
Propagule length/width ratio	–0.030	0.030	0.160	**–0.369****	–
Propagule weight	**–0.398****	**–0.570****	0.882**	0.920**	–0.153
Water dispersal (buoyancy)	0.049	–0.097	**0.372****	0.270**	0.113
Animal dispersal (epizoochory)	–0.117	**–0.212***	0.353**	0.230*	0.093
Wind dispersal (terminal velocity)	**–0.309****	**–0.403****	0.335**	0.558**	**–0.342****
Total germination	0.049	0.104	**–0.231***	**–0.386****	0.334**
RGR	**0.421****	**0.430****	**–0.312****	**–0.461****	0.222*
Total seedling establishment	0.048	–0.004	0.145	0.081	0.094
Autumn seedling establishment	0.050	0.084	–0.171	–0.180	–0.013

Table 5. Trait transformations and effects of plots within traits, invasion status (naturalized/invasive) and taxonomic hierarchy (genus, family, order) on the values of the traits studied. Plots within traits are not analyzed for seedling RGR because the data for this trait were pooled before the analysis. Positive parameter estimates for invasion status mean larger value of the trait for invasive species than for naturalized but non-invasive, shown both with and without taking into account species relatedness expressed by the taxonomic hierarchy. Likelihood ratio tests on taxonomic hierarchy show the significance for each trait, expressed for any species within genera, any genus within families and any family within orders, taking into account invasive status of the species. Likelihood ratio test could not be calculated for orders within classes due to singular convergence. Df = degrees of freedom; S.E. = standard error of the estimate; L. ratio = likelihood ratio test; *** P < 0.001; ** P < 0.01; * P < 0.05; (*) P < 0.1; NS = not significant.

Trait	Transformation	Plots within trait		Taxonomy		
	x	Df	F-test	Genus L. ratio	Family L. ratio	Order L. ratio
A. Seed production traits:						
Plant propagule number	ln(x)	6, 214	0.76 NS	65.20***	2.17 NS	21.93***
Population propagule number	(x+1)^0.1	6, 214	0.60 NS	54.63***	2.43 NS	9.40**
B. Dispersal traits:						
Propagule length/width ratio	x^-1	4, 220	0.18 NS	200.66***	13.63 ***	156.73***
Propagule weight	ln(x)	4, 220	0.05 NS	324.92***	24.91 ***	84.29***
Water dispersal (buoyancy)	(x+1)^-0.15	4, 221	0.31 NS	108.53***	38.58 ***	44.85***
Animal dispersal (epizoochory)	x	5, 224	0.65 NS	133.28***	49.77 ***	48.65***
Wind dispersal (terminal velocity)	x^2	4, 208	0.11 NS	317.91***	31.44 ***	48.57***
C. Establishment traits:						
Total maximal germination	arcsin√proportion	6, 214	0.71 NS	67.68***	1.89 NS	44.53***
Seedling RGR	x	–	–	4.61*	0.0020 NS	5.00*
Total seedling establishment	arcsin√proportion	6, 211	0.99 NS	39.78***	6.98 **	12.53***
Autumn seedling establishment	arcsin√proportion	6, 211	0.54 NS	30.76***	33.96 ***	24.61***

Propagule weight	Water dispersal (buoyancy)	Animal dispersal (epizoochory)	Wind dispersal (terminal velocity)	Total germination	RGR	Total seedling establishment
–						
0.171	–					
0.242[*]	0.328[**]	–				
0.690[**]	**−0.265**[*]	−0.049	–			
−0.322[**]	−0.172	−0.088	**−0.291**[**]	–		
−0.527[**]	0.211	0.163	**−0.593**[**]	0.205	–	
0.043	−0.068	0.096	−0.137	**0.362**[**]	0.028	–
−0.216[*]	**−0.283**[**]	−0.108	**−0.245**[*]	0.222[*]	0.022	0.544[**]

Invasion status (with phylogeny accounted for)				Invasion status (without phylogeny accounted for)			
Estimate	S.E.	Df	|t-test|	Estimate	S.E.	Df	|t-test|
0.51	0.300	161	1.72 (*)	0.62	0.260	220	2.39*
0.18	0.074	157	2.49 *	0.17	0.064	216	2.60**
−0.0019	0.016	163	0.12 NS	−0.12	0.029	224	4.10***
−0.63	0.120	162	5.27 ***	−0.22	0.280	224	0.80 NS
0.040	0.022	163	1.77 (*)	−0.049	0.026	225	1.89 (*)
−3.50	2.430	167	1.44 NS	−2.01	3.010	229	0.67 NS
−0.21	0.140	153	1.50 NS	−0.63	0.310	212	2.02*
0.041	0.044	159	0.94 NS	0.08	0.042	220	1.90 (*)
−0.0016	0.011	20	0.14 NS	0.0043	0.014	34	0.30 NS
0.0053	0.044	159	0.12 NS	0.0088	0.039	217	0.23 NS
0.0039	0.072	130	0.05 NS	−0.15	0.074	217	1.99*

difference in buoyancy remains only marginally significant but with phylogeny included its direction changes, suggesting that invasive species tend to have propagules floating for longer time than those of non-invasive species (Table 5).

Taking into account whether the species is invasive or naturalized but non-invasive, the effect of genus, describing species within genera, and the effect of order, describing families within orders, on the values of traits analyzed was always significant, while the effect of families, describing genera within families, appeared significant only for dispersal traits and seedling establishment traits. The values of likelihoods, testing patterns in species relatedness, appeared highest for genera, suggesting that most variation in the response variable is among species within genera (Table 5). This distribution of relatedness means that predictions of whether a species will become invasive cannot be based on traits of the relatives of this species at higher taxonomic levels.

Analyses without taking into account the plant invasion status (Fig. 2) confirmed that most trait variances consistently appear among species within genera, most strikingly so for propagule numbers, both per plant and for population (Fig. 2A), i.e. traits in which invasive species differ from non-invasives. Trait variability within localities in which the species were collected had only a negligible effect in all cases (Table 5).

Discussion

Data on reproductive characteristics of a large set of alien species are still rather scarce in the invasion ecology literature. This paper, by providing original quantitative information on reproductive characteristics of a number of alien species naturalized in the Czech flora, some of them invasive, and collected by standard methods aims to fill this gap. Our results suggest that reproductive traits, namely those related to seed production and dispersal, play a role in determining the invasiveness of alien plant species. Although individual traits had different values in our models and their significance was subject to change depending on whether phylogenetic relatedness among species was considered, the results indicate that invasive species are characterized by the production of more propagules, both at the level of individual plant/shoot and at that of the population, and by having lighter and more rounded propagules which are more easily dispersed by water and wind. The results therefore confirm the generally accepted view that traits related to propagules are key in discriminating invasive and non-invasive species (Pyšek & Richardson 2007).

In general, it is difficult to compare our results with those of previous papers since comparative studies including reproductive characteristics are rather scarce due to the lack of quality data for large sets of species (but see e.g. Hamilton et al. 2005). Yet the emerging patterns related to propagule size seem to be rather robust; several comparative studies have confirmed that invasiveness is correlated with small seed/fruit size (Cadotte & Lovett-Doust 2001, Lake & Leishman 2004, Hamilton et al. 2005, but see Crawley et al. 1996). This is because small seed mass is correlated with a high seed output (Henery & Westoby 2001), small seeds generally persist longer in the soil and form more persistent seed banks (Thompson et al. 1993), and small, long-lived and well-dispersed seeds are characteristic of plants adapted for rapid colonization of disturbed habitats, which makes them likely to become successful invaders (Rejmánek & Richardson 1996, Cadotte & Lovett-Doust 2001, Lloret et al. 2004, Hamilton et al. 2005).
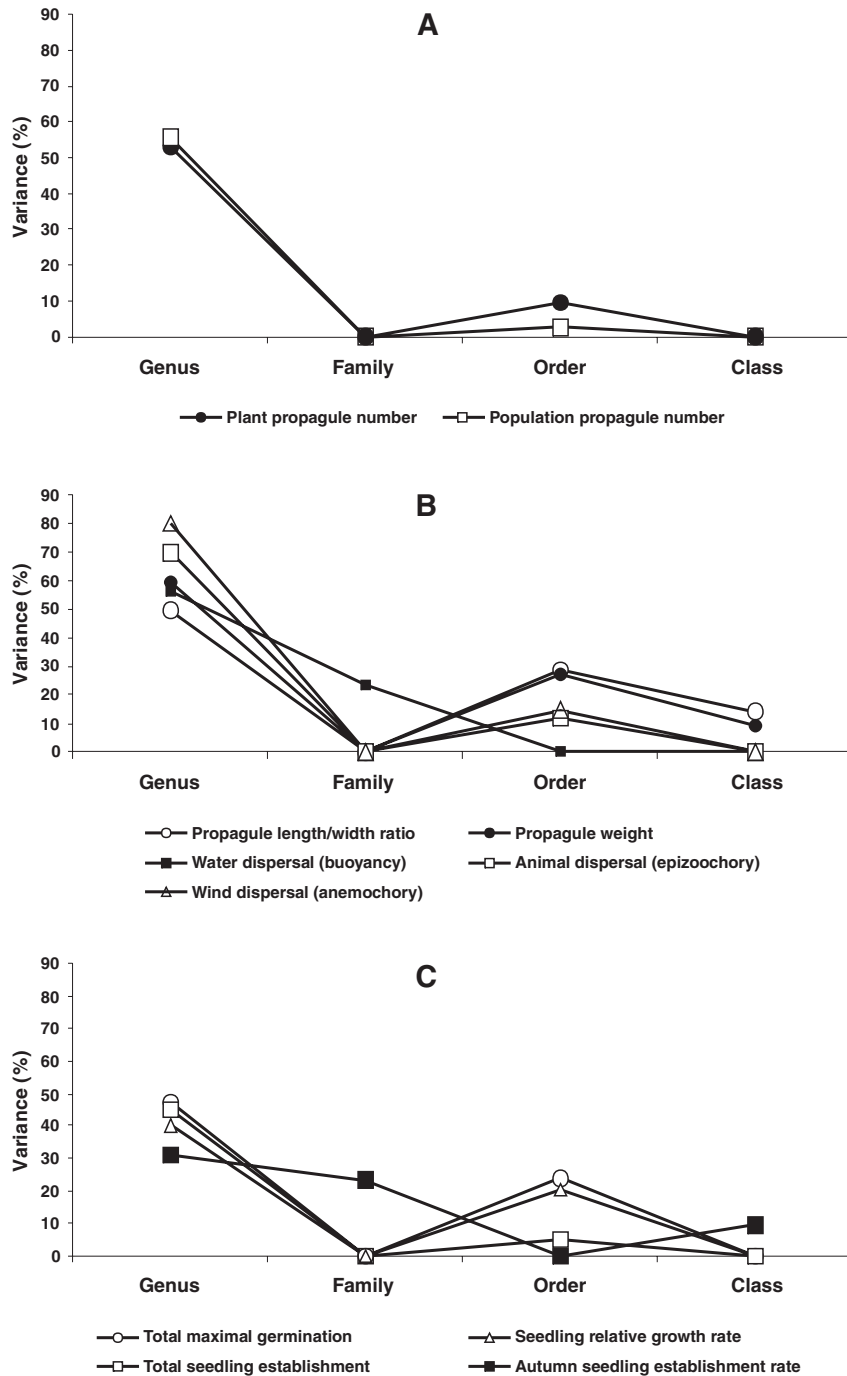
Fig. 2. – Taxonomic distribution of the variance (species within genera, genera within families, families within orders and orders within classes) in the individual species traits, estimated by the variance component analysis. (A) seed production traits, (B) dispersal traits, (C) establishment traits. Unlike likelihood ratio tests in linear mixed effect models (see Invasive status in Table 1), the results do not take into account the status of the species. Residual variance, describing variation within the individual species from replicated plots, appeared insignificant (see Plots within trait in Table 1), and is not shown.

Alien species are also often reported to be more fecund in congeneric comparisons but most of these relate to comparison of invasive species with their native congeners (Pyšek & Richardson 2007; but see Richardson et al. 1987, Mihulka et al. 2006). In this paper we employed two measures of fecundity, one was the seed production of an individual plant (or a shoot in the case of clonally growing species) and the other (by considering the maximum density a species is able to achieve) was the potential fecundity of the population of an alien species. Although both appeared significant in the models, population propagule production seems to be more important in contributing to whether a species becomes invasive or not.

There was also a very strong effect of propagule length/width ratio, that differs between invasive species and those that have reached the naturalization stage but are not invasive. Invasive species have more rounded propagules which may provide them with the advantage of easier movement on the soil surface at the local scale. Good dispersal ability, especially by wind and water is also assumed to contribute to invasion success. Interestingly, the capacity for efficient dispersal by individual vectors was correlated in our data; species that possess the ability to float for a long time also have a high capacity for dispersal by wind and animals. This suggests the existence of a dispersal syndrome that may contribute to invasiveness of aliens species able to use a variety of vectors in the process of their spread (Pyšek et al. 2009a).

That most trait variances appear among species within genera indicates that the prediction of whether a species will become invasive or not cannot be based on traits of a species' relatives at higher taxonomic levels. The fact that at higher taxonomic levels there is a weaker phylogenetic component of invasion success than at the level of species within genera implies that we cannot predict that a species belonging to a particular family, order or class would be more predisposed to invasion than other species belonging to other taxa at the same hierarchical level; in most cases, the variation in invasiveness is primarily associated with species level (Pyšek et al. 2009a). This does not mean that the effect of relatedness on the species traits analysed is unimportant. In all analyses, at least the effect of families within orders was also highly significant, and the output for several traits was different between the analyses that incorporated phylogenetic information and those that did not. While the results that did not consider phylogeny are specific to our data set, those with phylogeny included should be valid for any species within the taxonomic hierarchy applied. Phylogenetic relatedness of species exhibited greatest effect on the difference in propagule length/width ratio and size between invasive and non-invasive species. That the significant difference in propagule length/width ratio between invasive and non-invasive species disappeared after phylogeny was considered indicates that the present-day relationship is the result of one or a small number of independent, correlated evolutionary divergences between propagule length/width ratio and invasiveness (Hamilton et al. 2005). The opposite was true for propagule weight; small weight was significantly correlated with invasive status only after considering phylogenetic relatedness of species. The taxonomic distribution of variance for this trait (Fig. 2B) indicates that this result may be due to the propagule weight being linked to invasive status at the genus level, but not species or family levels. This seems to suggest the existence of significant correlated divergences between propagule weight and invasiveness in the phylogeny at the taxonomic level of genus. Furthermore, the direction of the marginally significant effect of buoyancy has changed after accounting for phylogenies, and only then it appeared that invasive species may have advantage in being able to float for longer time when dispersed by water.

Another reason which advocates for rather careful comparison of our results with previous studies is that the outcomes of comparative studies are to a large extent influenced by the context in which they are carried out – they differ in the range of species included, measures of invasiveness used, geographical scale, and the status of species they compare (Cadotte et al. 2006a, Pyšek & Richardson 2007). For example, studies comparing invasive aliens with native species convey a different message than those comparing invading and non-invading alien species. The distinction made in this paper, i.e. invasive species vs. naturalized but non-invasive (following definitions of Richardson et al. 2000, Pyšek et al. 2004), is the one with potential to contribute to deeper understanding of the determinants of invasiveness for which the transition from naturalized to invasion stage is crucial, yet rarely addressed in invasion ecology (Pyšek et al. 2008b, Murray & Phillips 2010, Phillips et al. 2010). This importance of addressing different stages of invasion in such analyses was illustrated in a previous paper based on the same species set as the one analysed here (Kubešová et al. 2010), since the traits correlated with invasion success may differ between stages (Williamson 2006, Pyšek et al. 2009a, b). Naturalized species in the Czech flora have smaller genomes than their congeners not known to be naturalized or invasive in any part of the world. However, there was no difference in the genome size of invasive species compared to naturalized but non-invasive. This suggests that small genome size provides alien plants with an advantage already at the stage of naturalization and need not be necessarily associated with the final stage of the process, i.e. invasion (Kubešová et al. 2010).

However, it needs to be borne in mind that the present paper is based on single trait analyses that, while indicative of the role individual traits may play, only capture a limited proportion of variation in invasive success, i.e. not that included in trait interactions (Küster et al. 2008). Also, the reproductive traits studied in this paper are mutually correlated, reflecting well-known demographic relationships such as the trade-off between propagule size and fecundity (Westoby et al. 1996, Henery & Westoby 2001, Moles et al. 2004, Hamilton et al. 2005) or between RGR and seed size (Fenner 1983, Swanborough & Westoby 1996, Reich et al. 1998). Single trait analyses therefore, due to the cross-correlation structure of our data, at this stage prevent us from identifying pure effects of individual traits unbiased by correlation with or mediated by other traits. Also, information on other characteristics that are known to affect invasion success such as residence time in the region or habitat associations (Pyšek et al. 2009a) need to be incorporated to account for the full understanding of the role of reproductive characteristics in the invasion process.

Souhrn

Práce přináší přehled reprodukčních vlastností 93 neofytů (druhů zavlečených po roce 1500) flóry České republiky a srovnává, zda se v těchto charakteristikách liší invazní druhy od naturalizovaných, avšak neinvazních druhů. Každý druh byl sbírán z několika lokalit na území České republiky a v terénu, na experimentální zahradě a v laboratoři byly měřeny vlastnosti týkající se produkce (počet propagulí na rostlinu a v populaci), rozšiřování (velikost, tvar a váha propagulí, plovatelnost, schopnost šířit se epizoochorně a větrem) a vzcházení (klíčivost, relativní růstová rychlost semenáčků a vzcházení semenáčků). Invazní druhy se od neinvazních statisticky průkazně lišily kulatějšími propagulemi, vyšší plodností, tendencí odložit vzcházení semenáčků na jaro příštího roku a lepší schopností šíření větrem. U několika vlastností se výsledky lišily podle toho, zda byla brána v úvahu fylogenetická příbuznost druhů, vyjádřená pomocí taxonomické hiearchie. Pokud ano, mají invazní druhy lehčí propagule, vyšší produkci na úrovni populace a na hranici statistické průkaznosti také v produkci propagulí na rostlinu a delší plovatelnost. Největší část variability je mezi druhy v rámci rodů, což ukazuje, že pravděpodobnost, zda bude druh invazní, nelze odvozovat od vlastností jemu příbuzných druhů na vyšších taxonomických úrovních.

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