

Regional species pools of vascular plants in habitats of the Czech Republic

Druhy cévnatých rostlin v biotopech České republiky

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Based on a combination of data from the Czech National Phytosociological Database and expert knowledge, a database of vascular plant species pools for 88 habitats, representative of the diversity of Czech vegetation, was compiled. This database contains 1820 native species, 249 archaeophytes and 278 neophytes, each assigned to one or more habitats. Besides the data on species occurrence in different habitats, the database contains information on a species' ecological optimum in the habitat or its dominance. The largest pools of native species were found in rather rare habitats of dry and warm herbaceous or woody habitats at low altitudes, some of which contain > 530 species (maximum of 695 species for thermophilous forest fringes). These were followed by common habitats on mesic soils. The smallest pools of native species were in saline, aquatic and bog habitats (< 90 species). Species pool sizes of archaeophytes and neophytes for different habitats were positively, yet weakly, correlated with the species pool sizes of native species. Habitats with native species pools < 350 species contained any number of archaeophytes. Habitats with < 100 native species contained < 5, and often no neophytes, but habitats with 100–350 native species contained different numbers of neophytes. Habitats with > 350 native species always contained > 5 archaeophytes and > 5 neophytes, and often many more. Two hundred and thirty two native species, 18 archaeophytes and 30 neophytes were identified as potential dominants in at least one habitat. However, potentially dominant species made up less than 3% of the species pool for 78 out of 88 habitats. Larger percentages (up to 14.6%) of potential dominants were included in habitats with small species pools and species-poor stands (e.g., aquatic, saline and mire habitats). The number of habitats in which a species occurred was used as a measure of its ecological range. Most ecological generalists were found among the native species, less among the archaeophytes and least among the neophytes. Out of the 36 species that occur as dominants in three or more habitats, 34 were native (many are grasses), one was an archaeophyte (*Cirsium arvense*) and one was a neophyte (*Impatiens parviflora*).

Key words: alien, archaeophyte, habitat classification, local and regional processes, native, neophyte, species richness, vegetation type

Introduction

Species pool is the set of species that are potentially capable of coexisting in a particular community (Zobel 1997). The concept of species pool explains local species richness in terms of historical and evolutionary processes operating at large spatial and temporal scales (Taylor et al. 1990, Cornell & Lawton 1992, Zobel 1992, Ricklefs & Schluter 1993). According to the species pool theory, species richness of a local plant community not only depends on local processes existing within this community, such as competition (Palmer 1994), but also to a large extent, on the availability of propagules of those species

that are able to disperse to and grow in the target community. In addition to studies on the variation in local species richness, the species pool theory is important in studies of habitat invasibility by alien plants (Chytrý et al. 2005, Stohlgren et al. 2006). Consistent with the species pool theory is the recognition in invasion ecology that the levels of invasion of particular habitats not only depend on habitat properties (habitat susceptibility to invasion), but also propagule pressure, i.e. the size of alien species pool (Williamson 1996, Lonsdale 1999, Daehler 2006, Richardson & Pyšek 2006, Richardson 2006). The species pool concept is also of great importance in applied fields such as restoration ecology (Zobel et al. 1998), where the success of restoration projects, especially those relying on spontaneous succession (Prach et al. 2001, Prach 2003, Ruprecht 2005), strongly depends on the migration of species from the local species pools into the restored sites.

When taking species pool effects into account, the key issue is the identification of the set of species that are in the species pool of the target community (Pärtel et al. 1996). Of the different attempts to tackle this problem (see an overview in Zobel et al. 1998), perhaps the most reliable is a combination of the relevé data existing in large phytosociological databases (Hennekens & Schaminée 2001) and expert knowledge of the habitat affinities of the species in the regional flora. In this way a relatively standardized list of species belonging to the species pool can be identified for each habitat occurring in the target region. If the target region is larger than a landscape in which species can migrate to a particular site within a few years, such lists correspond to the definition of regional species pool sensu Pärtel et al. (1996) and Zobel (1997) rather than to a local or actual species pool. The lists of regional species pools for particular habitats can be useful both in theoretical studies on the control of local species richness or habitat invasibility and in practical applications such as nature conservation or ecological restoration. However, even a simple comparison of the sizes and compositions of regional species pools among habitats can provide interesting ecological insights into the history of the formation of regional floras.

To facilitate future research into diversity and invasibility of Central European plant communities and future restoration projects, a database of the regional species pools of vascular plant for 88 habitats, which are representative of the vegetation diversity of the Czech Republic, was compiled. In this paper, statistical summary of the regional species pools of Czech habitats, extracted from this database, and some basic correlations between numbers of native and alien species are presented.

Materials and methods

The habitat classification used in this study (Appendix 1) was prepared in co-operation with I. Kühn, S. Klotz (Halle) and G. Karrer (Vienna) for the purpose of describing habitat affinities in the future database of species traits of German, Czech and Austrian flora. Habitat delimitation is largely based on phytosociological syntaxa, mainly at the level of alliance. Appendix 1 lists only the habitats occurring in the Czech Republic.

Species in the Czech flora were assigned to habitats in several steps. First, 24,283 relevés from the Czech National Phytosociological Database (Chytrý & Rafajová 2003) were assigned to habitats, using the assignment of these relevés to phytosociological syntaxa provided by the relevé's authors. Then, the percentage occurrence frequency and fidelity (according to Tichý & Chytrý 2006) of each species to each habitat, based on the

relevé data, were calculated using the JUICE 6.4 program (Tichý 2002). This provided the first approximation, because many rare species may be under-represented in relevés, as are species occurring in ecotonal or successional situations or small patches, which do not satisfy the phytosociological requirement for homogeneous plots (Westhoff & van der Maarel 1973).

This database was further improved and corrected by the first author, using handbooks on Czech flora (Hejný & Slavík 1988–1992, Slavík 1995–2000, Kubát et al. 2002, Slavík & Štěpánková 2004), papers on individual species, local and national vegetation studies (e.g., Moravec et al. 1995, Moravec 1998–2003, Kočí 2001, Havlová et al. 2004, Botta-Dukát et al. 2005, Havlová 2006, Kropáč 2006, Lososová et al. 2006, Chytrý 2007), and expert knowledge of species habitat affinity in the field. Often there were no reliable data on the occurrence of some species in some habitats; in such cases, species presence or absence in the habitat was assessed, with some degree of uncertainty, from the reliable information on its presence or absence in ecologically similar and close by habitats.

Some species recorded in single relevés from some habitats were deleted if such records represented sporadic exceptions to the habitat range of that plant (e.g., *Coronilla vaginalis* in a forest clearing or *Dryopteris carthusiana* growing in saline grassland). Seedlings and saplings were not included in the species pools of habitats in which they had little chance of survival (e.g., *Abies alba* in a meadow). Trees and shrubs were generally not included in species pools of meadows, pastures, annual anthropogenic vegetation, cliffs and very wet or inundated marshes.

The following groups of taxa were excluded from the database: (1) Species which disappeared from the flora of the Czech Republic before 2000 (Holub 2000). (2) Hybrids or hybridogenous taxa, with 19 exceptions, those that differ in habitat affinities from their parents or have at least one parent species not occurring in the Czech Republic (e.g., *Circaea xintermedia*, *Pinus x pseudopumilio*, *Prunus xfruticans*, *Sorbus xsudetica* and *Viola xwittrockiana* were all included). (3) Agamospecies of *Rubus* and *Taraxacum* were excluded and replaced by series and sections, respectively. However, agamospecies of *Alchemilla*, *Hieracium* and *Sorbus* were included. (4) Of 817 casual neophytes present in the Czech flora (Pyšek et al. 2002a), 119 relatively frequent species were included and 698 were excluded from the database. Excluded casual neophytes were those that occur as garden escapees but do not survive for long (e.g., *Allium cepa* and *Petunia hybrida*), do survive for long as garden escapees but are rare (e.g., *Arabis procurrens*), used to escape from gardens but do not escape today (e.g., *Chenopodium foliosum* and *Lathyrus ochrus*), are beginning to escape but are still rather rare (e.g., *Amaranthus caudatus*), or lack clear habitat affinity regardless of how common they are and for how long they have been present as casuals (e.g., *Artemisia dracuncululus*, *Spiraea douglasii*, *Ribes aureum*). In total, 2347 species were included in the database, of which 1820 are native, 249 archaeophytes and 278 neophytes.

Each species-habitat assignment was classified to one of the following categories: (1) occurrence – species can grow in the habitat, but it is not ecological optimum for this species, which often is rare in this habitat; (2) optimum – the habitat or part of it is ecological optimum for this species; (3) dominant – species can be assigned to the previous category and at the same time frequently attains a cover above 25% in areas $\geq 10 \text{ m}^2$ or $\geq 100 \text{ m}^2$ in herbaceous or woody vegetation, respectively; (4) constant dominant – same as for the previous category but also determines the general appearance of the habitat (e.g., *Calluna vulgaris* in heathlands), occurring in $\geq 40\%$ of the localities of the habitat.

The database reflects species' habitat affinities as recorded or observed in 1990–2007, i.e. in the current period of landscape development, following the socio-economic change of 1989. The only exception is the inland vegetation of succulent halophytes, which had disappeared by the 1970s (Šumberová 2007), but was included in the habitat list and its species pool reconstructed based on a detailed phytosociological survey from the 1960s (Vicherek 1973).

Taxonomy and nomenclature of plants follow Kubát et al. (2002), except for taxa of *Centaurea* sect. *Jacea*, which follow Štěpánek & Koutecký (2004). Classification of species as native/alien follows the list in Pyšek et al. (2002a) and recent terminological proposals (Richardson et al. 2000, Pyšek et al. 2004). Exceptions include *Arrhenatherum elatius*, which is now considered to be an archaeophyte rather than a neophyte (Chytrý et al. 2005), and *Cytisus scoparius*, *Imperatoria ostruthium*, *Mimulus guttatus* and *Myrrhis odorata*, which are considered to be naturalized rather than invasive. Names of phytosociological syntaxa follow Moravec (1998–2003) for forests, Chytrý (2007) for grassland and heathland vegetation and Moravec et al. (1995) for other vegetation types.

The basic statistical figures characterizing the database presented in this paper were obtained using the programs MS Excel, MS Access (www.microsoft.com) and Statistica (www.statsoft.com). Numbers of archaeophytes and neophytes had a strongly right-skewed distribution, which was transformed to normal by \log_{10} transformation before correlation and regression analyses. Number of native species was normally distributed and therefore used without transformation. Normality was tested using the Kolmogorov-Smirnov test at $P < 0.05$.

Results and discussion

Pools of native species

The largest regional pools of native species (Table 1) were identified in dry and warm herbaceous or woody habitats at low altitudes (thermophilous forest fringe vegetation – 695 species, tall mesic and xeric scrub – 672, broad-leaved dry grasslands – 549, peri-Alpidic basiphilous thermophilous oak forests – 535). It is remarkable that these habitats harbour so many species although occupying restricted areas in the Czech Republic. Concentration of many species in the dry low-altitude habitats may reflect their long historical continuity. Similar habitats may have occurred there in the Pleistocene and most of the species in their regional species pools may have survived in situ up to the present, because at low altitudes in the Czech Republic there were presumably many open areas and open-canopy forests throughout the Holocene (Ložek 1973, Sádlo et al. 2005). Thus, regional species pool sizes for these habitats may be a consequence of historical inertia rather than contemporary effects of the size of the area of these particular habitats (Aarssen & Schamp 2002, Pärtel 2002, Ewald 2003). Additional reasons for these habitats having large regional species pools include: (i) each of these habitats occur at a wide range of diverse sites (e.g., soils of varying quality), therefore they include a number of species with different niches; (ii) these habitats occur at the border of forest and naturally treeless areas, which results in ecotone effects on species diversity.

	No. of species										No. of dominant species										
	Native species	Archaeophytes casual	Archaeophytes naturalized	Archaeophytes invasive	Archaeophytes all	Neophytes casual	Neophytes naturalized	Neophytes invasive	Neophytes all	All species	Native species	Archaeophytes casual	Archaeophytes naturalized	Archaeophytes invasive	Archaeophytes all	Neophytes casual	Neophytes naturalized	Neophytes invasive	Neophytes all	All species	
12S Basiphilous spruce and fir forests	125	0	0	0	0	0	0	0	0	125	3	0	0	0	0	0	0	0	0	0	3
12T <i>Robinia pseudacacia</i> plantations	293	1	73	14	88	5	14	21	40	421	6	0	2	0	2	0	0	2	2	2	10
12U Plantations of broad-leaved non-native trees	289	1	47	13	61	20	32	29	81	431	1	0	0	0	0	1	0	5	6	7	
12V Spruce plantations	344	0	7	4	11	1	5	8	14	369	3	0	0	0	0	0	0	0	0	0	3
12W Pine and larch plantations	525	0	34	7	41	0	9	9	18	584	3	0	0	0	0	0	1	1	2	5	
13A Annual vegetation of ruderal habitats	202	16	178	17	211	76	45	27	148	561	3	0	3	2	5	0	0	2	2	10	
13B Annual vegetation of arable land	146	16	145	17	178	37	25	12	74	398	3	0	1	0	1	0	0	0	0	4	
13C Annual vegetation of trampled habitats	154	6	84	12	102	15	17	14	46	302	2	0	0	0	0	0	0	0	0	2	
13D Perennial thermophilous ruderal vegetation	386	6	160	19	185	49	58	37	144	715	6	0	2	3	5	0	0	2	2	13	
13E Perennial nitrophilous herbaceous vegetation of mesic sites	404	4	75	18	97	26	48	45	119	620	12	0	0	0	0	0	0	7	7	19	
13F Herbaceous vegetation of forests clearings and <i>Rubus</i> scrub	458	0	47	9	56	2	12	25	39	553	16	0	0	1	1	0	0	0	0	17	

These rare dry and warm habitats are followed, in terms of the regional species pool size, by widespread habitats on mesic soils (*Pinus* and *Larix* plantations – 525 species, mesic *Arrhenatherum* meadows – 505, oak-hornbeam forests – 481, pastures and park grasslands – 474). It is important to note that of the 525 native species in *Pinus-Larix* plantations, only 86 have their optima in this habitat. The rich regional species pool is therefore composed of species that find their suboptima there, which is a general feature of the occurrence of native species in human-made habitats.

In contrast, the smallest regional species pools of native species are found in saline, aquatic and bog habitats (inland vegetation of succulent halophytes – 15 species; continental vegetation of annual halophilous grasses – 31; macrophyte vegetation of water streams – 39; inland saline steppes – 57; peatland pine forests – 67; macrophyte vegetation of eutrophic and mesotrophic still waters – 82; raised bogs – 90). All of these habitats are relatively rare and subject to strong environmental stress. To some extent, however, the low numbers of species assigned to regional pools for some of these habitats can be due to limited data. Rarity or even extinction in the case of the halophilous habitats makes it difficult to identify all the species that should be in regional species pools.

The sizes of regional species pools are well reflected in the local species richness of particular habitats. However, the local species richness and regional species pool size are not formally compared in this paper, because the data on local species richness, in the form of phytosociological relevés, are less reliable than the present species pool data. Relevés originate from different sources (Chytrý & Rafajová 2003), from plots of varying size (Chytrý & Otýpková 2003) and were made by preferential sampling, which results in a bias towards species-richer sites (Diekmann et al. 2007, Hédli 2007, but see Botta-Dukát

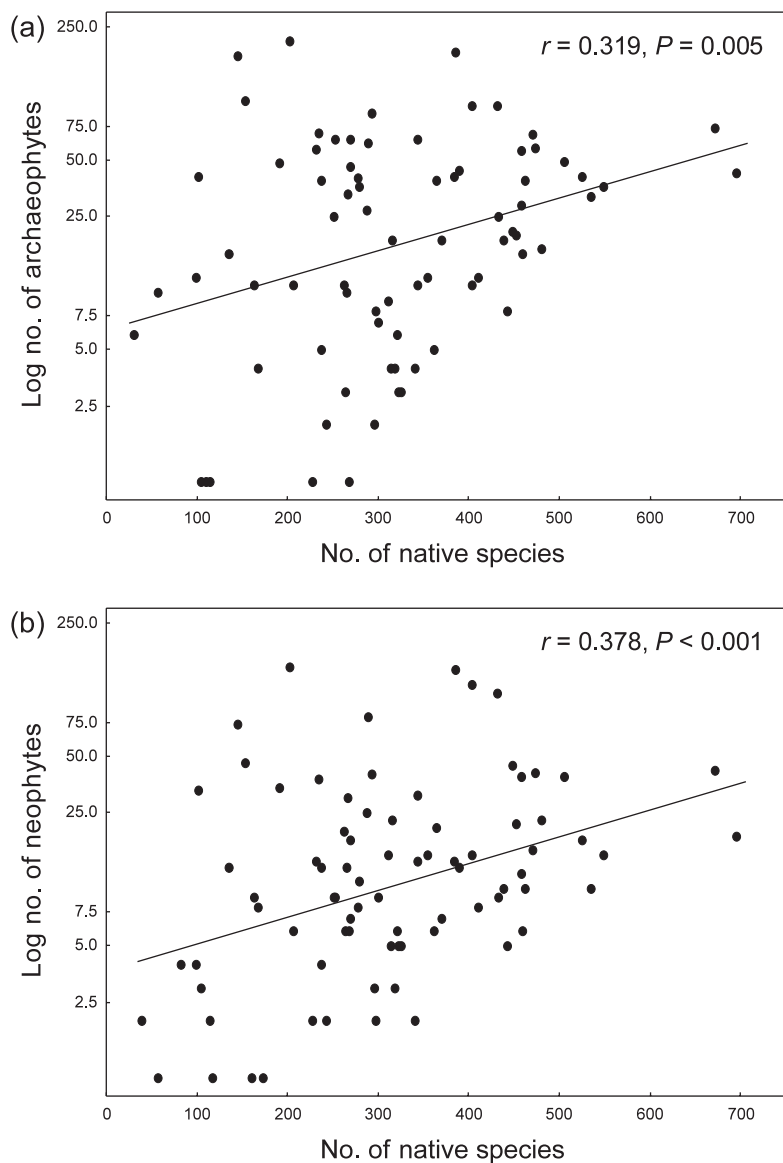


Fig. 1. – Relationships between the number of archaeophytes and neophytes, respectively, and the number of native species in the regional species pools of particular habitats. Regressions and correlations were calculated using log-transformed numbers of archaeophytes and neophytes; labels on vertical axes are back-transformed to original values.

et al. 2007) or artificial interactions between the magnitude of the bias and plot size (Chytrý 2001). Still, there are rough estimates of local species richness of individual vegetation types made during the preparation of the vegetation survey of the Czech Republic (Chytrý 2007), based on the relevés in the national phytosociological database (Chytrý &

Rafajová 2003). These analyses indicate good agreement between the local species richness of particular vegetation types and the regional species pool sizes presented here. For example, broad-leaved dry grasslands, basiphilous thermophilous oak forests and forest fringes were among the locally richest vegetation types, while bogs, saline and aquatic vegetation were among the poorest. These patterns might be indicative of the effect of the regional species pool size on the local species richness, although there are several pitfalls in the interpretation of correlations between these two variables (Zobel 1997, Herben 2000, Grace 2001).

Pools of alien species

There are significant positive correlations between the regional species pool sizes of archaeophytes and native species, and neophytes and native species (Fig. 1). These results are different from those obtained from phytosociological relevés of the Czech Republic (Chytrý et al. 2005), in which the relationships between the number of archaeophytes or neophytes, respectively, and the number of native species occurring in the relevés were insignificant, if calculated across all habitats. This difference between the regional species pools and the relevé data probably relates to the more general issue of scale-dependence of the native-alien relationships (Fridley et al. 2004, Herben et al. 2004, Stohlgren et al. 2006). In addition, correlation between neophytes and native species in the phytosociological data may be weak or absent due to the fact that neophytes are generally poorly represented in small plots, although making up a considerable proportion of the country's flora (Pyšek et al. 2002a, Chytrý et al. 2005). However, the relationships revealed in the present study are rather weak even for the regional species pools (Fig. 1).

The scatter plots of Fig. 1 indicate that habitats with native species pools < 350 species may contain any number of archaeophytes. Habitats with < 100 native species contain < 5, and often no neophytes, but habitats with 100–350 species may contain different numbers of neophytes. It is remarkable that habitats with > 350 native species always contain > 5 archaeophytes and > 5 neophytes, and often many more. Thus, habitats supporting many native species also tend to support aliens. This is consistent with the currently accumulating evidence of a positive relationship between native and alien species richness existing at larger spatial scales (Planty-Tabacchi et al. 1996, Lonsdale 1999, Stohlgren et al. 1999, 2006, Pyšek et al. 2002b, Deuschewitz et al. 2003, Kühn et al. 2003, Dark 2004, Espinosa-García et al. 2004, Herben et al. 2004, Gilbert & Lechowicz 2005, Pino et al. 2005, Palmer 2006).

In spite of the generally positive relationships between the regional species pool sizes of alien and native species, the largest pools of alien species are found in habitats other than the largest pools of native species (Table 1). Largest numbers of both archaeophytes and neophytes occur in herbaceous ruderal vegetation, on arable land, in scrub and pioneer woodland in forest clearings and plantations of non-native trees. In contrast, no aliens are included in the regional species pools of natural spruce forests, bogs, alpine grasslands and vegetation consisting of succulent halophytes. There is a strong positive relationship between the regional species pool sizes of archaeophytes and neophytes ($r = 0.804$, $P < 0.001$). The size of alien pools for particular habitats closely corresponds to the proportions of alien species recorded in phytosociological relevés from the Czech Republic (Chytrý et al. 2005). In that study, relevé data also indicated significant positive relationship between archaeophytes and neophytes.

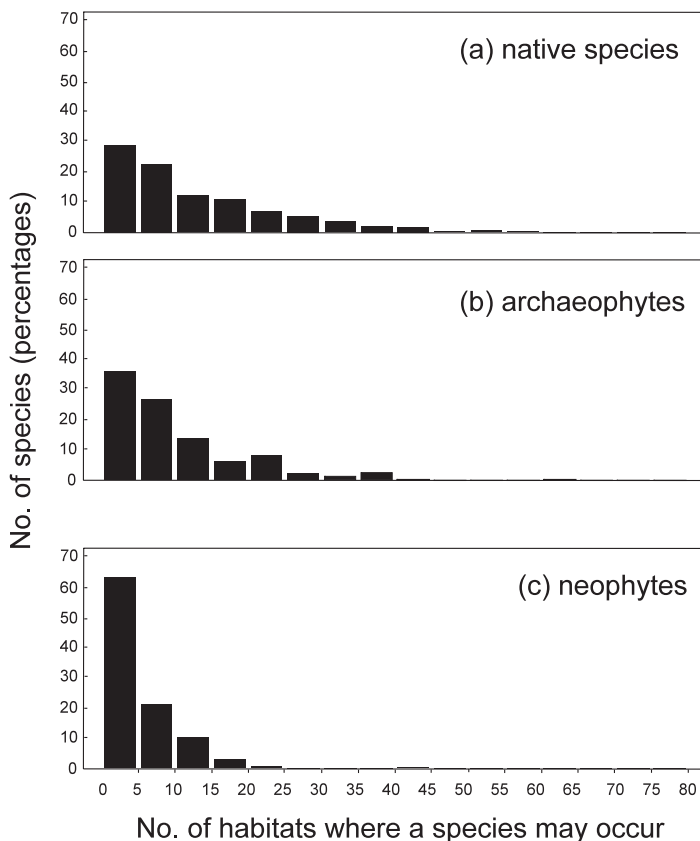


Fig. 2. – Percentage frequency distribution of species representation in regional species pools of different habitats. The longer the right tail of the distribution (such as in native species), the more habitat generalists there are in that species group.

Pools of dominant species

Species classified as dominants (including constant dominants) make up less than 3% of the regional species pool for 78 out of 88 habitats. Larger percentages of dominants were found only in habitats with small regional species pools and species-poor stands (macrophyte vegetation of water streams – 14.6%, inland vegetation of succulent halophytes – 13.3%, macrophyte vegetation of eutrophic and mesotrophic still waters – 11.6%, continental vegetation of annual halophilous grasses – 10.8%, raised bogs – 8.9%, peatland pine forests – 6.0%, inland saline steppes – 4.4%). Most species that are potential dominants are included in the species pools of nutrient-rich and disturbed habitats (Table 1). Most native dominants occur in herbaceous vegetation of forest clearings and *Rubus* scrub (16 species), scrub and pioneer woodland of forest clearings (13), perennial nitrophilous herbaceous vegetation of mesic sites (12) and tall mesic and xeric scrub (12). Most dominant archaeophytes were found in perennial thermophilous ruderal vegetation

Table 2. – Native and alien species occurring in most habitats, and the number of habitats (n = 88). Asterisks indicate alien species that were recorded in the highest numbers of habitats in the previous study (Chytrý et al. 2005), which was based on species occurrences in vegetation relevés.

Native species	Archaeophytes	Neophytes
<i>Festuca rubra</i>	78 * <i>Arrhenatherum elatius</i>	62 * <i>Epilobium ciliatum</i> 45
<i>Taraxacum</i> sect. <i>Ruderalia</i>	77 * <i>Cirsium arvense</i>	44 * <i>Impatiens parviflora</i> 45
<i>Agrostis stolonifera</i>	73 * <i>Lapsana communis</i>	40 * <i>Conyza canadensis</i> 34
<i>Deschampsia cespitosa</i>	67 * <i>Medicago lupulina</i>	40 * <i>Trifolium hybridum</i> 28
<i>Calamagrostis epigejos</i>	66 * <i>Tanacetum vulgare</i>	39 * <i>Robinia pseudacacia</i> 24
<i>Cerastium holosteoides</i>	63 * <i>Fallopia convolvulus</i>	38 * <i>Bidens frondosa</i> 22
subsp. <i>triviale</i>		
<i>Dactylis glomerata</i>	62 <i>Plantago major</i>	38 * <i>Agrostis gigantea</i> 21
<i>Veronica chamaedrys</i>	62 * <i>Convolvulus arvensis</i>	37 * <i>Aster lanceolatus</i> 19
<i>Agrostis capillaris</i>	61 * <i>Mentha arvensis</i>	37 * <i>Medicago sativa</i> 18
<i>Equisetum arvense</i>	60 <i>Myosotis arvensis</i>	35 * <i>Cytisus scoparius</i> 17
<i>Urtica dioica</i>	60 * <i>Lamium album</i>	33 * <i>Juncus tenuis</i> 17
<i>Galium aparine</i>	59 * <i>Linaria vulgaris</i>	33 <i>Lolium multiflorum</i> 17
<i>Poa angustifolia</i>	59 * <i>Lactuca serriola</i>	31 <i>Impatiens glandulifera</i> 16
<i>Avenella flexuosa</i>	57 <i>Tripleurospermum inodorum</i>	30 <i>Pinus nigra</i> 16
<i>Achillea millefolium</i>	56 <i>Veronica arvensis</i>	29 <i>Rumex thyrsoiflorus</i> 16
subsp. <i>millefolium</i>		
<i>Aegopodium podagraria</i>	56 * <i>Echium vulgare</i>	28 <i>Sisymbrium loeselii</i> 16
<i>Cirsium palustre</i>	56 <i>Vicia hirsuta</i>	28 <i>Populus × canadensis</i> 15
<i>Galium album</i>	55 <i>Chelidonium majus</i>	26 * <i>Veronica persica</i> 15
<i>Galeopsis bifida</i>	55 <i>Melilotus albus</i>	26 <i>Ribes rubrum</i> 15
<i>Heracleum sphondylium</i>	55 <i>Ballota nigra</i>	25 <i>Heracleum mantegazzianum</i> 14
<i>Ranunculus repens</i>	55 <i>Aethusa cynapium</i>	24 * <i>Lupinus polyphyllus</i> 14
<i>Rubus idaeus</i>	55 <i>Arctium lappa</i>	24 <i>Matricaria discoidea</i> 14
<i>Rumex acetosa</i>	55 <i>A. tomentosum</i>	24 <i>Oxalis fontana</i> 14
<i>Elytrigia repens</i>	54 <i>Bromus hordeaceus</i>	24 <i>Quercus rubra</i> 14
<i>Hypericum perforatum</i>	54 <i>Capsella bursa-pastoris</i>	24 * <i>Solidago canadensis</i> 14
<i>Poa trivialis</i>	54 <i>Carduus acanthoides</i>	24 <i>S. gigantea</i> 14
<i>Galeopsis tetrahit</i> s. str.	53 <i>Melilotus officinalis</i>	24 <i>Veronica filiformis</i> 14
<i>Angelica sylvestris</i>	52 <i>Vicia angustifolia</i>	24 * <i>Aster novi-belgii</i> s. str. 13
<i>Anthoxanthum odoratum</i> s. str.	52 <i>V. sativa</i>	24 * <i>Erigeron annuus</i> 13
<i>Carex hirta</i>	52 * <i>Cirsium vulgare</i>	23 <i>Galinsoga parviflora</i> 13
<i>Epilobium montanum</i>	52 <i>Geranium columbinum</i>	23 <i>G. quadriradiata</i> 13
		<i>Lonicera caprifolium</i> 13
		<i>Sedum spurium</i> 13
		<i>Sisymbrium strictissimum</i> 13
		<i>Solanum decipiens</i> 13

(5) and annual vegetation in ruderal habitats (5), and most dominant neophytes in perennial nitrophilous herbaceous vegetation of mesic sites (7) and plantations of broad-leaved non-native trees (6).

Two hundred and thirty two native species, 18 archaeophytes and 30 neophytes were identified as potential dominants in at least one habitat. These figures correspond, respectively, to 12.7%, 7.2% and 10.8% of the total number of species within these categories, which suggests that there are hardly any differences in the ability of native and alien species to become dominants.

Table 3. – Native and alien species that are dominant (including constant dominants) in ≥ 3 habitats, with numbers of habitats in which species are dominant and % of habitats in which they are dominant relative to all the habitats in which they occur.

Species	No. of habitats	% as dominant	Status
<i>Avenella flexuosa</i>	9	16	native
<i>Vaccinium myrtillus</i>	9	19	native
<i>Urtica dioica</i>	8	13	native
<i>Festuca ovina</i>	7	14	native
<i>Agrostis capillaris</i>	6	10	native
<i>Calamagrostis villosa</i>	6	19	native
<i>Brachypodium pinnatum</i>	5	12	native
<i>Impatiens parviflora</i>	5	11	neophyte
<i>Picea abies</i>	5	10	native
<i>Pinus sylvestris</i>	5	13	native
<i>Quercus petraea</i> agg.	5	16	native
<i>Calamagrostis epigejos</i>	4	6	native
<i>Phalaris arundinacea</i>	4	11	native
<i>Poa angustifolia</i>	4	7	native
<i>P. nemoralis</i>	4	9	native
<i>Aegopodium podagraria</i>	3	5	native
<i>Betula pendula</i>	3	7	native
<i>Calamagrostis arundinacea</i>	3	6	native
<i>Calluna vulgaris</i>	3	8	native
<i>Calystegia sepium</i>	3	11	native
<i>Carex humilis</i>	3	14	native
<i>C. rostrata</i>	3	13	native
<i>Chaerophyllum hirsutum</i>	3	8	native
<i>Cirsium arvense</i>	3	7	archaeophyte
<i>Fagus sylvatica</i>	3	11	native
<i>Festuca pratensis</i>	3	7	native
<i>F. rubra</i>	3	4	native
<i>Impatiens noli-tangere</i>	3	8	native
<i>Lemna minor</i>	3	19	native
<i>Molinia caerulea</i> s. str.	3	9	native
<i>Nardus stricta</i>	3	9	native
<i>Petasites albus</i>	3	12	native
<i>P. hybridus</i>	3	18	native
<i>Phragmites australis</i>	3	7	native
<i>Potentilla anserina</i>	3	9	native
<i>Quercus robur</i>	3	9	native

Species with the broadest habitat range

The number of habitats in which a species occurs can be used as a measure of the ecological range of that species. This measure is not without problems, because species occurring in, e.g., five forest habitats probably do not have a broader ecological range than a species occurring in three habitats, including one forest habitat, one grassland habitat and one man-made habitat. Still, a comparison of the number of habitats occupied by different species (Fig. 2, Table 2) provides valuable information on the distribution of ecological generalists and specialists among the plants in the Czech flora. Most generalists are native species, less are archaeophytes and least are neophytes. The low number of generalists among neophytes may reflect, to some extent, the short residence time of these species in this

country, which has prevented them from reaching all the habitats in which they are potentially able to grow. Ecological generalists in the native flora include many grasses, while the group of alien generalists mainly consists of dicotyledonous herbs. Very similar patterns were found in a previous study based on phytosociological relevés and a different habitat classification (Chytrý et al. 2005); the similarity of the results of these two studies indicate the robustness of our estimates of species ecological range.

Native species and grasses are also the most common dominants in different habitats (Table 3). Among 36 species that are dominant in three or more habitats, there is only one archaeophyte (*Cirsium arvense*) and one neophyte (*Impatiens parviflora*). These 36 species include two genera represented by three species (*Calamagrostis* and *Festuca*) and five genera represented by two species (*Impatiens*, *Petasites*, *Poa*, *Carex* and *Quercus*). This pattern suggests that the ability of a species to become dominant in plant communities depends on phylogenetical relatedness. Most of these species are dominant in less than 15% of the habitats in which they occur.

Conclusions

This study provides a basic description of the regional species pools for 88 habitats occurring in the Czech Republic. This data set will be used for various studies on the diversity of Central European flora and vegetation, its historical formation and patterns of plant invasions. In particular, there is great potential for comparative studies when similar databases become available for other regions of the world (e.g., species assignments to habitats and phytosociological syntaxa in the German BIOLFLOR database; Klotz et al. 2002). However, a knowledge of regional species pools of different habitats is also important for planning and monitoring of ecological restoration. For example, the same methods as used in the preparation of the present database were recently used to design seed mixtures for grassland restoration projects in different regions of the Czech Republic (Blažková et al. 2006).

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Souhrn

Článek shrnuje základní údaje získané z nově vytvořené databáze, která obsahuje tzv. „species pools“ cévnatých rostlin pro biotopy České republiky, tedy seznamy druhů, které jsou potenciálně schopny růst v daném biotopu. Pro tento účel jsme použili klasifikaci biotopů do 88 kategorií (appendix 1), které většinou odrážejí fytoecologické jednotky na úrovni svazů nebo skupin svazů. Databáze vychází z údajů obsažených v České národní fytoecologické databázi, které byly kriticky revidovány a rozsáhle doplněny s využitím terénních znalostí o výskytu druhů v různých biotopech. Databáze zahrnuje 1820 původních druhů, 249 archeofytů a 278 neofytů, z nichž každý je přiřazen k jednomu nebo více biotopům. Kromě údajů o prostém výskytu druhů v jednotlivých biotopech databáze obsahuje také informace o tom, zda má druh v těchto biotopech svoje ekologické optimum nebo zda se v nich vyskytuje jako dominanta porostů, případně jako častá dominanta porostů (tab. 1).

Největší „species pools“ původních druhů byly zjištěny v suchomilné a teplomilné bylinné i dřevinné vegetaci nižších nadmořských výšek (teplomilné bylinné lesní lemy – 695 druhů, vysoké mezické a suché křoviny – 672 druhů, širokolisté suché trávníky – 549 druhů, perialpidské bazilifilní teplomilné doubravy – 535 druhů). Tyto relativně vzácné biotopy jsou podle velikosti „species pools“ následovány hojnými biotopy mezických půd (borové a modřínové lesní kultury – 525 druhů, mezofilní ovsíkové louky – 505 druhů, dubohabřiny – 481 druhů, pastviny a parkové trávníky – 474 druhů). Nejmenší „species pools“ (méně než 90 druhů) mají biotopy vodní, slaniskové a rašeliništní. Velikosti „species pools“ archeofytů a neofytů pro jednotlivé biotopy jsou pozitivně, i když slabě, korelovány se „species pools“ původních druhů (obr. 1). Biotopy obsahující méně než 350 původních druhů mohou obsahovat různý počet archeofytů. Biotopy s méně než 100 původních druhů obsahují méně než 5, a často žádné neofyty, zatímco biotopy se 100–350 druhy mohou obsahovat velmi různé počty neofytů. Biotopy s více než 350 původními druhy vždy obsahují více než 5 archeofytů a více než 5 neofytů (často mnohem více).

Druhy, které se vyskytují jako dominanty porostů, jsou zastoupeny 232 původními druhy, 18 archeofyty a 30 neofyty. Tyto druhy tvoří méně než 3 % ze „species pool“ pro 78 z 88 biotopů. Větší procentická zastoupení (až 14,6 %) dominantních druhů byla zjištěna jen u biotopů s malým „species pool“ a druhově chudými porosty, např. u vodních, slaniskových a rašeliništních biotopů.

Počet biotopů, v nichž se druh vyskytuje, lze použít jako hrubou míru ekologické amplitudy druhu. Při použití tohoto kritéria bylo nejvíce druhů se širokou ekologickou amplitudou zjištěno ve skupině původních druhů, méně mezi archeofyty a nejméně mezi neofyty (obr. 2, tab. 2). Z 36 druhů, které se mohou vyskytovat jako dominanta ve 3 a více biotopech (tab. 3), je 34 druhů původních, jeden je archeofyt (*Cirsium arvense*) a jeden neofyt (*Impatiens parviflora*).

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Appendix 1. – Habitat classification used in this study and phytosociological syntaxa occurring in particular habitats. Missing items in the sequence of habitat codes indicate habitats that do not occur in the Czech Republic.

1. Vegetation of cliffs, screes and walls

- 1A. Calcareous cliffs (*Potentillion caulescentis*, *Cystopteridion*), including rare cases of walls colonized by natural vegetation of these alliances (e.g. ruins of medieval castles distant from the settlements)
- 1B. Siliceous cliffs and boulder fields (*Agrostion alpinae*, *Androsacion vandellii*, *Asplenion serpentini*), including rare cases of nutrient-poor acidic mobile screes
- 1C. Walls (*Centrantho-Parietarion*), excluding grassy or annual vegetation on wall crowns
- 1D. Mobile calcareous (to a small extent also siliceous) screes (*Stipion calamagrostis*)

2. Alpine and subalpine grasslands

- 2A. Alpine grasslands of siliceous bedrock (*Juncion trifidi*, *Nardo strictae-Caricion bigelowii*)
- 2E. Subalpine tall-grass and tall-forb vegetation (*Calamagrostion villosae*, *Calamagrostion arundinaceae*, *Adenostylin alliiariae*, *Dryopterido filicis-maris-Athyrium distentifolii*)

3. Aquatic vegetation

- 3A. Macrophyte vegetation of eutrophic and mesotrophic still waters (*Lemnion minoris*, *Utricularion vulgaris*, *Hydrocharition*, *Nymphaeion albae*, *Magnopotamion*, *Parvopotamion*, *Batrachion aquatilis*); rare and occasional occurrences of terrestrial species which do not survive for longer time when flooded are excluded
- 3B. Macrophyte vegetation of water streams (*Batrachion fluitantis*)
- 3C. Vegetation of oligotrophic lakes and pools (*Isoëtium lacustris*, *Littorellion uniflorae*, *Sphagno-Utricularion*), including transitions to 4H and 4I

4. Wetland and riverine herbaceous vegetation

- 4A. Reed-beds of eutrophic still waters (*Phragmiton communis*), including *Phragmites australis* stands in terrestrial habitats, but excluding wet meadows overgrown by *Phragmites*
- 4B. Halophilous reed and sedge beds (*Scirpion maritimi*)
- 4C. Eutrophic vegetation of muddy substrata (*Oenanthion aquatica*)
- 4D. Riverine reed vegetation (*Phalaridion arundinaceae*), including ruderalized stands of disturbed stream banks
- 4E. Reed vegetation of brooks (*Sparganio-Glycerion fluitantis*)
- 4F. Mesotrophic vegetation of muddy substrata (*Carici-Rumicion hydrolopathi*)
- 4G. Tall-sedge beds (*Magnocaricion elatae*, *Caricion gracilis*, *Caricion rostratae*), including transitions to 6D, 6E and 6F and wetlands with *Phalaris arundinacea* outside stream banks
- 4H. Vegetation of low annual hygrophilous herbs (*Eleocharition ovatae*, *Radiolion linoidis*, *Nanocyperion flavescens*), including transitions to 4I
- 4I. Vegetation of nitrophilous annual hygrophilous herbs (*Bidention tripartitae*, *Chenopodion glauci*)
- 4J. River gravel banks (*Myricarietum germanicae*, *Calamagrostietum pseudophragmitis*)
- 4K. *Petasites* fringes of montane brooks (*Petasition officinalis*); *Petasites* stands at low altitudes are assigned to 13E
- 4L. Nitrophilous herbaceous fringes of lowland rivers (*Senecionion fluviatilis*), including ruderalized stands of disturbed habitats

5. Vegetation of springs and mires

- 5A. Hard-water springs with tufa formation (occurrences of *Caricion davallianae* vegetation on tufa sediments, *Lycopodo-Cratoneurion commutati*)
- 5B. Lowland and montane soft-water springs (*Cardamino-Montion*, *Cardaminion amarae*)
- 5C. Alpine and subalpine soft-water springs (*Swertio-Anisothecion squarrosi*)
- 5D. Calcareous fens (*Caricion davallianae* vegetation outside tufa sediments, *Cladietum marisci*), including transitions to 6F
- 5E. Acidic moss-rich fens and peatland meadows (*Caricion fuscae*, *Caricion lasiocarpae*, *Caricion demissae*, *Drepanocladion exannulati*, *Sphagno warnstorffiani-Tomenthygnion*)
- 5F. Transitional mires (*Eriophorion gracilis*, *Sphagno recurvi-Caricion canescens*)
- 5G. Raised bogs (*Sphagnion medii*, *Oxycocco-Empetrium hermaphroditum*)
- 5H. Wet peatsoils and bog hollows (*Rhynchosporion albae*, *Leuko-Scheuchzerion palustris*), including transitions to 3C and to different types of meadows

6. Meadows and mesic pastures

- 6A. Mesic *Arrhenatherum* meadows (*Arrhenatherion elatioris*), including intensively managed mesic meadows
- 6B. Montane mesic meadows (*Polygono bistortae-Trisetion flavescens*)
- 6C. Pastures and park grasslands (*Cynosurion cristati*)
- 6D. Alluvial meadows of lowland rivers (*Deschampsion cespitosae*), including intensively managed wet meadows
- 6E. Wet *Cirsium* meadows (*Calthion palustris*)
- 6F. Intermittently wet *Molinia* meadows (*Molinion caeruleae*)
- 6G. Vegetation of wet disturbed soils (*Ranunculo repentis-Rumicicion crispi*)

7. Acidophilous grasslands

- 7A. Subalpine and montane acidophilous grasslands (*Nardion strictae, Nardo strictae-Agrostion tenuis*)
- 7B. Submontane *Nardus* grasslands (*Violion caninae, Nardo strictae-Juncion squarrosi*), including acidophilous grasslands on forest clearings (*Rumici-Avenellion flexuosae*)

8. Dry grasslands

- 8A. Hercynian dry grasslands on rock outcrops (*Alyssso-Festucion pallentis*)
- 8B. Submediterranean dry grasslands on rock outcrops (*Bromo pannonici-Festucion pallentis, Diantho lummitzeri-Seslerion*)
- 8C. Narrow-leaved sub-continental steppes (*Festucion valesiaca*)
- 8D. Broad-leaved dry grasslands (*Bromion erecti, Cirsio-Brachypodium pinnati*)
- 8E. Acidophilous dry grasslands (*Koelerio-Phleion phleoidis, Hyperico perforati-Scleranthion perennis*)
- 8F. Thermophilous forest fringe vegetation (*Geranion sanguinei, Trifolion medii*), including some acidophilous types of herbaceous forest fringes

9. Sand grasslands and rock-outcrop vegetation

- 9B. Open vegetation of acidic sands (*Corynephorion canescentis, Thero-Airion*)
- 9C. *Festuca* grasslands on acidic sands (*Armerion elongatae*)
- 9D. Pannonian sand steppes (*Festucion vaginatae*)
- 9E. Acidophilous vegetation of spring therophytes and succulents (*Arabidopsion thalianae*), including transitions to dry grasslands and 13A
- 9F. Basiphilous vegetation of spring therophytes and succulents (*Alyssso alyssoidis-Sedion*), including transitions to dry grasslands and 13A

10. Saline vegetation

- 10G. Continental vegetation of annual halophilous grasses (*Cypero-Spergularion salinae*)
- 10H. Inland vegetation of succulent halophytes (*Salicornion prostratae*)
- 10I. Inland saline meadows (*Juncion gerardii*)
- 10J. Inland saline steppes (*Puccinellion limosae*)

11. Heathlands and scrub

- 11A. Dry lowland to alpine heathlands (*Euphorbio cyparissiae-Callunion vulgaris, Genisto pilosae-Vaccinion, Loiseleurio procumbentis-Vaccinion*)
- 11D. Subalpine acidophilous *Pinus mugo* scrub (*Pinion mugo*), including rare *Pinus mugo* scrub with tall forbs
- 11H. Subalpine deciduous scrub (*Salicion silesiaca, Salicetum lapponum*)
- 11I. Willow carrs (*Salicion cinereae*), including wet scrub of *Frangula alnus* and *Spiraea salicifolia*
- 11J. Willow galleries of loamy and sandy river banks (*Salicion albae, Salicion triandrae*)
- 11L. Tall mesic and xeric scrub (*Berberidion*), including scrub of neophytic *Sarothamnus scoparius*
- 11N. Low xeric scrub (*Prunion spinosae*)
- 11R. Scrub and pioneer woodland of forests clearings (*Sambuco-Salicion capreae*), including scrub in ruderal habitats

12. Forests

- 12A. Alder carrs (*Alnion glutinosae*)
- 12B. Alluvial forests (*Alnion incanae*)
- 12C. Oak-hornbeam forests (*Carpinion*)

- 12D. Ravine forests (*Tilio-Acerion*), including forests on man-made screes
- 12E. Herb-rich beech forests (*Eu-Fagenion*, *Acerenion*), including herb-rich fir forests (*Galio-Abietenion*)
- 12F. Limestone beech forests (*Cephalanthero-Fagion*)
- 12G. Acidophilous beech forests (*Luzulo-Fagion*), including acidophilous fir forests (e.g. *Luzulo pilosae-Abietetum*) and *Larix decidua* forests in the area of its native distribution
- 12H. Peri-Alpidic basiphilous thermophilous oak forests (*Quercion pubescenti-petraeae*)
- 12I. Sub-continental thermophilous oak forests (*Aceri tatarici-Quercion*, *Potentillo albae-Quercetum*)
- 12J. Acidophilous thermophilous oak forests (*Sorbo torminalis-Quercetum*, *Genisto pilosae-Quercetum petraeae*)
- 12K. Acidophilous oak forests (*Genisto germanicae-Quercion*)
- 12L. Boreo-continental pine forests (*Dicrano-Pinion*), including rare acidophilous pine forests on sand
- 12O. Peri-Alpidic pine forests (*Erico-Pinion*)
- 12P. Peatland pine forests (*Vaccinio uliginosi-Pinetum sylvestris*)
- 12Q. Peatland birch forests (*Sphagno-Betulion pubescentis*)
- 12R. Acidophilous spruce forests (*Piceion excelsae*)
- 12S. Basiphilous spruce and fir forests (*Athyrio alpestris-Piceion*)
- 12T. *Robinia pseudacacia* plantations (*Robinietaea*), including plantations of *Ailanthus altissima*
- 12U. Plantations of broad-leaved non-native trees (*Acer negundo*, *Juglans nigra*, *Populus ×canadensis* and *Quercus rubra*), including stands in parks and gardens
- 12V. Spruce plantations (*Picea abies*; rarely also plantations of *Picea pungens* and *Pseudotsuga menziesii*)
- 12W. Pine and larch plantations (*Pinus sylvestris*, *P. nigra*, *P. strobus* and *Larix decidua*)
- 13. Anthropogenic vegetation**
- 13A. Annual vegetation of ruderal habitats (*Sisymbrium officinalis*, *Bromo-Hordeion murini*, *Malvion neglectae*, *Salsolion ruthenicae*, *Eragrostion*)
- 13B. Annual vegetation of arable land (*Caucalidion lappulae*, *Sherardion*, *Veronico politae-Euphorbion*, *Fumario-Euphorbion*, *Spergulo-Oxalidion*, *Aphanion*, *Scleranthion annui*, *Panico-Setarion*, *Veronico-Taraxacion*)
- 13C. Annual vegetation of trampled habitats (*Polygonion avicularis* p. p.)
- 13D. Perennial thermophilous ruderal vegetation (*Onopordion acanthii*, *Dauco-Melilotion*, *Arction lappae*, *Convolvulo-Agropyron*), including transitions to 6A
- 13E. Perennial nitrophilous herbaceous vegetation of mesic sites (*Galio-Alliarion*, *Aegopodion podagrariae*, *Rumicion alpini*), including herbaceous forest fringes on nutrient-rich soils and transitions to 13D
- 13F. Herbaceous vegetation of forests clearings and *Rubus* scrub (*Carici piluliferae-Epilobion angustifolii*, *Atropion bellae-donnae*), including transitions to 7B, 11A, 11L, 11R and 13E