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How do species dominating in succession differ from others?

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Abstract. Data on succession were collected from 15 seres starting on bare ground in man-made habitats (i.e. sites disturbed by various mining activities, bulldozed sites, ruderal urban sites, the exposed bottom of a destroyed water reservoir, and abandoned fields), all in the western part of the Czech Republic, Central Europe. The period for which the data on succession were available ranged from 12 to 60 yr. 56 species reaching dominance in some period of succession were selected (the criterion being: at least 25 % cover in at least one year in any sere); they were compared for biological and ecological traits with other species participating in the seres (167 species with at least 1 % cover in at least one year in any sere), and with the Central European flora as a whole. Significant differences between the species dominating in succession and others were found for the following traits: life form, life strategy, pollination mode, and ability of lateral spread. Dominant species differed from the regional flora in distribution of life strategies, pollination mode and immigration status. The results suggest that an 'ideal successional dominant' is a tall, wind-pollinated plant, often a geophyte capable of intensive lateral spread, requiring high nutrient supply and sufficient site moisture. The set of traits contributing to achieving dominance by a species in human-made habitats includes both features occurring independently of phylogenies (life strategy, pollination mode, plant height, moisture demands) and those which dominant species probably share due to their common ancestors (nutrient demands, capability of extensive lateral spread).

Keywords: Life history; Man-made habitat; Phylogenetic correction; Species trait; Succession.

Nomenclature: Tutin et al. (1964–1980).

Introduction

Of all species included in a regional flora, only some take an important part in succession; such species must be capable of colonizing and reaching a large cover in disturbed sites. The present paper addresses the question: how do these species differ in their biological and ecological traits from those which do not play an important part in succession in the Central European landscape?

Previous studies characterizing species traits in succession have usually dealt with differences between early and late successional species or evaluated the changes in species traits during succession (Noble & Slatyer 1980; Walker & Chapin 1987; Huston & Smith 1987; Rydin & Borgegård 1991; Brown 1992). In most of these studies, however, the potential for generalization was limited by the absence of quantitatitive comparisons between various kinds of successional seres. The present paper, by using relatively long-term data from a number of successional seres (Prach & Pyšek 1994a, b; Prach et al. 1997) attempts to select dominant species from a wide range of human-made habitats, thus providing a reasonably representative sample.

Data set and Methods

Cover data were obtained from published case studies and unpublished records for 15 successional seres starting on bare ground in human-made habitats located in the western part of the Czech Republic, Central Europe. The duration of time for which data on succession were available, ranged from 12 to 60 yr, depending on the sere. The cover of each species present was, in most cases, estimated annually (by phytosociological relevés and/or the point-quadrat method) in permanent plots usually established immediately after creation of the site. In some seres, comparable stages of different age were used to infer the course of succession, or this method was combined with annual sampling. The seres, described in detail elsewhere (Prach et al. 1993, 1997; Prach & Pyšek 1994a, b) are characterized in App. 1.

The data were used to select those species which are able to achieve dominance in any period of succession. The species present in the seres (only those reaching at least 1 % cover in at least one sere included) were divided into two groups: (1) '*dominants*' are those species whose cover in at least one sere in at least one year was higher than 25 % (56 species); (b) '*others*' are those which did not meet this criterion (167 species).

In addition, the set of dominants was compared with the Central European flora as a whole. For this purpose the list of Frank & Klotz (1990) was used (the only sufficiently complete survey available), excluding the species present in the studied successional seres. This yielded 2027 species, further indicated as '*flora*'.

For each species (for the flora only if available in Frank & Klotz 1990), information on the following traits was collected:

- *Life form* - Raunkiaer's scheme, taken from Frank & Klotz (1990);
- *Life history* - i.e. annuals, biennials, monocarpic perennials, and polycarpic perennials (from Grime et al. 1988);
- *Life strategy*, C-S-R scheme according to Grime et al. (1988); data from Frank & Klotz (1990);
- *Clonality*; clonal and non-clonal species were distinguished; see Prach & Pyšek (1994);
- *Immigration status* - native and alien species, the latter divided into archeophytes and neophytes; the classification was mainly based on Hejný & Slavík (1988-1992) and Slavík (1995);
- *Pollination mode* - insect, wind, and self-pollinated; Frank & Klotz (1990)
- *Dispersal mode* - dispersal by wind, water, ants, other animals, humans and self-dispersal; data from Frank & Klotz (1990);
- *Dispersule weight* - interval variable with particular categories reflecting dispersule weight was taken from Grime et al. (1988);
- *Lateral spread* - ability to spread laterally, taken from Grime et al. (1988); see Fig. 1 for the particular categories;
- *Regenerative strategy* - the following categories were relevant, being taken from Grime et al. (1988):
  - bs - species forming a persistent seed bank;
  - s - those with seasonal regeneration by seeds;
  - v - possessing lateral vegetative spread; and
  - w - producing numerous widely dispersed seeds
- *Seed bank type* (from Grime et al. 1988):
  - type 1 – most seeds germinating shortly after being shed;
  - type 2 – most seeds persistent until the next growing season;
  - type 3 – a small number of seeds persist in the soil; and
  - type 4 – a large persistent seed bank is formed;
- *Mycorrhiza* - presence or absence, disregarding the type, following Grime et al. (1988);
- *Height* - maximum height as given in Dostál (1958);
- *Nitrogen and moisture requirements* were expressed through Ellenberg's indicator values (Ellenberg et al. 1991).

The percentage representation of particular traits was then calculated for dominants, other species and, if available, for the flora. If a species was listed as belonging to more than one category (for pollination, dispersal, and regenerative strategy where combined traits are frequent) it was considered as contributing to each category and the frequency was calculated on the basis of summed-up data.

Data were analysed using analysis of variance and χ^2 -contingency tables (Sokal & Rohlf 1981). However, when analysing large comparative data sets, potentially confounding effects of phylogenetic relations should be taken into account (Harvey & Pagel 1991; van Groenendael et al. 1996; Kelly & Woodward 1996; Crawley et al. 1996; see also Westoby et al. 1995 and Harvey et al. 1995 for discussion). For that reason, evolutionary comparative methods were used to distinguish the effect of phylogenies on the traits of dominant species. The phylogenetic lineage of families was established according to Chase et al. (1993), using their second search. In the case of traits which were found to differ significantly between dominant species and others occurring in successional seres analysed, the percentage of species possessing the respective trait and the percentage of dominant species was calculated in those 14 families which had at least five species present in the data set (i.e including dominants and others as defined above). The difference in dominance and the trait analysed was then calculated in every node in the 'tree', and the relation between dominance and the trait analysed was tested using regression fitted through the origin (Harvey & Pagel 1991).

Families were mapped on the tree (e.g. van Groenendael et al. 1996) with respect to their importance in succession in man-made habitats.

Results

In total, 56 species were selected as dominants. Of these, nine reached 80 % cover in one sere (App. 1) and can be considered as monopolists (Falińska 1991). The sum of cover values of a species over all the seres probably best indicates its success in colonizing disturbed sites. This criterion yielded the top 10 most successful species (in decreasing order):

Calamagrostis epigejos > *Artemisia vulgaris* > *Chenopodium album*
> *Arrhenatherum elatius* > *Elymus repens* > *Betula pendula*
> *Phalaris arundinacea* > *Calamagrostis villosa* > *Cirsium arvense*
> *Deschampsia flexuosa*.

The following species participated in more than 50 % of the seres, regardless of their cover: *Elymus repens*, *Betula pendula* and *Calamagrostis epigejos* (App. 1).

Differences between dominants and regional flora

Dominant species recorded in the successional seres studied differ from the rest of the Central European flora in all the characteristics compared except for life form and mode of dispersal (Tables 1 and 2). C-, CR- and R-strategists were over-represented among the former, whereas CS- and CSR-strategists are under-represented (Fig. 1). A conspicuous difference was found in the mode of pollination, where the representation of wind-pollinated species amongst the dominants increased at the expense of species pollinated by insects (Table 1, Fig. 1). There was a less remarkable but still significant ($P = 0.01$) difference in the origin of species and immigration status. The group of species dominant in succession had a larger proportion of archaeophytes compared to the rest of the flora while neophytes were completely

Table 1. Difference in selected traits between dominants and other successional species, and other members of the Central European flora. The latter tests were performed only when there were available data in Frank & Klotz (1990); n.a. = not available. The null hypothesis was tested (χ^2 -test on contingency tables) that the groups distinguished do not differ in particular traits. See methods on trait description and information sources. NS = null hypothesis cannot be rejected at a significance level < 0.05.

	Dominants vs. other species			Dominants vs. flora		
	d.f.	χ^2	P	d.f.	χ^2	P
Life form	3[1]	10.70	0.013	3	1.43	NS
Life strategy	4[2]	23.44	< 0.001	4	18.01	0.001
Pollination mode	2	11.07	0.004	2	27.84	< 0.001
Origin	1[3]	3.05	NS	1	6.62	0.01
Lateral spread	4	17.06	0.002	n.a.	n.a.	n.a.
Life history	2[4]	3.34	NS	n.a.	n.a.	n.a.
Clonality	1	1.75	NS	n.a.	n.a.	n.a.
Dispersal mode	5	6.50	NS	5	9.49	NS
Dispersule weight	5	1.36	NS	n.a.	n.a.	n.a.
Mycorrhizae	3	0.46	NS	n.a.	n.a.	n.a.
Regeneration strategy	3	2.75	NS	n.a.	n.a.	n.a.
Seed bank type	3	1.49	NS	n.a.	n.a.	n.a.

[1]Chamaephytes excluded because of low representation; [2]CS-, SR- and S-strategies grouped; [3]Aliens grouped and tested against native;
[4]Annuals vs. monocarpic and polycarpic perennials.

absent from the seres (Fig. 1). Differences in distribution of dispersal modes were not significant ($P = 0.09$); dispersal by animals (epizoochory) was slightly over-represented among dominants (31.7 % vs. 24.5 %) whereas dispersal by ants (6.7 % vs. 9.7 %) and self-dispersal (5.8 % vs. 14.0 %) were the modes more represented in the Central European flora. No significant difference was found in the distribution of life forms (Fig. 1).

Dominant species had, on average, higher requirements for nitrogen than the remaining flora and the difference was highly significant ($P < 0.001$, Table 2). A significant ($P = 0.034$) difference in requirements for moisture was also found between the groups, with dominants showing higher demands for moisture (Table 2).

Differences between dominants and other species

Dominant species (App. 1) differed from others in the following traits: life form, life strategy, pollination mode, and ability to spread laterally (Table 1). Of the dominant species, 30.4 % are classified as pure C-strategists (the corresponding figure in other species being as low as 6.6 %) and none of them showed a SR- or S-strategy (Fig.1). Therophytes were under-represented among dominant species whereas the representation of geophytes in this group was four times higher than for other successional species (16.1 vs. 4.2 %; Fig. 1). Wind-pollinated species contributed twice as much to the dominants (38.7 %) than to the other species (19.3 %). Correspondingly, the latter had a larger proportion of self- and insect-pollinated species (Fig. 1). There was a remarkable shift to increased ability of dispersing laterally among dominants (Fig. 1). None of the remaining traits, i.e. life history, clonality, mode of dispersal, dispersule weight, regeneration strategy, type of seed bank, and the presence of mycorrhizae, were significanly different when dominants were compared with other species (Table 1).

Dominant species showed higher requirements for both nitrogen and soil moisture than species not achieving dominance (Table 2, Fig. 1).

Dominant species were on average significantly taller ($P < 0.01$) than the others and this was still true when woody species were excluded and herbs analysed separately (Table 3).

Table 2. Comparison of ecological requirements of species dominating in succession with those not capable of achieving dominance (others) with the rest of the Central European flora (as listed by Frank & Klotz 1990). Means ± S.D. are given; those significantly different in Kruskal-Wallis test share the indication between the values: *** = $P < 0.001$, * = $P < 0.05$. Total number of species in a particular category is given on the first line, numbers of species for which the respective value was obtained from Ellenberg et al. (1991) are given on lines 3 and 5.

	A. Dominants	P	B. Other species	P	C. Flora
	56	(A vs B)	168	(A vs C)	2027
Nitrogen	6.08 ± 2.14	*	5.29 ± 2.17	*	4.58 ± 2.27
	49		144		1238
Moisture	6.10 ± 1.99	*	5.42 ± 1.96	***	5.59 ± 2.52
	47		149		138

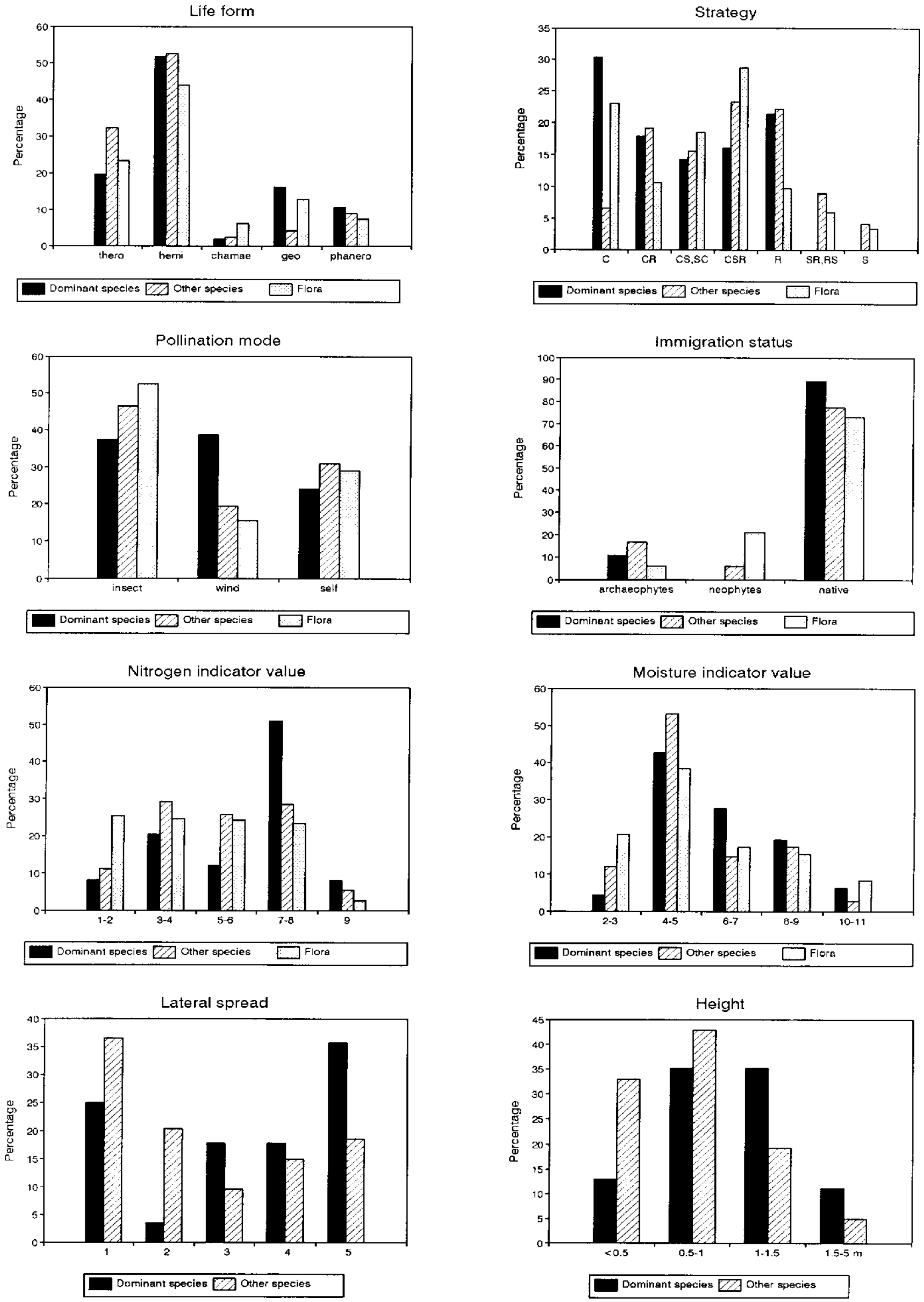

Fig. 1. Representation of particular traits among species dominating in succession ($n = 56$) in comparison with those not being able to achieve dominance (Other species, $n = 167$) and with the rest of the Central European flora as given in Frank & Klotz (1990) (Flora, $n = 2027$). Life forms are according to Raunkiaer's system, life strategies to that of Grime (1979). Indicator values were taken from Ellenberg et al. (1991). Categories of lateral spread (Grime et al. 1988): 1 = limited extent and duration; 2 = < 100 mm in diameter; 3 = 100 - 250 mm; 4 = 251 - 1000 mm; 5 = > 1000 mm. Data on lateral spread and height were not available for the Central European flora. Only those traits in which a particular group differed significantly are shown.

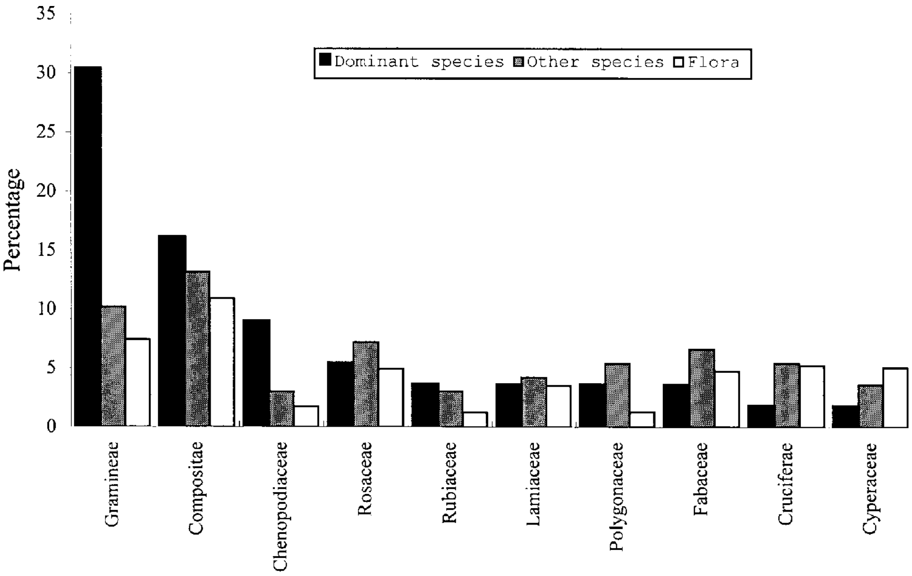

Fig. 2. Representatives of the 10 most important families (i. e. regarding dominants) among species dominating in succession, other species, and the rest of the Central European flora. The difference in representation of families between other species and the flora was significant ($\chi^2 = 18.2$, d.f. = 9, $P = 0.03$, test on contingency table), dominant species were not compared with the other two groups because of the low number of species in particular families.

Participation of families and phylogenetic corrections

Among dominant species, there was a remarkable over-representation of a few families (Fig. 2). The distribution of dominant families in the phylogenetic tree is illustrated in Fig. 3. The most important families, i.e. *Gramineae* (17 dominants), *Compositae* (9), *Chenopodiaceae* (5) and *Rosaceae* (3) are scattered over the tree. Given this concentration of dominants in a few families, the above-mentioned results may be re-analysed using evolutionary comparative methods. Given the restrictions imposed by the phylogeny, this was done at the family level. Only a few relationships are maintained when phylogeny is considered and these are weaker than without phylogenies being taken into account (Table 4). Species with a C-strategy are favoured but the S- and SR-strategies are strongly negatively associated with dominance. Among other traits, wind-pollination is – marginally significantly – related to dominance: the same holds for higher demands for moisture and for plant height (Table 4). The relationship between dominance and the remaining traits, i.e. life form, capability of lateral spread, and immigration status, turned out to be non-significant when phylogenetic correction was applied.

Table 3. Analysis of variance showing the effect of plant height on achieving dominance. Heights are given in m. Log-transformation of heights was used to achieve normality.

	Mean ± S.D.	d.f.	F-value	P
All species				
Dominants	2.75 ± 0.83	1, 222	8.86	0.003
Other species	1.95 ± 0.44			
Woody plants excluded				
Dominants	1.16 ± 0.10	1, 201	16.82	< 0.001
Other species	0.78 ± 0.03			

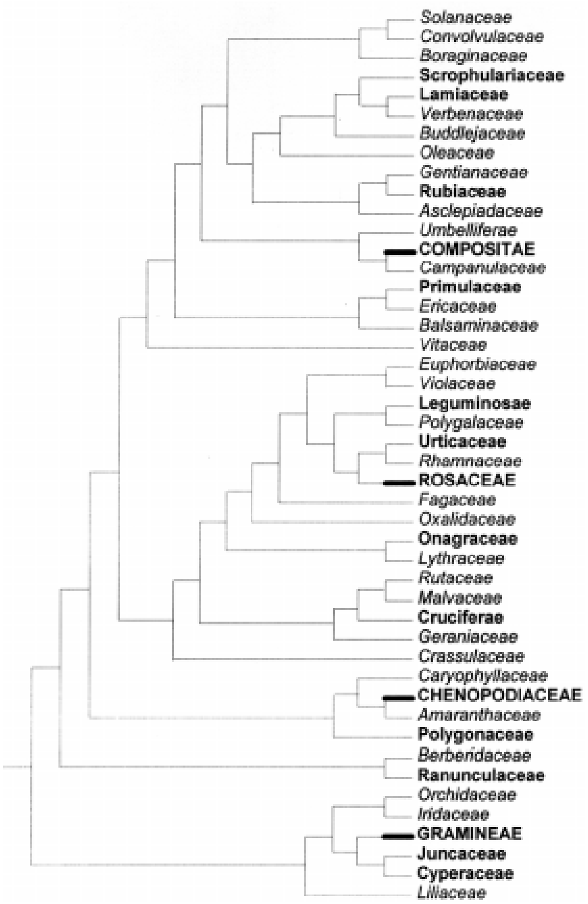

Fig. 3. Phylogenetic tree of large families (≥ 500 species), showing their importance in Central-European man-made habitats. Phylogeny based on Chase et al. (1993). Families including at least three dominant species are indicated by a thick line and upper case, those that have at least one dominant representative are shown in bold.

Table 4. Significance of difference between dominant species and others present in succession when using phylogenetical corrections. Pearson's correlation coefficient of the relationship between the percentage of dominant species in a family and the percentage of species possessing the trait given is shown ($n = 14$). See text for details. Significant relationships (including those with marginal significance, $P < 0.1$) are shown in bold.

	Trait	*R*	*F*	*P*
Life form	Therophyte	0.14	0.25	0.62
	Hemicryptophyte	– 0.01	0.00	0.96
	Geophyte	– 0.12	0.18	0.67
Life strategy	**C**	**0.54**	**4.90**	**0.047**
	CR	– 0.11	0.14	0.71
	CS	– 0.16	0.33	0.57
	CSR	0.13	0.22	0.64
	R	0.24	0.78	0.39
	S, RS	**– 0.64**	**8.11**	**0.015**
Pollination mode	Insect	– 0.36	1.79	0.20
	Self	– 0.29	1.06	0.22
	Wind	**0.48**	**3.64**	**0.080**
Origin	Alien	0.39	2.26	0.15
Lateral spread	High capability	0.24	0.76	0.40
Moisture demands[1]	Low	0.05	0.025	0.88
	Medium	– 0.30	1.19	0.29
	High	**0.48**	**3.49**	**0.086**
Nitrogen demands[2]	Low	0.04	0.018	0.89
	Medium	– 0.45	3.01	0.11
	High	0.38	2.02	0.18
Height	**Tall plants[3]**	**0.46**	**3.13**	**0.10**

[1] Low demand: species with Ellenberg indicator values for moisture: 1 - 4, medium: 5 - 8, high: 9 - 11.

[2] Low demand for nitrogen: 1 - 3, medium: 4 - 6, high: 7 - 9.

[3] > 1 m in height.

Discussion

As the successional seres studied cover a wide range of human-made habitats, the resulting set of species represent the variety of those dominating in disturbed habitats of the Central-European landscape. The different duration of particular seres (12 - 60 yr) implies that early- and mid-successional species are better represented in the species list than those typical of late successional stages. However, most (12) observed seres had already reached a stage dominated by late-successional species within the time spans studied, and represent more or less arrested successional stages where arrival of a new potential dominant is of a low probability (Prach & Pyšek 1994a).

The taxonomical bias expressed as the enormous success of grasses in reaching high cover in various stages of succession calls for evolutionarily comparative methods. The data sets used in the present paper are large enough to be biased by phylogenetic relationships between species, and the need to consider phylogenetic relation in comparative studies is widely accepted (Westoby et al. 1995; Harvey et al. 1995; Kelly & Woodward 1996; Beerling & Kelly 1996; van Groenendael et al. 1996). Using χ^2-contingency tables to analyse species count data when there is conspicuously unequal taxonomical representation of compared groups can lead to wrong conclusions (Crawley et al. 1996). The present study revealed that there is a certain set of traits which contribute to achieving dominance by a species under a certain disturbance regime and resource level (cf. Onipchenko et al. 1998; Díaz et al. 1998). The results indicate that some of these traits evolved independently in various phylogenetical lineages; this holds for those traits that were significantly correlated with dominance after using the phylogenetic correction (life strategy, pollination mode, plant height, and moisture demands). Another group of traits favouring dominance in man-made habitats are those which dominant species share due to their common ancestors. This is the case of a disproportionally high occurrence of species preferring nutrient-rich sites and which are capable of extensive lateral spread. The results indicate that species with these features dominate here because their common ancestors, exhibiting the same traits, were successful in this type of habitat.

To answer the question why the phylogenetic history persists in the phase of selection, i.e. why do offspring of nitrogen-demanding species continue to inhabit successional sites, it seems appropriate to consider the process of phylogenetic niche conservatism (Harvey & Pagel 1991). The dominant mode of evolution generates patterns of trait variation which are correlated with phylogeny and also maintained by the selective forces of present-day ecology (Westoby et al. 1995).

It appears that schemes summarizing biological and ecological traits (life forms and life strategies) are among the characteristics best correlated with species success in succession. It should be, however, borne in mind that the results obtained for life strategies *sensu* Grime (1979) must be considered as having only an illustrative value. The competitive strategy, found to be over-represented in dominants, is predicted to occur in competitively successful species, especially in productive environments (although other kinds of dominance which are possible in disturbed or unproductive habitats have been described also, see Grime 1979). Species with such a strategy are competitively superior to others, thus having more chance to become dominant.

The conclusion that the best predictive power was found in summary traits such as life form was also drawn when traits were related to the invasion success of alien plants (Pyšek et al. 1995). In studies on plant invasions, correlations between invasive behaviour and species traits have been repeatedly sought with differing success (Baker 1965; Noble 1989; Roy 1990). Species dominating in succession exhibit certain traits (C-strategy, high stature, high demand for nutrient and moisture) which are similar to those possessed by invaders successful in semi-natural habitats (Pyšek et al. 1995). However, among species dominant in the seres studied there is a low participation of aliens and the complete absence of neophytes (Fig.1).

Regarding many traits there is no information available for the whole regional flora as documented by Frank & Klotz (1990). Nevertheless, as it was possible to compare most of the traits in which dominants differed from other species present, it is obvious that the results of both kinds of comparison are similar (Table 1). Fig. 1 suggests that in some traits there is a more or less gradual change in their representation for particular categories. At the beginning of succession, species available from the species pool in the surrounding landscape, which are those possessing the set of suitable characters, will colonize the disturbed soil and participate in the succession. Of these colonizers, some become dominant. Similar results of both comparisons (i.e. dominant vs. others, dominants vs. flora) indicate that the same features which favour a species in the process of colonization contribute to its ability to become dominant. Some other traits, namely seed production and seed dispersal capacity could potentially give interesting results (Fenner 1987). Unfortunately, solid quantitative data are not available for the species set analysed.

Besides life forms and life strategies, there were several other traits with significant differences between tested groups of species: height, ability to spread laterally, and mode of pollination, demand for moisture and nutrients. It can be expected that species which are able to attain a higher stature are usually more competitive than shorter species and thus are more able to become dominant (e.g. Grime 1979; Tilman 1988; Keddy 1989; Rösch et al. 1997). Intensive lateral expansion is also associated with high competitive ability (Grime et al. 1988; etc.). To attain a higher stature and rapidly spread laterally, a plant needs more nutrients and moisture (Tilman 1988). The combination of all these traits apparently supports a species in reaching dominance.

A remarkably increased representation of wind-pollinated species among the dominants may be rather surprising, although self-pollination is often attributed to colonizing species. Kelly & Woodward (1996) found, using phylogenetic corrections based on a cladistically derived classification scheme, that wind-pollinated species had greater range sizes than non-wind pollinated species. Wind-pollination enables more intensive and widespread gene exchange than other modes of pollination, supporting thus a higher genetical plasticity of particular populations. This genetical plasticity may be advantageous for colonizing plants (Bazzaz 1996).

We did not find any differences in seed-dispersal modes despite the fact that wind-dispersed seeds are often attributed to species with high colonizing ability (e.g. Grime 1979; Fenner 1987). Intensive vegetative spread is another trait often predicted in species dominating in succession and in this respect, our results are in accordance with previous contributions (Grime 1979; Olsson 1987; Falińska 1991; van der Valk 1992; van Andel et al. 1993).

It must be emphasized that most of the considered traits are not independent variables, since there is a trade-off among them (Grime et al. 1988; van der Valk 1992; Bazzaz 1996, etc.). However, some species may possess a combination of traits which does not follow expected correlations between traits and theoretical trade-off. This is the case with highly competitive species which produce a large number of easily dispersed seeds and are able to rapidly spread vegetatively (e.g. *Artemisia vulgaris*, *Calamagrostis epigejos*, *Cirsium arvense* and *Phragmites australis*). Huston & Smith (1987) have called them ‘super-species’. This combination of traits seems to be very powerful in colonizing new space and achieving dominance, especially in productive environments.

Conclusions

For eight of the 15 species traits considered, significant differences were found between species dominating in succession on the one hand and others and local flora on the other hand. These results suggest that there are some features contributing to the chance of a species to become a dominant. Our conclusion does not support that of e.g. Gibson & Brown (1991) who found that species colonized a new site irrespectively of plant life-history traits. It may be concluded that an ‘ideal dominant’ in succession is a tall, wind-pollinated plant, often a geophyte capable of intensive lateral spread, requiring high nutrient supply and sufficient site moisture.

It also appears that some of the traits contributing to achieving dominance occur independently of phylogenies (life strategy, pollination mode, plant height, moisture demands) and others originated due to common ancestors (nutrient demands, capability of extensive lateral spread) and are perpetuated under the given combination of disturbance and resources.

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For App. 1, see p. 392.

App. 1. Survey of dominant species recorded in 15 succession seres in man-made habitats. Species are arranged according to the sum of cover values recorded in all seres. Only species with > 25 % cover in at least one sere are included. The number of seres in which the species was present and the sum of maximum covers from particular seres are also shown, while the sere in which the maximum cover was achieved is indicated. The life history traits significantly affecting species' capability of becoming dominant are shown on the left: STR = life strategy (according to Grime et al. 1988); LF = life form (Raunkiaer system): th = therophyte; h = hemicryptophyte; g = geophyte; ph = phanerophyte; ch = chamaephyte; LS = lateral spread (according to Grime et al. 1988, see Methods); POLL = pollination mode (from Frank & Klotz 1990): i = insect; w = wind; s = self-pollinating.

STR	LF	LS	POLL	Species	Maximum cover (%)	Number of seres	Cover sum (%)	Sere
C	g	5	w	*Calamagrostis epigejos*	95.0	8	363.2	Acidic bottom
CR	h	3	is	*Artemisia vulgaris*	87.5	5	207.0	Urban moderate
R	th	1	w	*Chenopodium album*	67.5	6	183.9	Urban poor
C	h	4	w	*Arrhenatherum elatius*	87.5	5	182.0	Mesic old field
CR	h	5	w	*Elymus repens*	62.5	8	165.6	Xeric old field
SC	ph	5	w	*Betula pendula*	50.0	8	155.7	Sandy damp
C	h	5	w	*Phalaris arundinacea*	90.0	5	141.2	Peat damp
C	g	5	w	*Calamagrostis villosa*	90.0	2	135.0	Bulldozed mound
SC	h	4	w	*Deschampsia flexuosa*	62.0	3	118.6	Bulldozed plot
C	ph	5	i	*Sambucus nigra*	68.8	3	117.6	Urban rich
R	th	1	i	*Papaver rhoeas*	87.5	2	102.5	Xeric old field
SC	ph	5	i	*Crataegus* spp.	98.0	2	101.0	Mesic old field
CR	h	3	is	*Tanacetum vulgare*	50.8	2	97.0	Spoil heap
CS	g	2	w	*Carex gracilis*	58.0	3	95.4	Emerged bottom
CSR	h	4	w	*Juncus effusus*	47.0	6	95.3	Emerged bottom
C	h	4	w	*Urtica dioica*	53.8	6	93.3	Urban rich
C	ph	5	w	*Pinus sylvestris*	70.0	3	90.0	Sand pit
CSR	h	4	w	*Poa palustris*	37.5	5	89.2	Wet old field
C	g	4	is	*Petasites hybridus*	87.5	1	87.5	Wet old field
CR	h	5	is	*Ranunculus repens*	62.5	3	86.3	Wet old field
C	g	4	w	*Phragmites australis*	80.0	2	85.0	Wet spoil heap
R	th	1	w	*Chenopodium suecicum*	75.0	1	75.0	Urban moderate
C	ch	3	is	*Ballota nigra*	62.5	2	63.7	Urban rich
CS	h	3	w	*Festuca rupicola*	62.5	1	62.5	Xeric old field
SC	h	5	w	*Brachypodium pinnatum*	62.5	1	62.5	Mesic old field
CSR	h	3	w	*Poa angustifolia*	37.5	3	61.9	Xeric old fields
SC	h	4	w	*Molinia caerulea*	48.0	2	61.8	Damp sand
R	th	1	is	*Sisymbrium loeselii*	47.5	2	61.2	Urban poor soil
R	th	1	ws	*Rumex maritimus*	59.0	2	60.2	Emerged bottom
SC	h	5	w	*Calamagrostis canescens*	52.5	1	52.5	Damp peat
CSR	h	4	is	*Galium album*	37.5	2	52.5	Xeric old field
R	h	1	i	*Melilotus albus*	50.0	1	50.0	Urban poor
C	ph	5	i	*Prunus spinosa*	50.0	1	50.0	Mesic old field
CSR	h	3	w	*Holcus lanatus*	38.6	2	45.3	Spoil heaps
CSR	h	3	i	*Potentilla erecta*	38.7	2	45.0	Damp sand
C	g	5	w	*Typha latifolia*	40.0	1	40.0	Wet spoil heap
CSR	h	5	i	*Glechoma hederacea*	37.5	2	37.6	Mesic old field

Seres considered:

- Large spoil heaps from open-cast brown coal mining, xeric and moist parts distinguished; the duration of succession for which the species exchange was reconstructed: 1 - 40 yr (data from Prach 1987, completed by unpublished records);
- Abandoned sand pit; 1 - 20 yr (Kočár & Prach unpubl.);
- Reclaimed sites in areas deforested due to air pollution, formerly covered by *Picea abies*. To facilitate replanting of *Picea*, the sites were bulldozed, creating plots with a grass cover, the topsoil removed and mounds formed by the dumped material; 1 - 18 yr (Pyšek 1992);
- Barriers around a newly constructed fishpond formed by sandy subsoil or organic (peaty) topsoil; 1 - 13 yr (Prach unpubl.);
- Ruderal urban sites in the town of Plzeň; particular seres were distinguished according to the nutrient status, i.e. poor, moderate and rich; 1- 12 yr (data from Pyšek 1978);
- Exposed bottom of a destroyed water reservoir, an acidic zone was considered separately; 1 - 12 yr (Frantík, Osbornová & Prach unpubl.);
- Abandoned fields; three seres were distinguished according to the soil moisture conditions, i.e. xeric (1 - 60 yr), mesic (1 - 55 yr) and wet (1 - 18 yr) (data from Osbornová et al. 1989 and Prach unpubl.);

For other characteristics of the seres see Prach et al. (1993, 1997); Prach & Pyšek (1994a, b) and the references given above.