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CLONAL PLANTS - WHAT IS THEIR ROLE IN SUCCESSION?

Karel Prach[1] & Petr Pyšek[2]

1) Department of Plant Ecology, Institute of Botany, Academy of Sciences of the Czech Republic, CZ-379 82 Třeboň, and Faculty of Natural Sciences, University of South Bohemia, CZ-370 01 České Budějovice, Czech Republic; fax +42 38 45985

2) Institute of Applied Ecology, University of Agriculture Prague, CZ-281 63 Kostelec nad Černými lesy, Czech Republic; fax +42 203 97458

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Abstract: Fifteen successional seres from man-made habitats in central Europe were compared and the occurrence of clonal species assessed on the basis of cover data. The effects of soil moisture and nitrogen (expressed using Ellenberg indicator values) on the performance of clonal plants were also considered. Clonal species formed the dominant component of vegetation cover in the majority of the seres studied. In moist sites, their dominance was more pronounced and the peak in their relative cover occurred earlier in succession. The relative importance of species with guerilla type growth tended to increase with time in most seres and after 10 years these were mostly more important than those exhibiting phalanx type growth. The prevalence of guerilla species after 10 years was more obvious in moist seres. Clonal species were able to become dominant regardless of soil conditions, whereas the dominance of non-clonal species tended to be restricted to very wet and nutrient-poor sites. Clonal plant species appeared to maintain their dominance for a longer period than non-clonal plants.

INTRODUCTION

Clonal growth often allows effective horizontal vegetative spread (clonal dispersal sensu BEGON et al. 1986). This ability makes it possible for a species to rapidly colonize available space and thus influence its success in vegetation succession. So far, however, the participation of plants in succession has mostly been discussed in a general sense (GRIME 1979, GRUBB 1988, MORTIMER 1989, WALLER 1988), and where quantitative data have been provided these are usually concerned with only one sere (RYDIN & BORGEGÅRD 1991). It has been hypothesized (PRACH 1988) that the role of extensive clonal dispersal in succession is evident both (a) in the early stages, due to the rapid capture of space made available following disturbance (see also WALLER 1988), and (b) in late-successional stages, due to the rapid filling of gaps in more or less closed vegetation cover (cf. GRIME 1979).

However, a detailed evaluation of the success of clonal species in succession has not been made and an understanding of their behaviour in succession in the field is based, to a large extent, on speculation (CALLAGHAN et al. 1992). Hence the main aim of this paper, which is based on the mutual comparison of a number of seres from Central European man-made

Table 1. Overview of successional seres included in the analysis.

No. Locality	Region	Habitat type	M	N	Successional age of the oldest plots	Year of sampling[a)]	Type of observation	Method	Plot size (m)	Source
1 Dřínov	NB	acidic emergent bottom[1]	7.65	5.99	9 yrs	1	PP	PQ,Rel	5x5	FRANTÍK et al., unpubl.
2 Dřínov	NB	emergent bottom[1]	7.89	6.11	10	1	PP	PQ,Rel	5x5	FRANTÍK et al., unpubl.
3 Nový rybník fishpond	SB	peaty barrier[2]	8.58	5.70	9	1	PP	PQ,Rel	5x5	PRACH, unpubl.
4 Nový rybník fishpond	SB	sandy barrier[2]	7.13	3.36	9	1	PP	PQ,Rel	5x5	PRACH, unpubl.
5 Krušné hory Mts.	NB	reclaimed plots[3]	5.60	3.93	15	1,4,5,15	I	Rel	5x5	PYŠEK 1992
6 Krušné hory Mts.	NB	mounds[3]	5.45	5.25	15	1,4,5,15	I	Rel	5x5	PYŠEK 1992
7 Halámky	SB	abandoned sand pit	5.25	5.92	18	2,6,12,18	PP	Rel	5x5	PRACH, unpubl.
8 Plzeň	WB	ruderal sites-poor[4]	4.84	5.93	12	1	PP,I	Rel	v	PYŠEK 1978
9 Plzeň	WB	ruderal sites-moder[4]	5.25	7.45	12	1	PP,I	Rel	v	PYŠEK 1978
10 Plzeň	WB	ruderal sites-rich[4]	5.22	7.52	12	1	PP,I	Rel	v	PYŠEK 1978
11 Bohemian Karst	CB	aband. oldfields-xeric	4.37	5.75	67	1,4,6,8,13,32,55,67	I	PQ,Rel	5x5	OSBORNOVÁ et al.1989
12 Bohemian Karst	CB	aband. oldfields-mesic	4.67	5.59	47	1,2,8,15,28,36,47	PP,I	PQ,Rel	5x5	OSBORNOVÁ et al.1989
13 Bohemian Karst	CB	aband. oldfields-wet	6.57	6.86	13	1,2,4,5,13	PP,I	Rel	5x5	OSBORNOVÁ et al.1989
14 Most	NB	spoil heaps[5]	4.49	6.59	37	± 1	PP,I	Rel	1x1,5x5	PRACH 1987
15 Vissonta	H	spoil heaps[6]	4.39	5.12	20	1-10,16-20	PP,I	Rel	5x5	BARTHA 1990

1 - [a)] sampled every year; CB - central Bohemia, NB - northern Bohemia, SB - southern Bohemia, WB - western Bohemia, H - Hungary. Soil conditions were characterized by Ellenberg indicator values (ELLENBERG et al. 1991) calculated on the basis of species presence in the initial 10 years of succession. M - moisture, N - nitrogen. Sampling years are given for those seres in which the year-by-year sampling was not carried out. PP - permanent plots, I - course of succession was inferred from comparison of differently aged sites. Combination of both means that succession was inferred from arranging the subsets of data, obtained from permanent plot sampling, on the time axis on the basis of comparison of stages of a different age. PQ - point quadrat, Rel - relevé method, v - variable plot size.

[1] Exposed muddy bottom of a water reservoir, altitude 260 m a.s.l.; sulphur accumulation and its subsequent oxidation caused a decrease in pH value in sere no. 1 during the first years of succession; [2] Recently (1983) constructed pond ca. 1 ha in size at 430 m a.s.l.; barriers of allochtonous material (no. 3 - peat, no. 4 - sand) surrounding the pond were studied; [3] Reclaimed plots were created by bulldozing away the upper humus soil layer to make spruce replanting in areas deforested by air pollution easier; mounds were built by accumulating the material removed from plots; [4] Succession in urban habitats of the town of Plzeň (175 000 inhabitants, altitude 300 m a.s.l.) was inferred from series of permanent plot (each 6 years of duration) starting at different successional age (Poor: seres no. 1,7, Moderate: no. 2,11, Rich: no. 3,12 in PYŠEK 1978); differentiation of sites according to soil fertility was assessed visually; no soil analyses were carried out; [5] Spoil heaps after brown coal mining at the altitude of 250-270 m a.s.l., built predominantly by uniform Tertiary grey clay; [6] Spoil heaps after brown coal mining located in drier climatic district; two differently aged seres were sampled annually.

habitats, is to contribute to this lack of information and answer the question: Is there any regular pattern in the participation of clonal plants in succession in man-made habitats and if so, can it be related to soil conditions?

MATERIAL AND METHODS

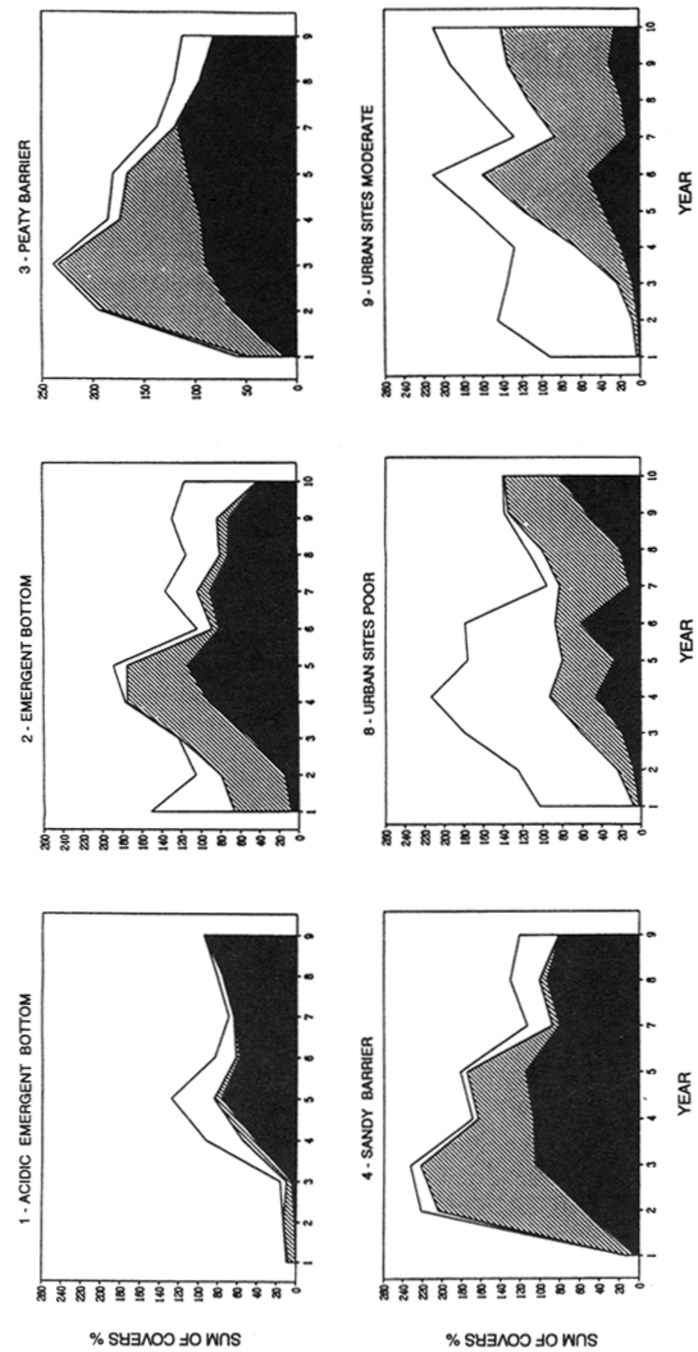
Data from 15 successional seres studied in various central European man-made habitats were collected. All the seres represent succession starting on bare soil and cover a wide range of habitats with respect to soil moisture and nutrient status (see Tab. 1 for basic characteristics of the seres; more detailed information may be found in original sources referred to in the table).

Species performances in all seres were characterized using cover data. Point-quadrat data and direct cover estimations, where used by original authors, were directly taken from the original sources; in the seres sampled by the relevé method (Braun-Blanquet scale; see MUELLER-DOMBOIS & ELLENBERG 1974), the following transformation of values of the Braun-Blanquet scale was used: 5, 87.5%; 4, 62.5%; 3, 37.5%; 2, 15%; 1, 2.5%; +, 0.1%; r, 0.02%. In seres with several replicates, the mean value from all plots was considered. All species achieving the mean cover value of at least 1.0 % in at least one sampling year were included in analyses.

Information on clonal growth was extracted from various floras (DOSTÁL 1954, TUTIN et al. 1964-80, ROTHMALER 1986, HEJNÝ & SLAVÍK 1988-92) and species lists (GRIME et al. 1988). The role of species possessing the ability for extensive horizontal dispersal, i.e. those corresponding to the guerilla type of growth (and further termed as guerilla plants to distinguish them from those exhibiting a phalanx strategy; see LOVETT DOUST & LOVETT DOUST 1982, and BEGON et al. 1986), was also evaluated. Those species capable of producing vegetative offspring at a distance of 0.5 m or more during one year of growth were considered as guerilla species. Field observation of the growth pattern of the species was also used to determine the type of clonal growth of each particular species.

To characterize soil conditions in particular seres, Ellenberg indicator values for moisture and nitrogen were used. By this approach, an ordinal scale is used to express the relationship of a species to particular environmental factors (ELLENBERG et al. 1991). Mean values were calculated on the basis of species presence for each sampling year of each sere. Soil conditions were expressed as the mean value calculated for the initial 10 years of succession (or for years within this period for which data were available in the case of those seres that were not sampled year by year).

Because of different sampling frequency and duration of the seres studied, only those sampled less annually in permanent plots during the first 10 years of succession were analysed in detail (seres nos. 1-4, 8-12, 14 and 15; see Tab. 1 and Fig. 1a). Data were treated using standard statistical methods (SOKAL & ROHLF 1981).


1 - ACIDIC EMERGENT BOTTOM
2 - EMERGENT BOTTOM
3 - PEATY BARRIER
4 - SANDY BARRIER
8 - URBAN SITES POOR
9 - URBAN SITES MODERATE
SUM OF COVERS %
YEAR

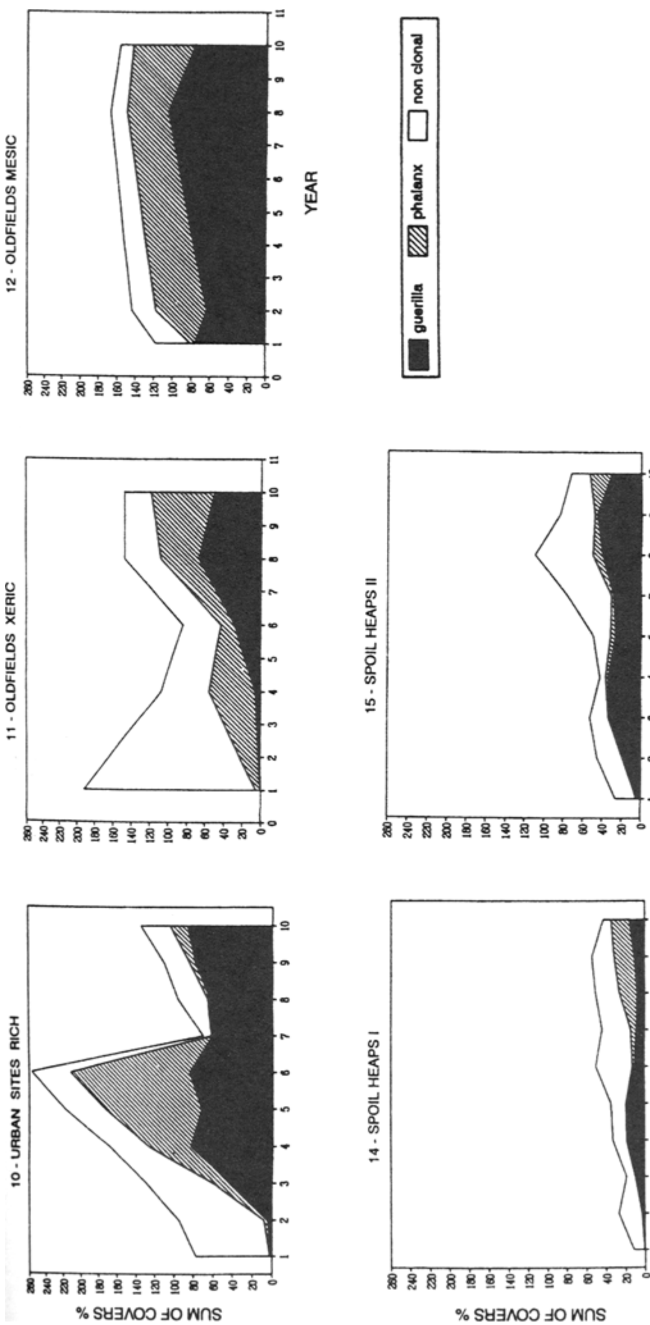
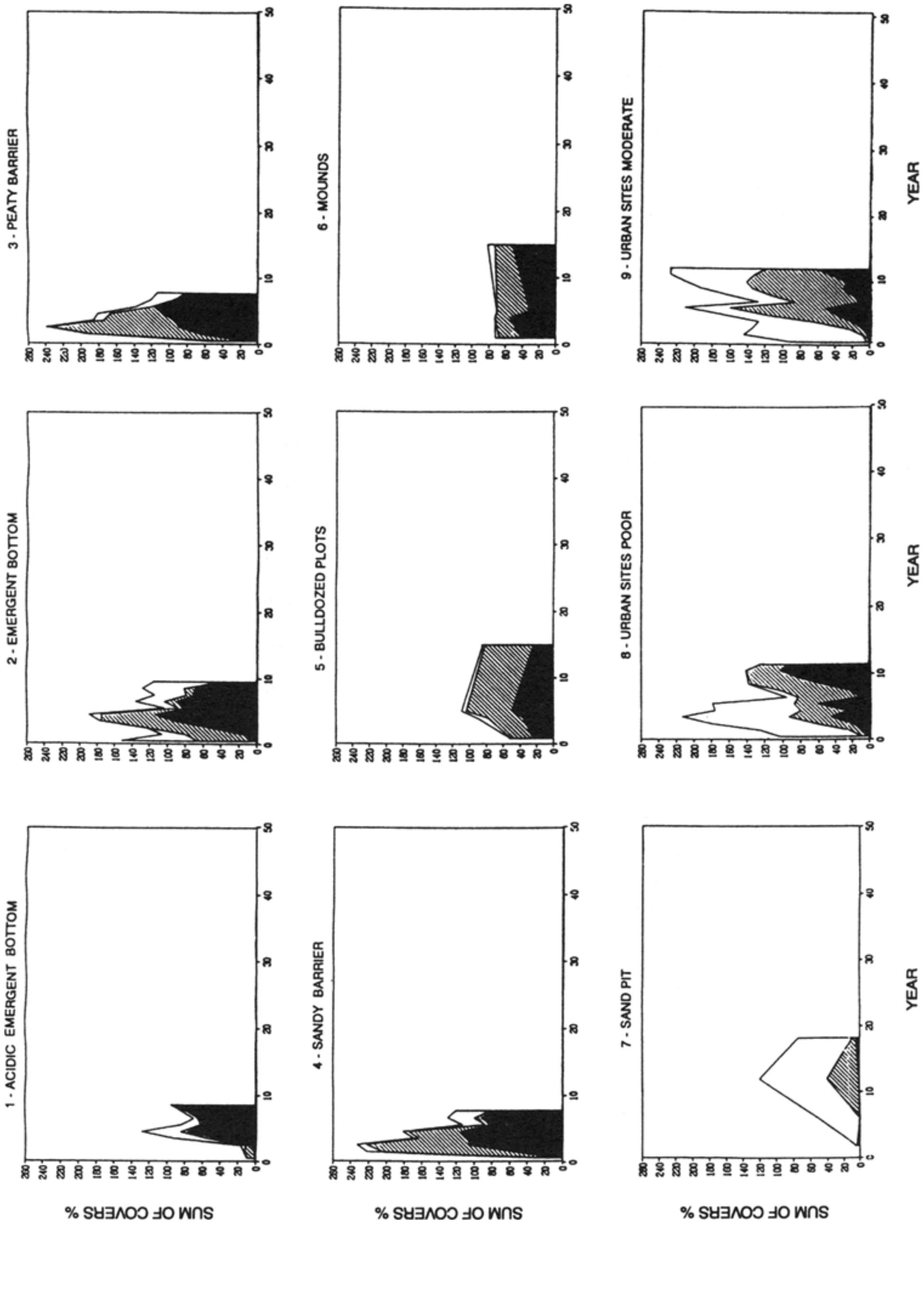


Fig. 1a. Changes in cover of clonal and non-clonal plants during succession: Seres in which the sampling interval made it possible to carry out a detailed analysis of changes during the first 10 years. The whole area corresponds to the total cover and is composed of clonal plants capable of guerilla type growth, clonal plants exhibiting phalanx type growth, and non-clonal plants. Note that sums of cover of all species belonging to the given group were used so that the total value may exceed 100%. See Tab. 1 for characteristics of the seres.


1 - ACIDIC EMERGENT BOTTOM
2 - EMERGENT BOTTOM
3 - PEATY BARRIER
4 - SANDY BARRIER
5 - BULLDOZED PLOTS
6 - MOUNDS
7 - SAND PIT
8 - URBAN SITES POOR
9 - URBAN SITES MODERATE
SUM OF COVERS %
YEAR

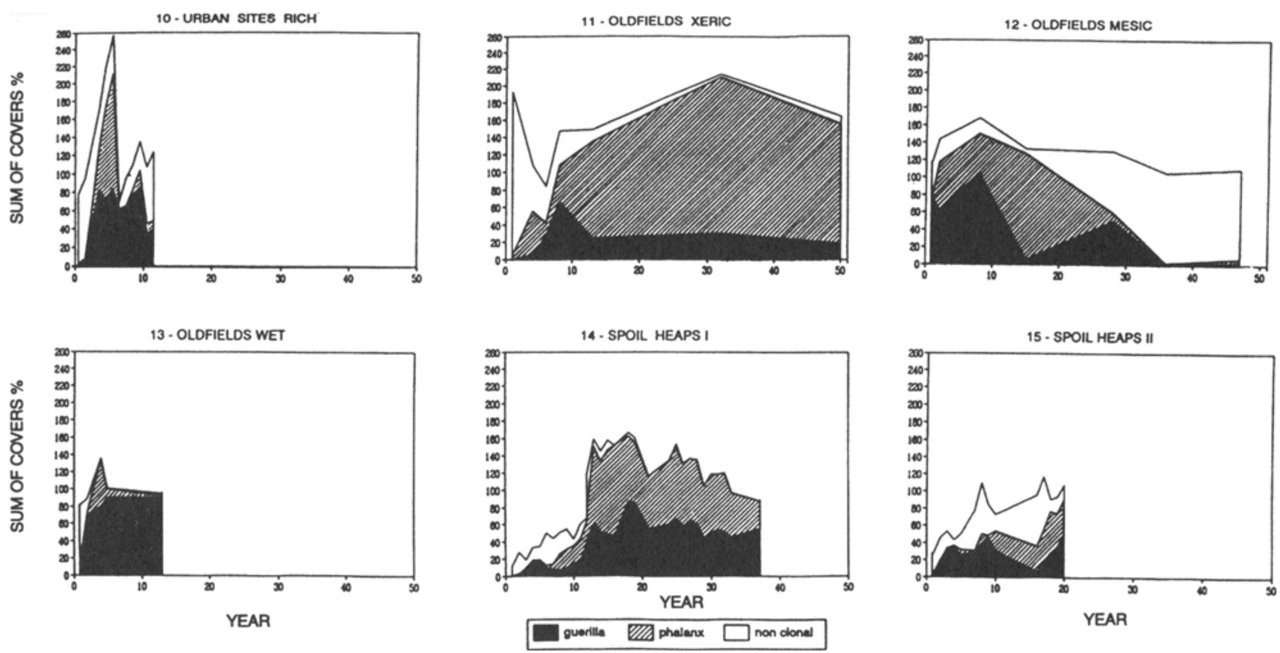


Fig. 1b. Changes in cover of clonal and non-clonal plants during succession: Complete data for all the seres studied. The whole area corresponds to the total cover and is composed of clonal plants capable of guerilla type growth, clonal plants exhibiting phalanx type growth, and non-clonal plants. Note that sums of cover of all species belonging to a given group were used so that the total value may exceed 100%. See Tab. 1 for characteristics of the seres.

Table 2. Maximum cover (expressed as the sum of cover of species present) reached during the first 10 years of succession and the year at which it was attained compared between (a) clonal and non-clonal species, and (b) phalanx and guerrilla clonal plants. Means ± s.d. from 15 seres are shown. The significance level of the difference between means (Kruskal-Wallis test) is shown between corresponding values. *, $P < 0.05$; **, $P < 0.01$; n.s., non significant.

	Clonal		Non-clonal	Phalanx		Guerilla
Maximum cover	128.7 ± 64.6	**	66.3 ± 49.6	69.6 ± 42.4	n.s.	72.0 ± 35.8
Year of maximum cover	6.9 ± 2.9	*	4.0 ± 3.0	5.3 ± 2.8	n.s.	6.4 ± 2.6

RESULTS

Proportion of clonal plants in succession

The total cover of clonal plants (expressed as the sum of cover of all clonal species present in a given year) tended to increase from the onset of succession to a maximum value and then decrease in the majority of seres (2-5, 7, 9-14). The changes in the presence of clonal plants during the first 10 years of succession are compared in Fig. 1a for those seres analysed in detail; Fig. 1b allows a comparison of all the seres studied over the period of time for which the data were available. Considering all seres, the maximum total cover of clonal plants during the first 10 years of succession was significantly higher than the maximum cover of non-clonal species. The peak in cover was attained earlier in non-clonal species (Tab. 2).

During the initial 10 years of succession, clonal plants were the dominant component of plant cover, at least for a certain period, in all seres subjected to the year-by-year analysis (their maximum relative cover was in all cases higher than 0.5, see Fig. 2a, b). The relative cover of clonal plants, which may be considered as a measure of their success in comparison with non-clonal species, increased with soil moisture and was not significantly affected by nitrogen (Fig 2a, b). The dominance of clonal plants was expressed earlier in moist seres (Fig. 2c).

Neither the maximum total cover nor the year in which it was reached differed between guerilla and phalanx species during the first 10 years of succession (all seres used for comparison, Tab. 2). However, the phalanx species seemed to decrease their proportion in later stages of succession whereas that of guerilla species did not exhibit any clear pattern. After 10 years of succession, the total cover of guerilla species (mean cover ± s.d. = 61.4 ± 33.2) was significantly higher (Kruskal-Wallis test, $P < 0.05$) than that of phalanx species (27.8 ± 31.6). At that time, the prevalence of plants with the guerilla type of growth was significantly more pronounced in most sites. Nitrogen had no significant effect on the representation of both groups (Fig. 3).

Clonality and dominant species replacement

In total, 27 clonal and 14 non-clonal dominant species (i.e. those having attained in at least one year the highest cover value of all species present in that year) were observed in the seres

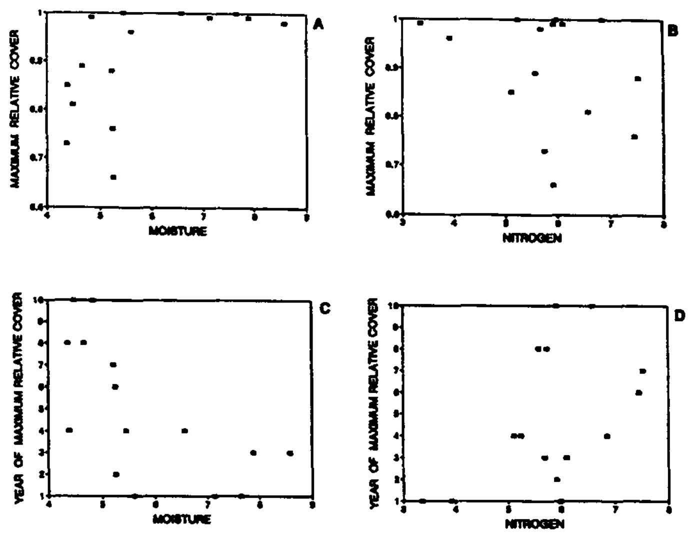


Fig. 2. Successional performance of clonal plants related to soil conditions. (A, B) Maximum relative cover of clonal plants represents the maximum contribution of the sum of cover of clonal species to the total cover recorded during the first 10 years of succession. (C, D) The year at which the maximum cover was attained is related to soil conditions (expressed as Ellenberg indicator values calculated on the basis of species presence). The values of Kendall correlation coefficient and their significance levels are: (A) 0.44, $P < 0.05$; (B) -0.07, n.s.; (C) -0.57, $P < 0.01$; (D) 0.32, n.s.

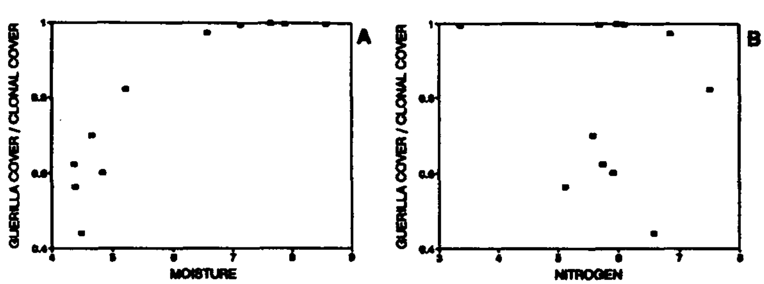


Fig. 3. Representation of plants with guerilla type of growth after 10 years of succession (± 3 years in those seres for which data from year 10 were not available) related to (A) soil moisture (Kendall correlation coefficient 0.52, $P < 0.05$) and (B) nitrogen (-0.09, n.s.). Ellenberg indicator values calculated on the basis of species presence were used to express soil conditions. Seres 5,6,7 and 13 were not included because of insufficient data.

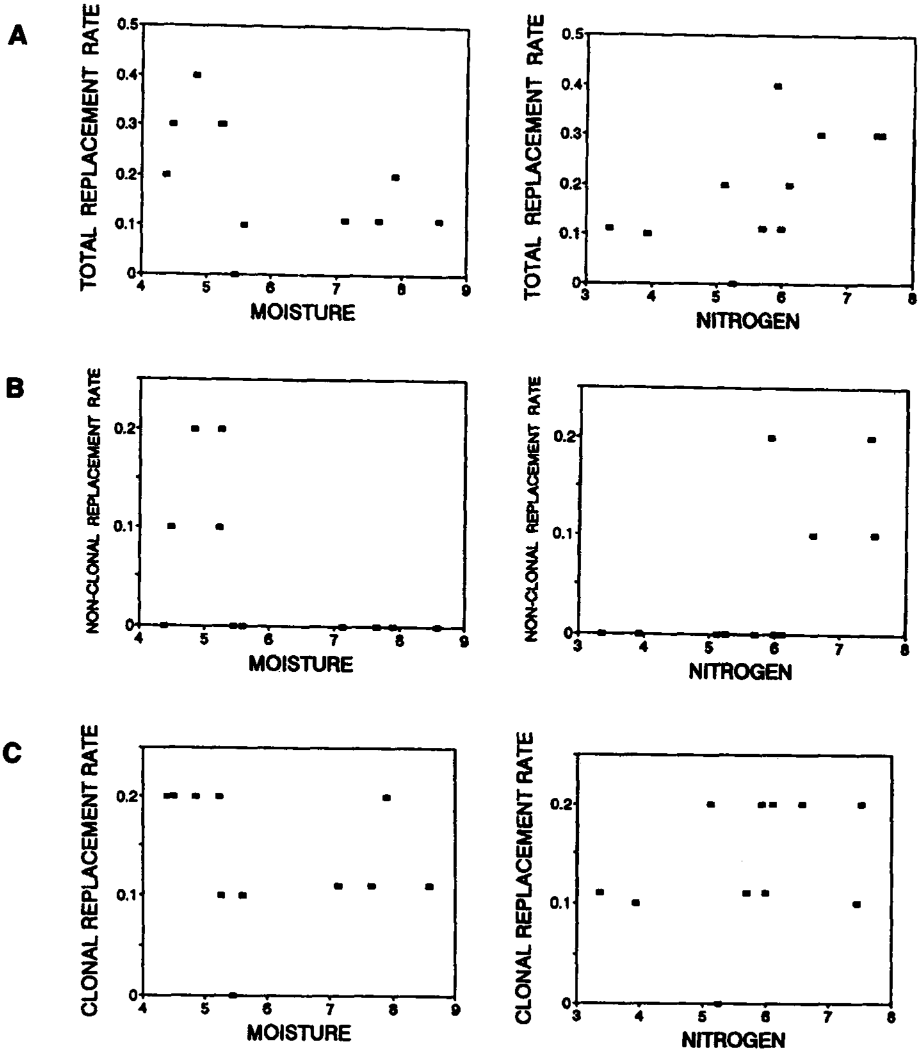


Fig. 4. Annual exchange rate of dominant species (expressed as number of replacements/total number of years considered which was 10, except of the seres 1, 3, 4 followed for 9 years only) related to soil conditions. Ellenberg indicator values calculated on the basis of species presence were used to express soil conditions. Only seres sampled annually during the first 10 years of succession (1-4, 8-10, 14-15) and those in which the dominance did not change between two successive samplings (5, 6) were considered (n = 11). (A) Total exchange rate: Kendall correlation coefficient -0.31, n.s. (moisture), 0.51, $P < 0.05$ (nitrogen). (B) Non-clonal species taking over the dominance: -0.43, n.s. (moisture), 0.52, $P < 0.05$ (nitrogen). (C) Clonal species taking over the dominance: -0.23, n.s. (moisture), 0.27, n.s. (nitrogen).

studied (Tab. 3). Having reached dominance, clonal species maintained it longer than non-clonal dominants: dominance persistence (see Tab. 3 for the definition) for the former (mean ± s.d. = 0.69 ± 0.28, n = 21) was significantly higher (Kruskal-Wallis test, $P < 0.05$) than for the latter (0.38 ± 0.40, n = 13). Species with the guerilla type of growth (0.77 ± 0.17, n = 8) did not differ from those with the phalanx type of growth (0.65 ± 0.33, n = 13) with respect to the persistence of dominance ($P > 0.05$).

The rate of replacement of dominant species (expressed for a given sere as the number of year to year replacements having occurred during the first 10 years of succession) is shown in Fig. 4 for situations in which (a) a clonal species replaced either a clonal or non-clonal species, (b) a non-clonal species replaced a clonal or non-clonal species, and (c) a replacement of any kind occurred, i.e. the total rate of exchange. The latter decreased with moisture (although not significantly) but increased with nitrogen ($P < 0.05$). The pattern of exchange for non-clonal species replacing others was basically the same with the relationship to moisture being also marginally significant ($P = 0.09$). However, the ability of clonal plants to become dominant was not affected by any of the soil factors considered (Fig. 4).

DISCUSSION

As expected from the nature of the data, no simple and unambiguous pattern of succession was displayed by clonal plants in the seres studied; however, some trends were recognized. Undoubtedly, the role of clonal plants in man-made habitats is of great importance. Their initial increase and subsequent culmination and decrease in many seres may be explained by the close correlation between clonality and life form: annuals and biennials which are typical of initial successional stages (as in seres nos. 8-11, 13 and 14) are usually non-clonal. On the other hand, woody species, of which most are non-clonal, prevail in later stages of succession (especially in seres 7, 10, and 12). Perennial herbs as well as grasses and grass-like species are mostly clonal (see Tab. 3) and usually play the most important part as mid-successional species (GRIME 1979, BEGON et al. 1986, GRAY et al. 1989, BROWN 1992). Rates of expansion, persistence and dominance of these life-forms largely seem to determine the success of clonal plants. Further, the early culmination of clonal plants' cover appears to reflect the fact that in many seres, total plant cover also culminates early in succession (see Fig. 1). This can be explained by temporal overcrowding which is being frequently observed after an initial period of colonization.

In some seres in the present study (seres nos. 3-6, especially), clonal plants were the most important part of vegetation from the very onset of succession. Hence the results from these seres appear to support hypotheses suggesting that clonal plants are associated with the initial succession of recently disturbed habitats (WALKER & CHAPIN 1987, WALLER 1988). In some secondary successions, species surviving disturbance by means of vegetative propagules may also be favoured in very early stages (WALKER & CHAPIN 1987; e.g. sere no. 6). Examples of clonal perennials attaining dominance in the very early stages of succession are given in Tab. 3.

The analysis of those seres from which more detailed data were available provided more exact results. Soil moisture appears to be the factor significantly supporting the success of

Table 3. Overview of dominant species recorded in 15 successional seres. Seres in which the species occurred as dominant (i.e. attaining in at least one sampling year the highest cover of all species present in that year) are listed using the numbers corresponding to those used in Tab. 1. Clonal species which became dominant during the first 3 years of succession are marked with asterisk. Guerilla type of growth is indicated (G). Probability of a species persisting as dominant (*DomPers*) was expressed as $Yr_{ret}/(Yr_{ret} + Yr_{repl})$ where Yr_{ret} is the number of years the species retained its dominance if two successive years are compared, and Yr_{repl} stands for the number of years in which it was replaced by another species. Only data from year-by-year sampled seres (see Tab. 1) were used for calculation of the *DomPers* characteristic; from other seres, only data for those species were considered which retained their dominance during two (or more) subsequent samplings. n.a. - data not available to express the characteristic.

Species	Seres	*DomPers*
Clonal:		
Agropyron repens G	8,13	0.63
Arrhenatherum elatius	11,12,14	0.93
Artemisia vulgaris	9,11,14	0.88
Ballota nigra	10	0.5
Brachypodium pinnatum G	12	n.a.
Calamagrostis epigeios G	1,2,4,8,14	0.86
Calamagrostis villosa G	5,6 *	0.96
Cardaria draba G	13,14 *	0.66
Carex gracilis	2 *	0.0
Cirsium arvense G	12 *	n.a.
Coronilla varia	13	n.a.
Deschampsia flexuosa	5	1.0
Festuca rubra	15	1.0
Festuca rupicola	11	1.0
Galium album	13	n.a.
Galium palustre	3 *	0.5
Glechoma hederacea G	12 *	0.5
Holcus lanatus	14	0.66
Juncus effusus	1 *	0.66
Lathyrus tuberosus	15	1.0
Molinia caerulea	4 *	0.67
Petasites hybridus G	13	n.a.
Phalaris arundinacea G	3 *	1.0
Ranunculus repens G	13 *	n.a.
Tanacetum vulgare	8,14	0.6
Tussilago farfara G	15 *	0.86
Urtica dioica G	10	0.67
Non-clonal:		
Atriplex nitens	14	0.5
Betula pendula	1	0.0
Carduus acanthoides	14	0.0
Chenopodium album	8,9,10,13	0.5
Chenopodium viride	9	0.0

Species	Seres	*DomPers*
Crataegus sp. div.	12	1.0
Lactuca serriola	15	0.0
Melilotus alba	8	0.0
Papaver rhoeas	11,13	n.a.
Pinus sylvestris	7	1.0
Polygonum lapathifolium	13,14	0.5
Rumex maritimus	2	0.0
Sambucus nigra	9,10	1.0
Sisymbrium loeselii	8	0.5

clonal species; they exhibited the fastest and most successful performance in wet seres. The less successful colonization and later culmination of clonal plants in drier sites correspond to the fact that annuals and biennials, which are usually non-clonal, often attain higher productivity and persist longer during succession in dry sites (SCHAFALE & CHRISTENSEN 1986, OSBORNOVÁ et al. 1989).

With respect to the guerilla and phalanx growth forms of clonal plants (LOVETT DOUST & LOVETT DOUST 1982), the present study showed that there was a major difference between both in the timing of their performance. Species capable of the guerilla type of growth are often more successful later in succession than phalanx species; this may be explained by their ability to produce widely spaced modules that have greater chance of penetrating into more or less closed vegetation cover (BEGON et al. 1986). This is in agreement with the conclusions of others who stress the importance of increasing vegetative expansion in the later stages of succession when establishment from seed becomes limited by dense cover and a compact litter layer (GRIME 1979, RYDIN & BORGEGÅRD 1991).

Because of the limitations of the data set used, this study was not able to reveal any functional relationship between the participation of clonal plants in succession and environmental conditions. For that, experimental studies conducted in real seral stages, focused on the growth pattern of clonal plants under different environmental conditions, and on competition amongst them and non-clonals, and on gap dynamics, are needed.

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