

THE EFFECT OF SUCCESSIONAL AGE AND DISTURBANCE ON THE ESTABLISHMENT OF ALIEN PLANTS IN MAN-MADE SITES: AN EXPERIMENTAL APPROACH

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Abstract

The hypothesis that younger successional stages are less resistant to invasions than older stages was verified experimentally in two kinds of primary successional seres (sand pit and peat-bog disturbed by peat extraction) in southern Bohemia, Czech Republic. Three comparable successional stages aged 0 (i.e. the year of disturbance), 10 and 25 years were selected in both sites. Eight species alien to Czech flora were sown into particular sites and stages and their establishment was recorded. MANOVA revealed significant ($P < 0.001$) differences in the number of established seedlings between the successional stages and sites. The difference in seedling numbers among the three successional stages was significant (GLM, $P < 0.05$) in seven species in the disturbed peat-bog. In the sand pit, significant differences were found in four species and the results from this site were more variable, showing no clear trend. In general, the 10 years old stages seemed most convenient for seedling establishment. The role of disturbance regime on seedling establishment was studied in the second experiment conducted in wet meadows near the town of Třeboň, southern Bohemia, Czech Republic. *Heracleum mantegazzianum* and *Impatiens glandulifera* were sown into plots varying in species composition, biomass and cover, and their germination was recorded. The correlation between the number of seedlings and any of the community characteristics measured was significant for neither species. The only trend observed was that the numbers of established *Impatiens glandulifera* seedlings decreased with increasing stand height. The results indicate that it is very difficult to find a community characteristic acting as a simple predictor of establishment success.

Introduction

Establishment of alien plants invading regions outside their native distribution range is a crucial step in the process of plant invasions (di Castri 1990). This stage of the process is rather poorly understood because of considerable lack of data, however it can be expected that the probability of successful seedling establishment would increase with the level of disturbance creating open space in a closed canopy (Crawley 1989). With respect to the successional status, young successional stages are predicted to be more susceptible to invasion by alien species than older stages (Rejmánek 1989; Hobbs and Huenneke 1992), and there is some support for this hypothesis coming from both theoretical models (Rejmánek 1989) and field data (Lepart and Debussche 1991). The latter, however, mostly compare *a posteriori* successional stages with respect to the representation of alien species (Kowarik

1995). The major methodological flaw associated with such an approach is, however, that it is impossible to separate the effect of successional status from that of the input of diaspores which need not be constant over time (Crawley 1986). The later successional stages may then seem more resistant to invasions because, at least in part, the input of diaspores would decrease over time. To determine whether or not such an assumption is true, experimental data are needed.

The present paper explores the experimental verification of the hypothesis that younger successional stages are less resistant to invasions than older stages. Furthermore, the invasion success appears to be affected by such community characteristics as total cover and biomass (Rejmánek 1989; Hobbs 1989), i.e. those principally affected by disturbance regimes. There is some support for the hypothesis that disturbances in plant communities promote invasions (Hobbs and Humphries 1995). For that reason, the effects of various disturbance regimes on the seedling establishment during invasion are also addressed.

Study sites and methods

Effect of successional stage

The effect of successional age on the establishment of alien species seedlings was studied in two kinds of primary successional seres running in (1) sand pit land, (2) peat-bog disturbed by peat extraction. The localities were situated close to each other in southern Bohemia, Czech Republic (1-longitude 14°57'E, latitude 48°50'N; 2-longitude 14°48'E, latitude 48°57'N) at the altitude of 445-460 m a.s.l. Mean annual temperature was about 7°C, annual sum of precipitation was about 650 mm (50-year average).

Three comparable successional stages aged 0 (i.e. the year of disturbance), 10 and 25 years were selected in both sites. The age of particular successional stages was inferred from historical maps and site history records. The initial stages were completely free of vegetation. Ten years old stages in the sand pit were characterized by trees and shrubs up to 3 m in height (*Pinus sylvestris*, *Betula pendula*, *Salix caprea*) and by a sparse herbaceous layer. In the disturbed peat bog, ten year old stages were covered by scattered trees and shrubs (*Betula pendula*, *Pinus sylvestris*, *Rubus fruticosus* agg.), rather compact herb layer consisted mostly of *Molinia coerulea*. The oldest stages in both seres were covered by a dense pine-birch forest with low cover in the herbaceous layer.

A single measurement of ground water table was carried out in July 1994, using bore-holes installed in each successional stage. The sites and stages were similar from the viewpoint of moisture conditions. The position of ground water table slightly fluctuated around 1 m below surface.

Eight species considered as invasive in the Czech Republic (Pyšek et al. 1995) were used for experimental sowing (Table 1). The species were selected to cover a wide range of life forms and taxonomical groups. Seed availability and germination characteristics were also taken into account. In each site and successional stage, each species was sown into 4 randomly selected 1 × 1 m plots, giving the total of 24 plots per species. The seeds were sown in March 1995, before the onset of growing period, except for *Robinia pseudoacacia* and *Physocarpus opulifolius* which were sown later

Table 1. Species used in experiments on seedling establishment, their basic characteristics, and number of seeds sown in particular plots.

Species	Life form	Origin	Seeds per 1 m ²		
			Peat bog	Sand pit	Meadow
<i>Acer negundo</i>	tree	N America	200	200	–
<i>Ailanthus altissima</i>	tree	Asia/China	150	150	–
<i>Bidens frondosa</i>	annual	N America	400	400	–
<i>Heracleum mantegazzianum</i>	perennial	Asia/Caucasus	1000	1000	500
<i>Lupinus polyphyllus</i>	perennial	N America	45	90	–
<i>Physocarpus opulifolius</i>	shrub	N America	500	500	–
<i>Pinus strobus</i>	tree	N America	100	100	–
<i>Robinia pseudoacacia</i>	tree	N America	200	200	–
<i>Impatiens glandulifera</i>	annual	Asia/Himalayas	–	–	500

(May) to avoid possible frosts. *Robinia pseudoacacia* was treated before germination by hot water (90°C, 3 times for 15 seconds – Grime *et al.* 1981).

The number of seedlings were counted immediately after germination. Another census was carried out at the end of the vegetation period in October 1995. The data (seedling numbers) were analyzed by generalized linear models (GLM) (McCullagh and Nelder 1989) using the S-PLUS package (Anonymous 1995a, b) and after log-transformation also by MANOVA (Scheiner 1993).

Effect of community characteristics and disturbance regime

The experiment examining the role of disturbance regime on seedling establishment was conducted in a complex of wet meadows attached to a large fishpond, near the town of Třeboň, southern Bohemia, Czech Republic at the altitude of 430 m a.s.l.; latitude 48°61' N; longitude 14°55' E (see Jeník and Květ 1984; Prach 1993 for details on the site).

An homogenous, uncut sward dominated by sedges (*Carex gracilis*, *C. vesicaria*, *C. nigra*, *C. canescens*) and a grass *Calamagrostis canescens* was used as a study plot. Prior to the experiment reported in the present paper, the meadow was subjected (1984–1991) to various treatments (fertilization, mowing, trampling, burning) in a long-term experiment on response of species composition and productivity of a wet grassland to various kinds of disturbance (Prach and Soukupová, in press). As a result, the treated plots varied in species composition, biomass and cover, providing a convenient subject for testing the effect of these characteristics on the establishment of alien species.

Heracleum mantegazzianum and *Impatiens glandulifera* were sown in plots previously subjected to particular treatments at the beginning of January, the former in 1993 and the latter in 1994. In each plot, five subplots 1 × 1 m received 500 seeds of each species (Table 1). Seedlings and establishing plants were counted regularly.

Results

Effect of successional stage

Numbers of seedlings that became established and survived until the end of vegetation period are shown for particular sites and successional stages in Table 2.

Table 2. Establishment of seedlings and their survival until the end of the first vegetation period represented as the percentage of the total number of the seeds sown. Means from 4 plots are given in sand pit and disturbed peat bog, that from 5 subplots in the moist meadow (see Methods for details). The figures from the moist meadow experiment are based on the total number of seedlings germinated in 1994 and 1995, and are pooled over treatments.

Site	Sand pit			Peat bog			Meadow (pooled data)
	0	10	25	0	10	25	
<i>Acer negundo</i>	0.9	0.9	11.0	0.8	3.0	0.1	–
<i>Ailanthus alitissima</i>	5.0	0.2	0.2	10.0	16.0	0	–
<i>Bidens frondosa</i>	0	0	0	0	0	0	–
<i>Heracleum mantegazzianum</i>	0	0	0	0	0	0	0
<i>Lupinus polyphyllus</i>	0	3.0	1.0	5.0	2.0	0	–
<i>Physocarpus opulifolius</i>	0	3.0	0	0.2	6.0	0	–
<i>Pinus strobus</i>	5.0	0	0	0	5.0	0	–
<i>Robinia pseudoacacia</i>	2.0	2.0	4.0	6.0	5.0	0	–
<i>Impatiens glandulifera</i>	–	–	–	–	–	–	0.4

MANOVA revealed significant ($P < 0.001$) differences in the number of established seedlings among the successional stages and localities. The interaction between successional stage and site was significant at the same level, indicating that the differences between sites and successional stages have no additive character.

The difference in established seedling numbers among the three successional stages was significant (GLM, $P < 0.05$) in seven species in the disturbed peat-bog. Generally, the 10 year old stages seemed as those most convenient for seedling establishment. In the sand pit, significant differences were found for four species and the results from this site were more variable, showing no clear trend (Fig. 1).

Effect of community characteristics and disturbance regime

Some seedlings of *Heracleum mantegazzianum* appeared in all but one treatment in 1993 and none survived into the next year. Another cohort germinated in spring 1995 and no seedling survived into the next year. *Impatiens glandulifera* germinated in the year when sown. In the heavily manured plot, 25.8% of seedlings survived, the plants set fruit and a vital population established the following year (Table 3).

A similar germination response was found for both species, the number of *Heracleum* seedlings in particular plots being positively correlated with that of *Impatiens* ($r = 0.66$, $P = 0.05$). The highest seedling numbers of both species were recorded in the burned plot. The germination was, on the other hand, very low in trampled plots and especially in those subjected to moderate liming. No correlation between the

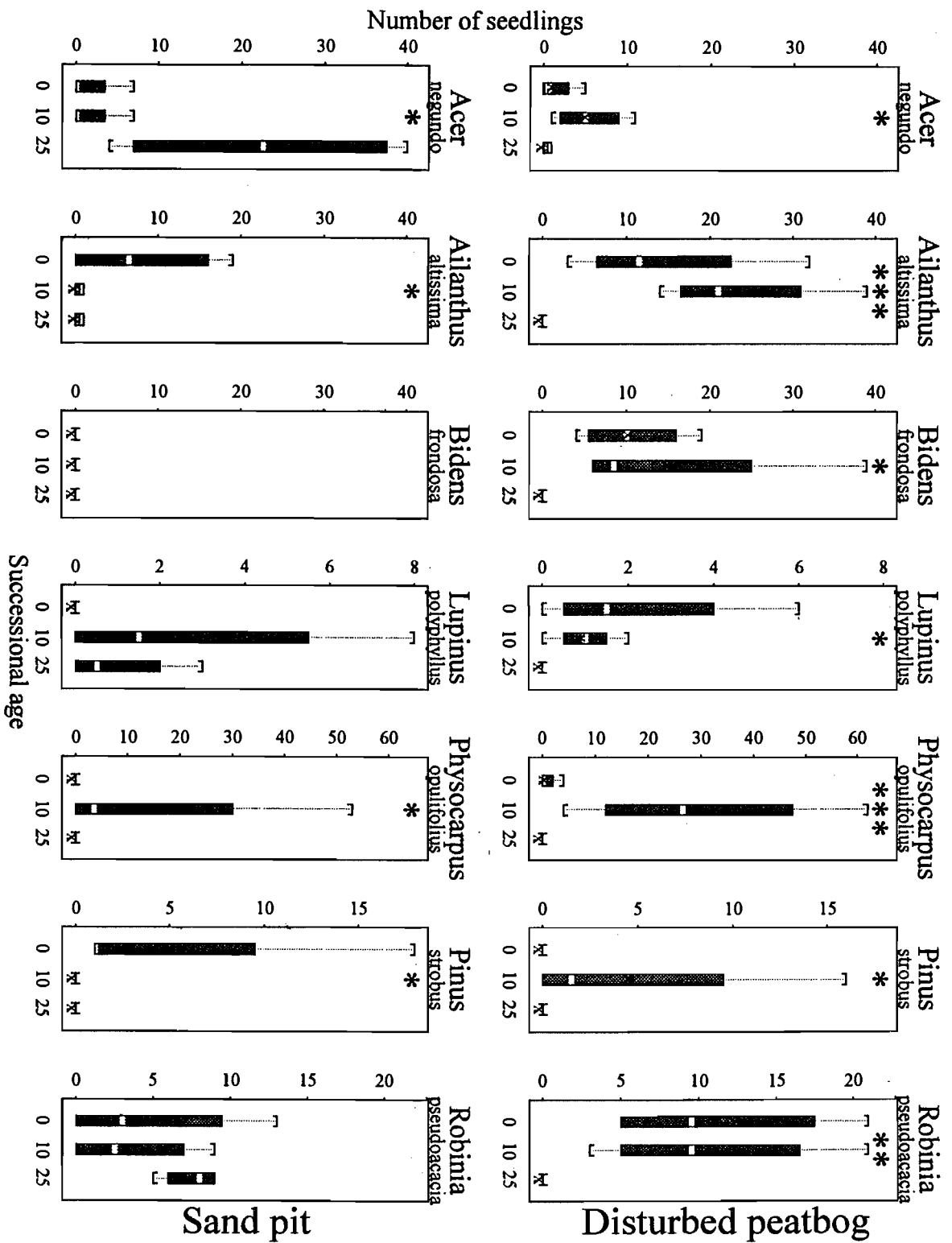


Fig. 1. Numbers of established seedlings (per 1 m²) shown for particular sites (sand pit, disturbed peat bog) and successional stages (0, 10, and 25 years old). Note the different scale used to stress the comparison between sites and stages for each species. Significant differences in seedling numbers among the three successional stages as revealed by GLM are indicated (* p<0.05; ** p<0.01; *** p<0.001).

Table 3. Community characteristics and seedling establishment in the moist meadow experiment. Cover (%) was measured by the point-quadrat method, oven-dry biomass (48 hours at 85°C) is given in g.m⁻². Species diversity is expressed by Shannon index (log₂ base). Stand height is given in cm. Seedling numbers represent means from five 1 × 1 m subplots. No *Heracleum* seedlings were observed in 1994. No later recruitment of *Impatiens glandulifera* was observed except as indicated below.

Treatment	Community characteristics						Seedling establishment		
	Living biomass	Litter	Dicott cover	Monocot cover	Stand height	Species diversity	Heracleum		Impatiens
							1993	1995	1994
Control	277	400	47	88	80	2.87	11	11	49
Manuring intensive	276	300	35	98	95	2.57	10	16	31 [#]
Manuring moderate	293	290	43	106	95	2.58	16	3	0
Cutting intensive	304	0	71	115	44	3.48	14	7	50
Cutting moderate	245	39	92	143	57	2.50	10	25	70
Liming intensive	494	440	58	147	80	2.95	17	22	57
Liming moderate	280	261	79	101	77	2.67	0	1	0
Liming, manuring	437	442	68	114	85	2.40	37	19	75*
Burning	287	62	77	127	51	2.97	53	109	100
Trampling	395	101	60	191	58	4.03	5	4	49

[#] Eight plants flowered in 1994, and two of these set seed. In 1995, 41 plants survived in the plot until the reproductive period.

* Ten plants flowered, none of them set seed.

number of seedlings for either species for any of the measured community characteristics was significant. The only trend observed was that the numbers of established *Impatiens* seedlings tend to decrease with increasing stand height ($r = -0.51$, $P = 0.07$).

Discussion

Although the results vary with respect to particular species, a trend observed in this study was that mid-successional stages were the most favourable for the establishment of alien species. This pattern may be partly explained by the facilitation model of succession (Connell and Slatyer 1977). In the initial stages of succession in both the sand pit and the peat bog, topsoil moisture appears to be the main factor controlling seedling survivorship, especially in the summer (Bastl, unpublished data). The establishment of aliens might have also been restricted by some other rather severe abiotic conditions, such as the lack of nutrients.

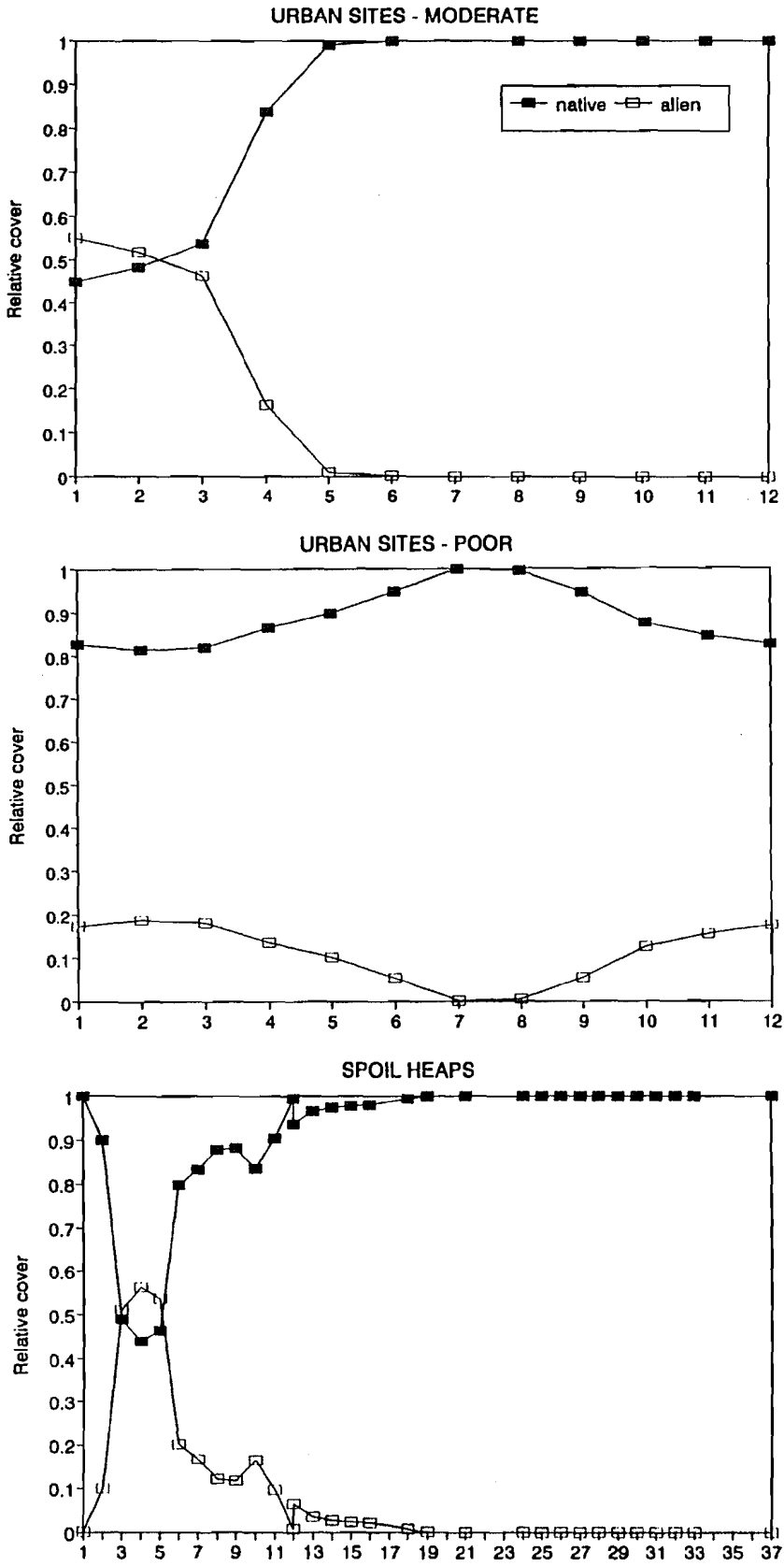
Ten years after the colonization of the sites, moisture conditions tend to improve by the growth of native species. On the other hand, after the canopy becomes closed later in the course of succession, the lack of light, compact litter layer, and competition from the established herb layer are probably other factors inhibiting seedling performance in more advanced successional stages. The negative effect of litter on seedling establishment was repeatedly indicated in various experiments (Facelli and Pickett 1991; Sydes and Grime 1981a,b; Pyšek 1990).

The hypothesis predicting easier invasion of younger sites (Rejmánek 1989) does not seem to be fully supported by the present study. The pattern observed is more complicated and stresses the importance of timing in succession, i.e. that following a precocious arrival, establishment may be prevented because of the absence of resources whereas late entry may be prevented by established vegetation and natural enemies (Crawley 1989). Moreover, the available data largely do not take into account that the higher representation of invaders in early successional communities may be due to higher rates of species introductions. Hard data to separate this effect from the community resistance to invasion are not available, and there are indications of a contradicting pattern (Crawley 1986). Viewed from this perspective, our results may be taken as unbiased by the varying rate of seed introductions.

At a more detailed scale, represented by the wet meadow experiment, it appears very difficult to find a community characteristic that acts as a simple predictor of establishment success. The concept of "plant's eye view" and that of safe sites are difficult to record and quantify, still they play a crucial role in the process of seedling establishment (Harper 1977; Johnstone 1986). Strong disturbances, such as addition of large amounts of nutrients, probably enhance invasions (Hobbs and Huenneke 1992) as indicated by the heavily manured plot, the only one in the wet meadow experiment in which a population of *Impatiens glandulifera* was established. Nevertheless, the absence of clearcut results stresses the necessity to assess each particular invasion as a context-specific process (Lepart and Debussche 1991; D'Antonio 1993). The available experimental studies indicate that the effect of disturbance on the outcome of invasion depends on the invading species, invaded community, and the type of disturbance involved (Hobbs and Huenneke 1992; Knapp 1992).

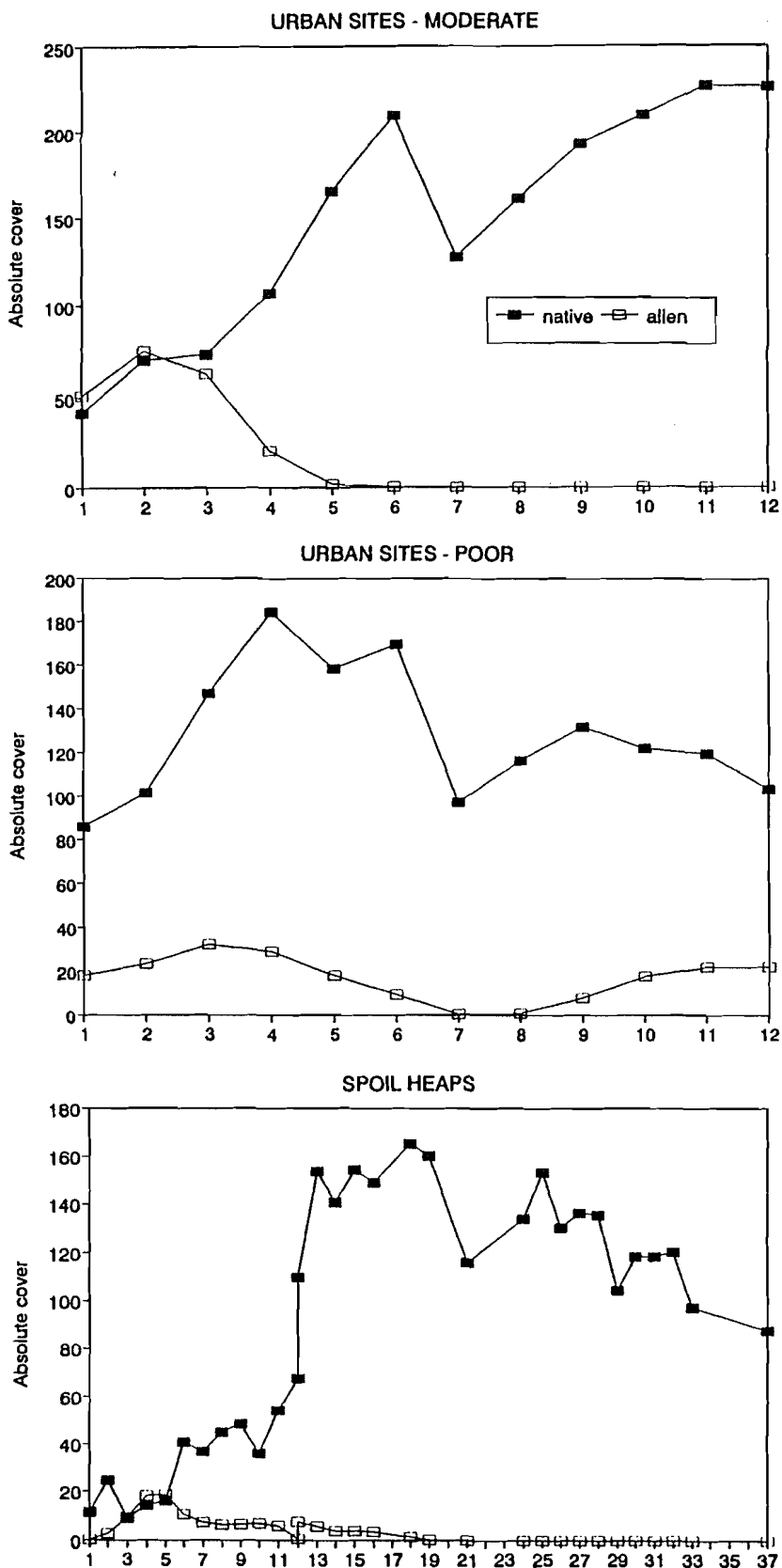
The present study also documents that successful seedling establishment, a crucial step in the process of invasion, by far does not mean the start of successful invasion. In older successional stages and under a closed canopy, the further elimination of seedlings is probable due to competition for resources with established vegetation (Crawley 1989). Similarly, in the closed meadow sward the dense cover of resident species prevented the growth of seedlings following establishment and no seedling survived except in two experimental plots.

Field experiments in which seeds are introduced into relatively intact vegetation clearly indicates that for successful establishment of colonizers a large quantity of seeds must be introduced (Bazzaz 1986). For example, experimental introduction of seeds of *Melaleuca quinquenervia* and *Schinus terebinthifolius* (at least of 2 million of the former and 20,000 of the latter) both major invaders in Florida, into an array of communities representing various successional stages, degrees of disturbance, hydroperiods, fire regimes, and soil types yielded establishment rates between 0.01 and 2.62 percent (Myers 1983; Ewel 1986). Similarly in both species, introduced seeds yielded more seedlings in disturbed communities than in mature ones, and in all cases the number of surviving seedlings in mature communities was lower than that in man-made (Myers 1983; Ewel 1986). However, in many communities seed introductions were complete failures and yielded no surviving seedlings (Ewel 1986). Despite careful design of these experiments in order to exclude the possibility that timing of the seed-introduction experiments did not coincide with the chance juxtaposition of conditions required to ensure both germination and seedling establishment, the establishment rates obtained were still very low and confirm that repeated



a.

Fig. 2. Participation of alien species in successional series of man-made habitats: urban sites – nutrient poor; urban sites – moderate in nutrients; and spoil heaps from coal mining. All the series were located in the western part of the Czech Republic, and are described in details in Prach *et al.*(1993), Prach and Pyšek (1994a,b). Only the series with significant representation of alien species are →



b.

shown. (a) relative cover, (b) absolute cover. Alien species were also present in reclaimed plots in the areas deforested due to air pollution, in nutrient rich urban sites, wet spoil heaps and xeric abandoned fields. However, in these habitats, their cover did not exceed 5%. Aliens were absent from the rest of the sites (sand pit, peat bog, emergent bottom, mesic and wet abandoned fields).

introductions of a large number of disseminules may be necessary for initial establishment of colonizers (Martins and Jain 1979).

The barriers alien species have to cope with during particular phases of invasion are reflected in representation of aliens in a wide array of successional seres in man-made habitats of central Europe. Among the 15 seres analysed (Prach *et al.* 1993; Prach and Pyšek 1994a,b), the alien species only play an important part in urban areas (Fig. 2), i.e. in sites with sufficiently high and permanent input of diaspores (Kowarik 1995), and partly in spoil heaps from coal mining. The presence of aliens in drier and nutrient poor sites such as spoil heaps may be from reduced competitive ability of native species in these less favourable habitats.

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