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# URBAN ECOLOGY

## PLANTS AND PLANT COMMUNITIES IN URBAN ENVIRONMENTS

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# SOME RESPONSES OF FLORA AND VEGETATION TO URBANIZATION IN CENTRAL EUROPE

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## Abstract

The urban flora and vegetation respond sensitively to man-made disturbance. In the historical dimension we analyse the spread and decline of native and alien species, changes in relative abundance, and the establishment of aliens in vegetation types. In the spatial dimension floristical changes on a city-country gradient and within city zones are examined. Finally, we document the ecological dimension by examining trends in species richness, relative abundance and the confinement of species to distinct levels of impact. These results reveal both general responses and striking differences between species differing in time of immigration (native vs. alien species, archeophytes vs. neophytes) in their reaction to urbanization.

## 1. Introduction

For most parts of the central European landscape, human impact has been recognized as the most important influence on the composition of the flora and vegetation during the last 5000 years. The effects of man's activities can be analysed nowhere better than in large cities and their surroundings. Here the change from virtually uninfluenced natural sites to strongly altered man-made sites is often gradual, with many differently influenced vegetation types. Alterations of the urban biosphere have been studied on many levels, including energy flows, nutrient cycles, water and material budgets (*e.g.* Duvigneaud and Denayer-De Smet, 1977), the characteristics of urban climate (*e.g.* Kratzer, 1956), soils (*e.g.* Alaily *et al.*, 1986), and wildlife adapted to the man-made environment (Klausnitzer, 1987; Sukopp and Werner, 1983; and Sukopp, this volume).

The goal of this paper is to show how increasing human impact disrupts pristine patterns of abundance and distribution of vascular plants, producing new combinations of species and plant communities. The resulting man-made changes in urban flora and vegetation are analysed in the *historical dimension* (spread and decline of species, alterations of vegetation types: section 3) and in the *spatial dimension* (city-country gradient, city-zonation: section 4). Before studying the *ecological dimension* (species' and communities' response to increasing human impact: section 6) some *theoretical concepts* suitable for the assessment of man's impact are discussed (section 5).

## 2. The study area

Berlin (West) offers good opportunities for such investigations because of the extensive background of research in urban ecology during the last 30 years (Scholz,

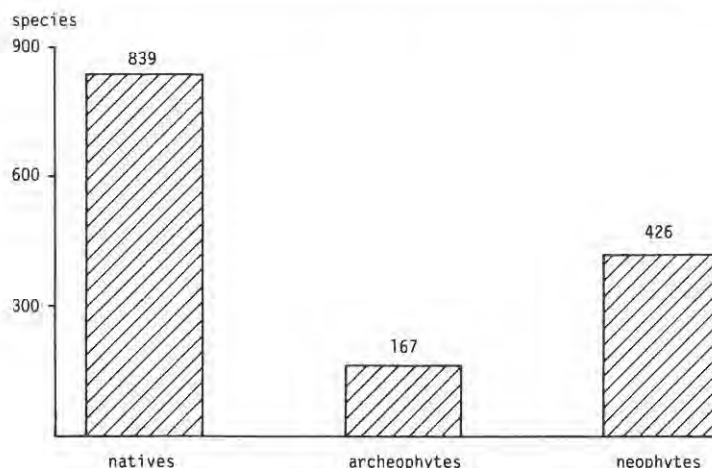


Fig. 1. Composition of the flora of Berlin (West) by native and alien species, the latter divided into archeophytes and neophytes (according to Auhagen and Sukopp, 1982, number of neophytes changed by Kowarik, 1988).

1987) and a whole range of sites varying from natural to man-made. The natural site conditions are sandy and loamy soils from the last ice age, a mean annual temperature of 8.7°C, and annual precipitations of about 600 mm. On sandy soils the natural or semi-natural vegetation is dominated by oaks and pine (*Quercion robur-petraeae*), on loamy soils by hornbeam, oaks, and lime (*Carpinion betuli*), and only on special sites by beech (*Querco-Fagetum*). On wet sites, there are alder-dominated forests and mires (Sukopp *et al.*, 1980). The conurbation of Berlin developed in the 19th century when the number of inhabitants increased from 147,000 in 1786 to 1,579,000 in 1890. Today there are about 3 million people in Berlin including ca 2 million in the western sectors on 480 km<sup>2</sup>.

22% of Berlin (West) is covered by less disturbed forests, fens, bogs, and water communities. But the majority of Berlin's vegetation results from different types of land use. Agricultural communities, covering 7% of the total area, are a reminder of the pastoral landscape of the early 19th century. The greatest part of the green city is covered by typical urban or industrial vegetation, surprisingly dependent on direct human impact and on far-reaching man-made changes of abiotic factors (establishment of an 'urban heat island', alkalization and eutrophication of soils, changes in water regime, see reviews in Sukopp *et al.*, 1980; Alaily *et al.*, 1986).

### 3. The historical dimension: spread and decline of species

Historical reviews of man-made changes in Central Europe have shown that human activities resulted first in an increased diversity in flora and vegetation culminating in the cultural landscape of the late 18th century. A decline followed, beginning with industrialization in the middle of the last century and accelerating with the industri-

alization of agriculture since 1950 (e.g. Ellenberg, 1963; Sukopp, 1972, 1976; Haeupler, 1976; Jäger, 1977; Fukarek, 1988). There is some evidence that these changes are quicker in urban-industrial areas, indicating similar future tendencies in rural areas not yet affected by urbanization. Taking Berlin as an example, changes concerning the spread and decline of native and alien species are analysed (section 3.1) as well as alterations of resident vegetation types and the establishment of new ones by the invasion of aliens (section 3.2).

### 3.1 Native and alien species in the flora

Dividing Berlin's present-day flora according to the time of species' introduction reveals the huge impact of man (Fig. 1): 839 native species, as opposed to 593 aliens whose invasion was enabled directly or indirectly by human activities. Mainly due to the introduction of agriculture and stock-farming 167 archeophytes<sup>1</sup> reached the area of Berlin up to 1500 A.D. The discovery of America and the following commercial activities improved the conditions for the spreading of aliens (Jäger, 1977). A wave of 426 neophytes (aliens invading after 1500 A.D.)<sup>1</sup> swamped the resident vegetation (see table 1 in section 3.2). This invasion did not take place continuously but was encouraged by industrialization in the last century, as Fig. 2 shows with a coincidence between population development and the number of two groups of aliens (naturalized neophytic ruderal plants excl. trees and shrubs according to Scholz, 1960, and alien trees and shrubs according to Kowarik, 1985).

The human impact not only changed the composition of the urban flora but obviously disrupted species' abundance patterns. Fig. 3 shows dramatic changes of the proportion of abundance classes comparing the spectra for 1864 (Kutschkau, 1982 after Ascherson, 1864) and 1987 (Kowarik, 1988). A high percentage of those species which had been frequent in the last century became more or less rare (abundance classes 1,2). 640 native species, 113 archeophytes, but only 68 neophytes are affected by decline during the last hundred years (Kutschkau, 1982). According to Berlin's 'Red Data Book' (Sukopp *et al.*, 1982) 58% of the native species, 37% of the archeophytes, but only 12% of the neophytes are endangered (Fig. 4). This endangerment must be attributed mainly to human changes to site conditions. The most important ones are: construction of buildings and roads, sealing of soils, drainage activities, eutrophication of soils, and the loss of ecotones (Sukopp and Auhagen, 1982).

On the other hand 237 neophytes are more frequent today than in 1864. Among the most successful are *Acer negundo*, *Ailanthus altissima*, *Bidens frondosa*, *Clematis vitalba*, *Matricaria discoidea*, *Parietaria pensylvanica*, *Prunus serotina*, *Robinia pseudacacia*, *Rumex thyrsoflorus*, *Sisymbrium loeselii*, and *Solidago canadensis*. Only 28 archeophytes (e.g. *Crepis capillaris* and *Plantago major*, gained by the establishment of lawns) and 97 native species (e.g. *Acer platanoides*, *A. pseudoplatanus*, *Agrostis stolonifera* agg., *Artemisia vulgaris*, *Festuca trachyphylla*) increased their abundance during the last hundred years. Similar results from other cities, e.g. Halle and Warsaw (Klotz, 1984; Sudnik-Wojcikowska, 1986, 1987), support the

<sup>1</sup> Without regard to the species meanwhile extinguished.

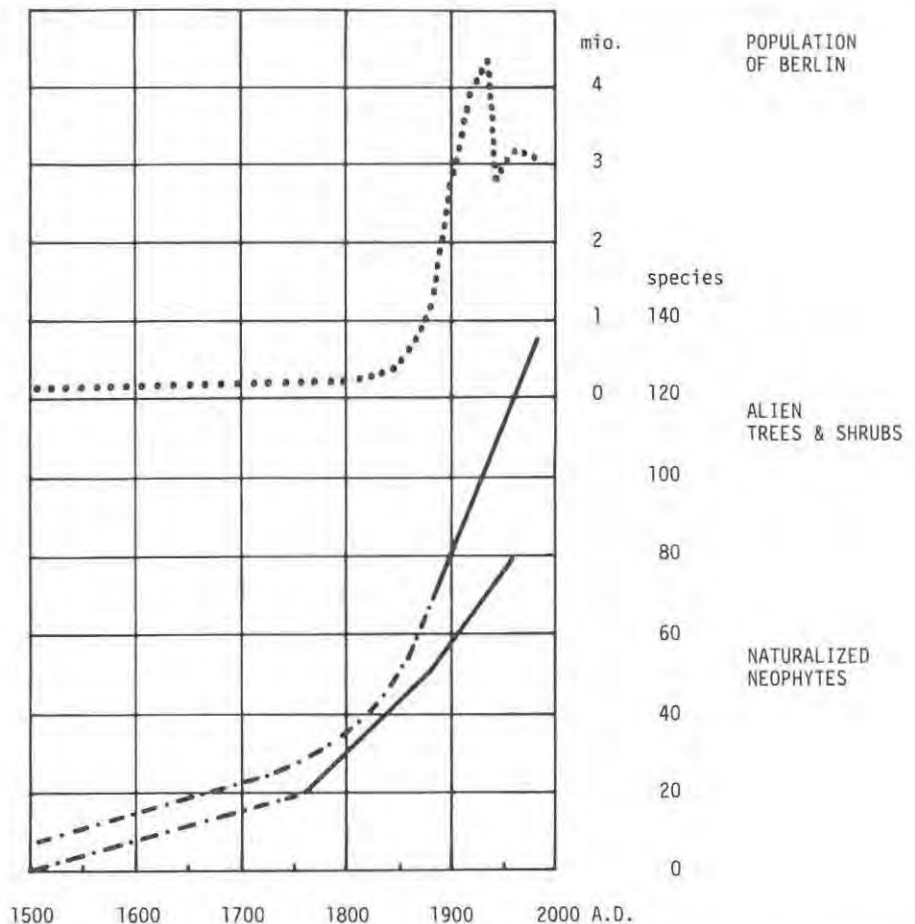


Fig. 2. Coincidence between the population growth and the number of two groups of alien species (naturalized neophytic ruderal plants excl. trees and shrubs according to Scholz, 1960, and alien trees and shrubs according to Kowarik, 1985).

generalisation that mainly native species suffer from the urban environment, whereas neophytes seem to be better adapted to severely changed conditions. The differences between the response of these groups to increasing human impact are analysed in section 5.3

### 3.2 Native and alien species in the resident vegetation

The introduction of aliens, their spontaneous spread, and, of course, the factors favouring this process have greatly affected the resident vegetation. Native plant communities were partly changed by the invasion of archeophytes and later on of neophytes, and new communities established themselves on man-made sites. In table 1 Berlin's vegetation is grouped into 52 phytosociological alliances (after Sukopp, 1979 according to the Braun-Blanquet approach). Data about the mean

Table 1. Native species and aliens (divided into archeophytes and neophytes) in Berlin's vegetation (mean percentage in vegetation relevés of phytosociological alliances; n: number of vegetation relevés, n<sub>s</sub>: mean number of species).

vegetation types (phytosociological alliances)	n	n <sub>s</sub>	natives (%)	aliens (%)	
				archeo- phytes	neo- phytes
<b>segetal and ruderal vegetation</b>					
1 Aphanion	96	17.1	40.2	53.9	5.9
2 Panico-Setarion	111	10.9	40.8	42.6	16.6
3 Sisymbrium	271	13.5	41.1	27.2	31.8
4 Fumario-Euphorbion	178	15.0	44.1	29.0	26.9
5 Spargulo-Oxalidion	23	16.0	45.4	37.2	17.4
6 Arnoseridion	15	14.6	45.4	47.4	7.1
7 Dauco-Melilotion	79	18.3	55.6	19.6	24.8
8 Polygonion avicularis	316	9.8	59.7	29.3	11.1
9 Arction	223	13.7	62.4	16.1	21.4
10 Robinia pseudacacia-stands	46	15.1	67.4	4.8	27.8
11 Convolvulo-Agropyron	235	11.0	67.7	14.5	17.7
<b>dry grassland and meadow vegetation</b>					
12 Alysso-Sedion	92	10.1	61.9	26.7	11.4
13 Arrhenatherion elatioris*	345	19.6	74.8	15.0	10.2
14 Armerion elongatae	178	16.5	75.0	8.9	16.1
15 Koelerion glaucae	9	14.8	78.1	6.9	15.0
16 Corynephorion canescentis	53	7.5	84.9	1.6	13.4
17 Molinion	27	24.2	96.3	1.7	2.1
18 Calthion	120	22.4	96.5	2.0	1.6
19 Filipendulion	36	18.1	97.8	0.4	1.8
<b>shrub and forest vegetation**</b>					
20 Geo-Alliarion	90	12.0	72.9	12.9	14.2
21 Rubo-Salicion	27	10.4	73.4	6.2	20.4
22 Crataego-Prunion	50	10.2	75.6	9.4	15.0
23 Aegopodion podagrariae	66	11.4	80.8	7.4	11.9
24 Epilobion angustifolii	7	11.3	81.6	8.0	10.4
25 Fagion sylvatici	81	12.0	81.9	0.4	17.7
26 Salicion albae	27	13.1	84.4	4.7	10.9
27 Alno-Padion	52	14.3	86.3	1.9	11.8
28 Carpinion betuli	103	15.7	87.4	0.8	11.8
29 Frangulo-Salicion	12	17.4	88.0	1.9	10.2
30 Vaccinio-Piceion	38	10.2	89.1	0.3	10.7
31 Trifolion medii	14	18.5	89.2	4.2	6.7
32 Quercion robori-petraeae	261	13.9	91.1	0.6	7.9
33 Alnion glutinosae	71	15.8	93.5	2.3	3.9
<b>wetland and water vegetation</b>					
34 Chenopodion rubri	14	12.9	61.5	21.8	16.8
35 Convolvulion sepium	58	12.8	78.0	8.4	13.5
36 Bidention	47	13.1	78.5	12.3	9.1
37 Agropyro-Rumicion	127	12.0	84.3	12.2	3.5
38 Nanocyperion	20	11.0	89.1	10.2	0.4
39 Oenanthion aquaticae	34	9.1	91.6	5.6	2.9
40 Phragmition	187	9.8	94.5	1.0	4.6
41 Magnocaricion elatae	94	11.8	95.4	1.4	3.1
42 Potamogetonion	20	3.3	96.6	0.0	3.4
43 Sphagnion magellanici	21	9.1	97.8	0.0	2.2
44 Glycerion fluitantis	27	6.0	98.0	0.5	1.5
45 Hydrocharition	18	4.9	98.2	0.0	1.9
46 Nymphaeion	28	4.4	98.6	0.0	1.4
47 Lemnion minoris	37	1.8	98.7	0.0	1.4
48 Caricion canescenti-fuscae	27	10.3	99.0	0.0	1.0
49 Littorellion	5	3.8	100.0	0.0	0.0
50 Sphagno-Utricularion	6	3.7	100.0	0.0	0.0
51 Rhynchosporion albae	2	7.8	100.0	0.0	0.0
52 Eriophorion gracilis	35	8.5	100.0	0.0	0.0

\* incl. lawns, \*\* incl. skirt vegetation.

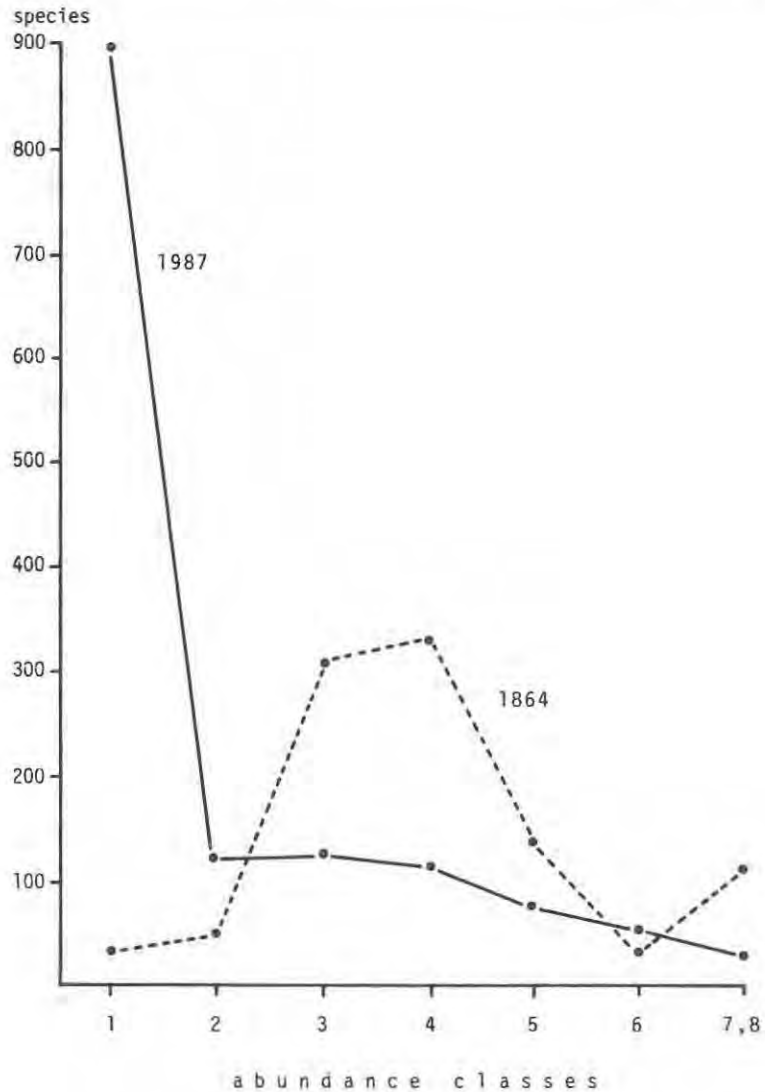


Fig. 3. Comparison between the abundance patterns of the flora of Berlin (West) in 1864 (Ascherson, 1864 according to Kutschkau, 1982) and 1987 (according to Kowarik, 1988; abundance class 1: very rare species, abundance class 8: very frequent species).

percentage of native and alien species (the latter divided into archeophytes and neophytes) in vegetation relevés can be used to indicate how community structure has been modified. Such an analysis illustrates the important role of aliens in urban vegetation (Kowarik, 1988): in 21 alliances their mean percentage exceeds 20% including 13 alliances with more than 30% aliens. Only 4 alliances of wetland



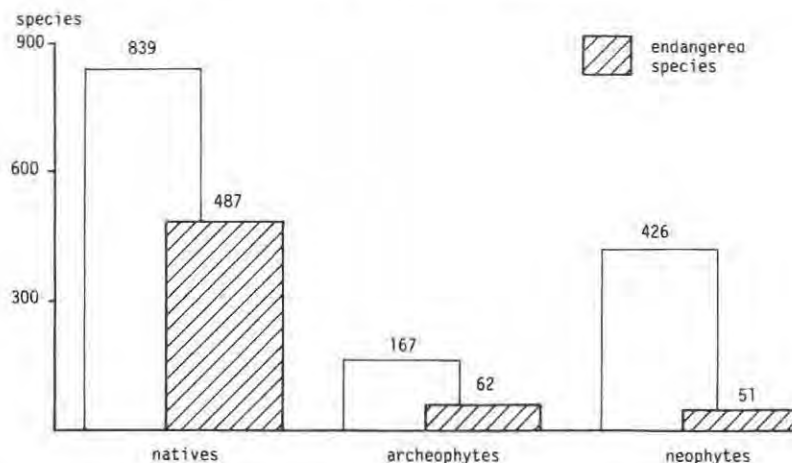


Fig. 4. Endangerment of the flora of Berlin (West): striking differences in natives, archeophytes and neophytes (same sources as in fig. 1).

vegetation are absolutely free of non-native species, and an additional 5 are almost unaffected.

At first sight, these results appear to conform to the idea that disturbance facilitates the establishment of aliens, stressed for example by Elton (1958), Sukopp (1962), Harper (1965), Bazzaz (1983), and Crawley (1987). The vegetation of intensively disturbed urban-industrial or rural sites is dominated by aliens. Archeophytes, formerly introduced with agriculture, still play an important role in the vegetation of fields cultivated in the outskirts of Berlin (e.g. *Aphanion*: 53.9%, *Arnosseridion*: 47.4% archeophytes). In this vegetation the percentage of neophytes (6–7%) is as low as in pine-oak-forests (*Quercion robori-petraeae*: 7.9% neophytes). On urban sites, in contrast, neophytes are more frequent than archeophytes (e.g. *Sisymbrium*: 31.8% neophytes). There is much evidence that the percentage of native species increases with succession, e.g. from annual pioneer vegetation (*Sisymbrium*: 41.1%) to biennial (*Dauco-Melilotion*: 55.6%) and perennial vegetation of tall herbs (*Arction*: 62.4%) or of ruderal grassland (*Convolvulo-Agrophyron*: 67.4%). *Robinia pseudacacia* stands represent the most common and well developed vegetation type on calcareous ruderal soils of bombed inner city sites. The fact that still 33.6% of the species growing in these pre-forests are aliens, underlines the potential success of introduced species on man-made sites.

Wet meadows (e.g. *Calthion*: 3.6% aliens) are significantly poorer in aliens than dryer meadows and lawns (e.g. *Arrhenatherion*: 25.2% aliens). In the sparse pioneer vegetation of dry sandy soils (*Alyssum-Sedum*) aliens reach a percentage of 38.1%. This obviously limiting effect of moisture (often coinciding with a higher presence of bare gaps) can be related to the origin of aliens, which are often native in warmer regions (Scholz, 1960). These species preadapted to drier sites are excluded in wetlands by competition from native species; mires are virtually free of aliens. The susceptibility of wetland vegetation to the invasion of aliens is higher, however, if the sites are affected by natural disturbances ('natural dynamic' in the sense of Westhoff,

1971; Trepl, 1983). Ecologically 'open' sites resulting from flooding in river valleys, for example, facilitate the penetration of aliens into the alliances *Chenopodion rubri* (38.5% aliens), *Bidenton*, and *Convolvulion sepium* (both about 22% aliens).

This effect can be seen even by comparing forest data: *Salicion albae* (15.6%) and *Alno-Padion* (13.7%), both accompanying river borders, are richer in aliens than *Quercion robori-petraeae* (8.5%). But the fact that still 18.1% of the species growing in beech forests (*Quercio-Fagetum*) are aliens cannot be related exclusively to natural disturbance. In Berlin, beeches are recorded in the neighbourhood of historical gardens and recreation areas. Here, the propagation conditions for aliens have been better over a longer time than in other parts of Berlin's forests. This explanation, although simple, suggests that the minor presence of aliens in forests cannot be ascribed solely to the resistance of natural vegetation against invasions as commonly assumed. Additional historical studies of spreading processes are often necessary to understand the present distribution patterns (see e.g. Schroeder, 1972 and Trepl, 1984 stressing the important role of historical events for the spread of *Amelanchier* species and *Impatiens parviflora* in Central Europe): 'whether or not a community can be invaded also depends on our temporal frame of reference' (Oriens, 1986: 142f).

#### 4. The spatial dimension: city-country gradient and city zonation

Comparisons between cities and their surroundings have shown that very often settlements are not poorer but richer in species than more or less undisturbed landscapes of the same size. A grid-mapping of southern Lower Saxony (Haeupler, 1974), for example, showed an increase from 350 species in  $5 \times 5 \text{ km}^2$  grids entirely covered by forests to 400–600 species in grids including larger cities. Pysek and Pysek (this volume) found a higher diversity of flora and vegetation in towns compared to villages. There is some evidence that the species richness of settlements as well as the presence of aliens coincides with the amount of human population (see also fig. 2), already demonstrated by Linkola (1916), who compared the flora of Finnish farms, villages, and towns. Data from Polish settlements (Falinski, 1971) are given in table 2.

Within the city area minimal species number has been found in the inner city. In Warsaw, for example, the mean number of species in  $1.5 \times 1.5 \text{ km}^2$  grids decreases from the outskirts with 305 species to 178 species in the inner city (Sudnik-Wojcikowska, 1987). In Berlin (West) the most species are found in the transition zone between the densely built up inner city and the suburbs (zone 2 in table 3, Kunick, 1974, 1982). The presence of native and alien species in city zones of Berlin (West) as opposed to data from local floras of the surrounding Brandenburg districts (table 3) illustrates the actual city-country gradient. The lowest percentage of aliens is found in the Spreewald district (20.7%), which is dominated by wet forests, whereas the flora of the more industrialized Spremberg district already includes 25.2% aliens (Klemm, 1975). From the outer fringe of Berlin (zone 4) to the centre (zone 1) their percentage increases from 28.5 to 49.8% (Kunick, 1982). This city-country gradient can be attributed to two reasons, not mutually exclusive:

- (1) Settlements including harbours, railway stations, parks, and gardens are

Table 2. Proportion of native and alien species in varying types of settlements in Poland (from Falinski, 1971).

type of settlement	natives	aliens
forest settlements	70–80%	20–30%
villages	70%	30%
small towns	60–65%	35–40%
medium towns	50–60%	40–50%
cities	30–50%	50–70%

distribution centres of intentionally or unintentionally introduced aliens (mainly neophytes). It only depends on the duration of spreading processes for isolated sites to be invaded by aliens. Although, the asiatic *Impatiens parviflora* cultivated in botanic gardens needed about 50 years for the transition from urban garden sites to undisturbed forests, today it is the most common widespread alien in forests of Central Europe (Trepl, 1984). Conversely, it can be difficult for autochorous native species (such as *Primula elatior*, see fig. 5) to bridge man-made barriers such as housing areas and invade open sites in the inner city. Here, plants dispersed by wind have an advantage in reaching isolated sites.

(2) The higher proportion of aliens in the inner city can be explained as preadaptation to man-made changes of abiotic factors. The fact that some thermophilous neophytes like the mediterranean *Chenopodium botrys* or the chinese *Ailanthus altissima* are mainly confined to the inner city of Berlin (Sukopp, 1971; Kowarik and Böcker, 1984, see fig. 6 in Sachse *et al.*, this volume) can be related to the urban 'heat island' and the existence of ruderal calcareous soils. Further expansion of these species to the outskirts seems to be checked by their requirements of higher temperatures. Göttsche and Wittig (1983) showed that urban floras are characterized by an obviously higher proportion of thermophilous species. Even in little villages and towns changes

Table 3. Percentage of native and alien species (archeophytes, neophytes) in city zones of Berlin (West) and in the floras of surrounding rural districts of Brandenburg. Sources for 1: Auhagen and Sukopp (1982, number of neophytes changed by Kowarik, 1988); 2–5: Kunick (1974, 1982); 6–10: Klemm (1975).

	area (km <sup>2</sup> )	species (n)	percentage of		
			natives	archeophytes	neophytes
1 Berlin (West)	480	1432	58.6	11.7	29.7
City zones Berlin					
2 zone 1 (inner city)		380/km <sup>2</sup>	50.2	15.2	34.6
3 zone 2		424/km <sup>2</sup>	53.1	14.1	32.8
4 zone 3		415/km <sup>2</sup>	56.6	14.5	28.9
5 zone 4 (outer fringe)		357/km <sup>2</sup>	71.5	10.2	18.3
Brandenburg districts					
6 Spremberg	370	982	74.8	8.1	17.1
7 Ruppiner Land	1740	1092	75.7	8.9	15.4
8 Priegnitz	3350	1114	77.5	9.1	13.4
9 Dahme	120	771	78.4	10.6	11.0
10 Spreewald	180	745	79.3	10.4	10.3

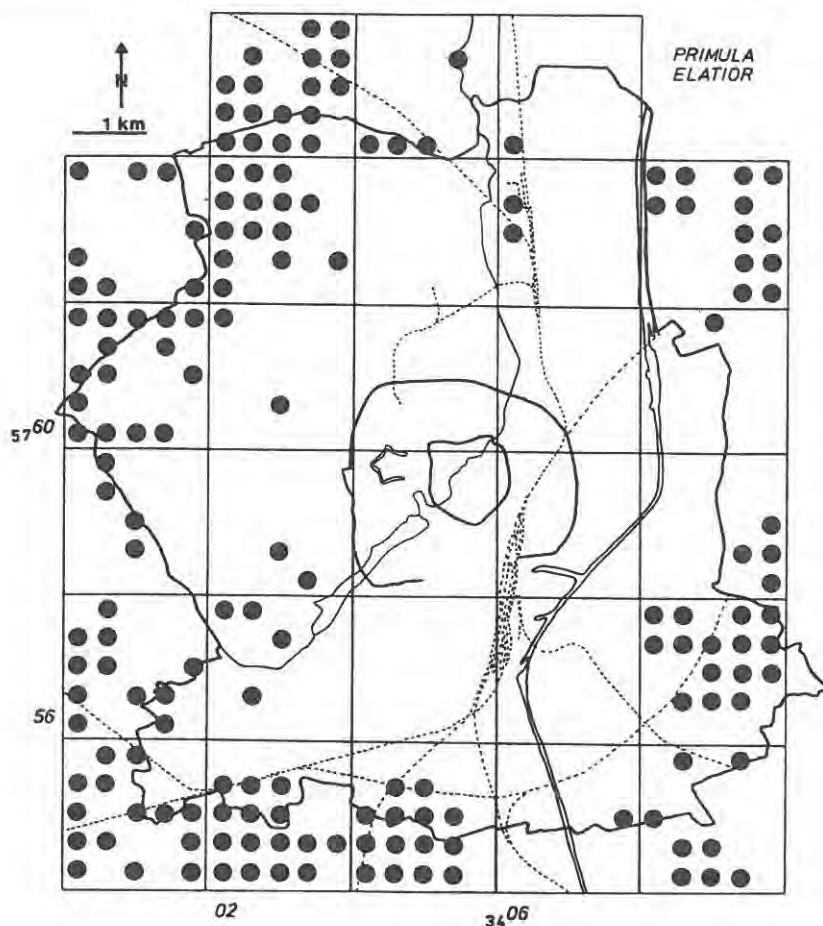


Fig. 5. Distribution pattern of *Primula elatior* as a native species confined to the outskirts of Münster (from Wittig *et al.*, 1985).

in climate and soils promote the occurrence of species with higher requirements for temperature or nutrients (Saarisalo-Taubert, 1963). In several central European cities, *Hordeum murinum* is approved as a good indicator for urban conditions (fig. 6, see also maps in Sudnik-Wojcikowska, 1986; Kunick, 1987). The urban distribution patterns of particular species cannot be generalized, however, because in warmer regions their temperature requirements are also fulfilled in the countryside. The confinement of *Ailanthus altissima* to urban-industrial sites, for example, increases from the Mediterranean to the colder continental and northern parts of Central Europe (Kowarik, 1983; Gutte *et al.*, 1987).

Information about the ranges of species more or less confined to different parts of the city can be transformed into zonation maps. In Berlin (West) Kunick (1974, 1982) differentiated four zones of similar floristic composition (see table 3) corresponding to the zonal character of cities which had been stressed in models by

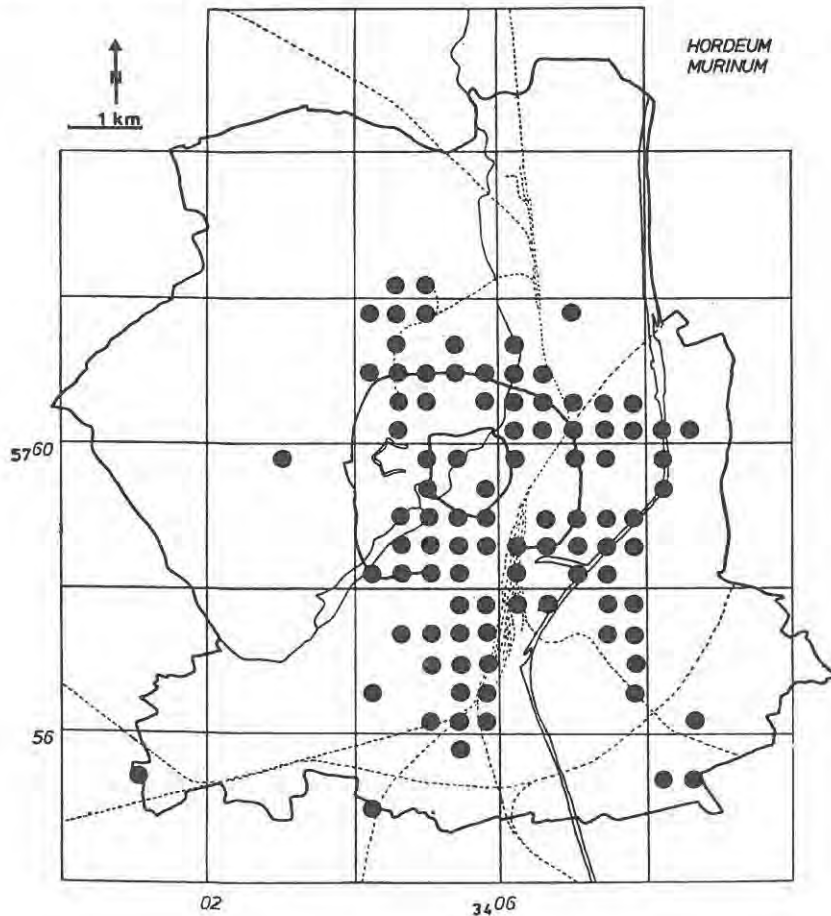


Fig. 6. Distribution pattern of *Hordeum murinum* as an alien species confined to the inner city of Münster (from Wittig *et al.*, 1985).

Sukopp (1973, fig. 7), Klotz *et al.* (1984), and Wittig *et al.* (1985). Although such spatial differentiation results from human impact, generally increasing from the outskirts to the inner city, further investigations are necessary to understand species' responses to human impact as an ecological factor. Because of the heterogeneous structure of each city zone which usually includes extrazonal elements (*e.g.* parks with forest species in the inner city, or railway sites with ruderal species in the outskirts) the analysis of spatial distribution patterns should be coupled with ecological site-orientated studies (section 6).

##### 5. Theoretical concepts for the assessment of man's impact

There is no doubt about the important role of disturbances for abundances and



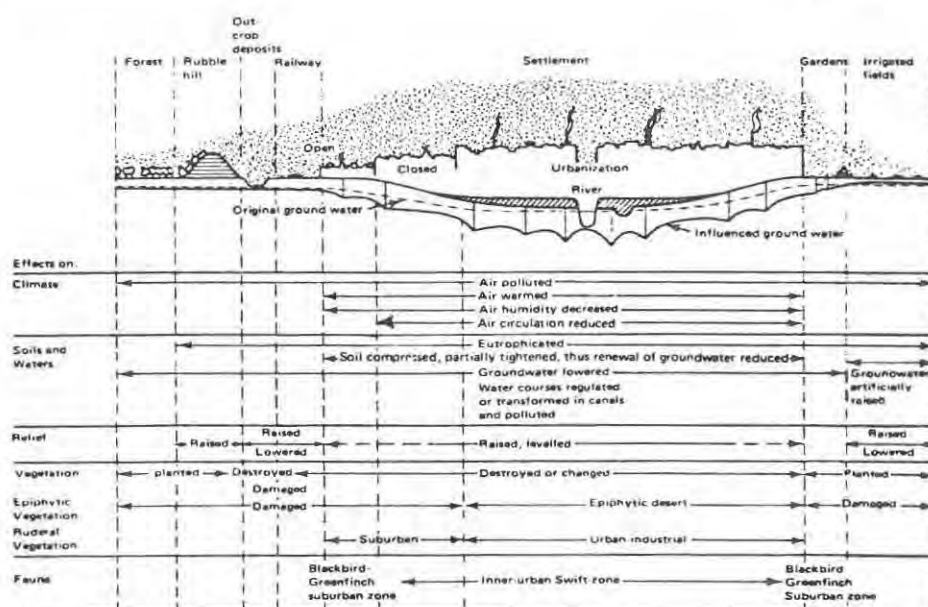


Fig. 7. Idealized cross-section of a large city with varying ecological features (Sukopp, 1973).

distribution patterns of species (e.g. papers in Mooney and Godron, 1983). In addition to general analysis of disturbance effects (e.g. Peet *et al.*, 1983; Trepl, 1983), which does not distinguish between natural and man-made components of disturbance regimes, it is useful to study the distinct human impact on urban flora and vegetation excluding natural disturbances. Although some human disturbances closely mimic natural disturbances (for example, certain silvicultural practices contrast only in detail with some windfall patterns), man-made disturbances are usually of contrasting type, scale, intensity and frequency (Reiners, 1983). Plowing grasslands, distributing exotic biocides, alkalization of formerly acid soils, or construction of buildings and roads, for example, are unique disturbances compared with natural disturbances. Generally they result in urban-industrial areas showing special response patterns of species. Before studying some of these effects (section 6), theoretical concepts which might be applied to the assessment of man's impact should be discussed.

There is a long tradition in Central Europe and Fenno-Scandinavia of classifying species according to different aspects of human impact (e.g. time and mode of introduction, degree of naturalization), as in the early 'Adventivfloristik', closely connected with the work of Thellung (e.g. 1905, 1918/19) and Linkola (1916/21; see also Trepl, this volume, and reviews in Ziska, 1985; Sudnik-Wojcikowska and Kozniowska, 1988). Less well known is the first attempt of Bernatsky (1904), who classified not species but vegetation types according to different degrees of human impact. Later, some well-established concepts dealing with the same subject were promulgated by Westhoff (1949, 1951), v. Hornstein (1950, 1954), Jalas (1955),

Tüxen ('Ersatzgesellschaftskonzept', see 1956), Ellenberg (1963), Falinski (1967, 1987), Sukopp (1972), Long (1974) and others.

Some of these concepts have been judged to be more or less synonymous (e.g. van der Maarel, 1975; Dierschke, 1984) although a comparison (Kowarik, 1988) reveals elementary differences concerning (a) the definition of the undisturbed 'natural' state, (b) the applicability to species, plant communities, or vegetation complexes, and (c) the ordering system including elements from ordination and classification, respectively. However, other concepts differ only in terminology, scale, or whether they are defined in functional terms. Concepts allowing an assessment of man's impact on vegetation, sites, or complexes of vegetation can be divided into two groups:

(1) The concepts of Westhoff, v. Hornstein and Ellenberg relate man-made changes to a former state of nature not yet affected by human activities ('nature I'). On an ordination scale man's impact is evaluated by the distance between the present and the pristine vegetation ('ursprüngliche Vegetation' in the sense of Tüxen, 1956). Because of this time-orientated comparison these concepts can be summarized as historically orientated concepts, which can be applied to plant communities, vegetation and ecosystem complexes. Falinski's synanthropization-concept is closely related to this group. It is related to the pristine vegetation, too, but it classifies vegetation complexes according to the presence of aliens, and in some cases this method excludes an ordination according to the human impact. Similarly to Falinski, Godron and Forman (1983) characterize types of landscapes differing in the level of human modification by changes in the origin, size, shape, number and configuration of patches.

(2) In contrast to the above mentioned concepts, Tüxen's 'Ersatzgesellschaftskonzept' (e.g. applied by Miyawaki and Fujiwara, 1975), Jalas' 'hemeroby' system (enlarged by Sukopp, 1972, 1976; Kowarik, 1988), and Long's 'artificialisation' concept do not evaluate the human impact by 'measuring' the distance to the pristine vegetation. They assess the present level of human impact by reference to a future state of self-regulation ('nature II'). In concepts related to Tüxen's 'Ersatzgesellschaftskonzept' this state is represented by the potential natural vegetation in the sense of Tüxen (1956), in the hemeroby concept by the final stage of a succession (according to a proposition of Kowarik, 1988).<sup>1</sup> Nature II can also establish on irreversibly changed sites, admitting those components of human impact which are stable (in a biological time frame).

On severely changed sites, e.g. on derelict railway territories, succession can lead to stages without connections to the pristine vegetation. For this reason, concepts referring to the pristine vegetation are unsuitable to assess how human impact decreases with succession, even on irreversibly changed sites. In these cases, which are not exceptional for urban-industrial areas, it is advantageous to use concepts referring to 'nature II', because they allow a differentiated assessment of natural development even on severely changed sites. For this reason, the hemeroby system is used in the following sections in order to analyse some aspects of the response of urban flora and vegetation to human impact. On sites not affected by severe human impact the use of concepts referring to nature I or II leads to similar results.

<sup>1</sup> The differences between both reference points are discussed in another paper (Kowarik, 1987).

### 5.1 The hemeroby system as a basic concept

In Central Europe the hemeroby concept (firstly promulgated by Jalas, 1953, 1955, and enlarged by Sukopp, 1972, 1976 and Kowarik, 1988) has become a well established concept, used in vegetation science as well as in landscape planning (e.g. Bornkamm, 1980). Hemeroby is an integral expression for the sum of those effects of past and present human activities on the current site conditions or vegetation, which prevent the development to a final stage (Kowarik, 1988). Of course the use of this holistic concept cannot replace the analysis of single factors, but it can provide some general insight into the response of species, plant communities or sites to the total human impact as an ecological factor. It should be stressed that the different degrees of hemeroby reflect the influence of man-made, not natural, disturbances. Table 4 shows the hemeroby scale, including examples of vegetation and site types. The human impact increases from H0 to H9.

## 6. The ecological dimension: species' and communities' response to different levels of human impact

### 6.1 Material and methods

As a basis for the study of response patterns of species and communities to man's

Table 4. Hemeroby scale (Jalas, 1955, enlarged by Sukopp, 1972, 1976; Kowarik, 1988) with examples of vegetation and site types.

degree of hemeroby	types of sites / vegetation
H0    ahemerobic	almost not existing in Central Europe (only in parts of high mountains)
H1    oligohemerobic	virtually uninfluenced primary forests, growing flat or raised bogs, vegetation of rocks and sea-shores
H2    oligo- to mesohemerobic	extensively drained wetlands, forests with minor wood withdrawal, some wet meadows
H3    mesohemerobic	more intensively managed forests, developed undisturbed secondary forests on man-made sites, dry grassland, traditionally managed meadows
H4    meso- to $\beta$ -euhemerobic	monocultural forests, disturbed secondary forests, skirt vegetation, less ruderalized dry grassland
H5 $\beta$ -euhemerobic	young planted forests, intensively managed meadows and pastures, ruderal vegetation of tall herbs, strongly ruderalized dry grassland on man-made sites
H6 $\beta$ -eu- to $\alpha$ -euhemerobic	traditionally managed field vegetation, trampled lawns, ruderal rough meadows
H7 $\alpha$ -euhemerobic	intensively managed segetal and garden vegetation
H8 $\alpha$ -eu-hemerobic to polyhemeric	segetal vegetation affected by strong herbicide impact (e.g. maize fields), ruderal pioneer vegetation, annual trampled lawns
H9    polyhemeric	pioneer vegetation on railway territories, rubbish places, dumps, salted motorways
—    metahemerobic	no vegetation of vascular plants



impact, a dataset was compiled including 5136 vegetation relevés made by different authors following the Braun-Blanquet approach (see Kowarik, 1988). These relevés taken as a whole represent the vegetation of Berlin (West) according to the list of Sukopp (1979).

The first step was to ordinate the relevés on the hemeroby scale given in table 4. The criterion for the assignment of each relevé was an assessment of the intensity of human impact on the site conditions, which was made directly at the site, or derived from descriptions of published vegetation relevés and additional information from experts. (The occurrence of distinct species was not used as indicator for a certain level of human impact.)<sup>1</sup>

Having assigned each of the 5136 vegetation relevés to one of the nine degrees of hemeroby, a computer analysis was run in order to produce hemeroby spectra for each species reflecting its distribution on the hemeroby scale. As an example fig. 8 shows the spectrum for *Euphorbia peplus*, representing the current occurrence of this species typical of gardens in Berlin (West). *Euphorbia peplus* has a range over 7 degrees of hemeroby, but its ecological optimum on this scale lies near degree 7. In contrast, *Prunus serotina*, an alien introduced from northern America which is mainly confined to semi-natural forest, actually has an optimum on extensively influenced sites (near degree 3, fig. 9). Finally, the native *Poa palustris*, formerly confined to wet sites, has been able to invade drier urban sites and is an example of a species without a significant optimum level of human impact (fig. 10).

These spectra showing the response pattern of each species to different levels of human impact were used to analyse the effect of increasing human impact on species richness (section 6.2), on the occurrence of rare and frequent species (section 6.3), on the confinement of species to distinct levels of impact (section 6.4), and on the reaction of vegetation units (section 6.5). As it is a special phenomenon, the spread of native species to man-made sites is analysed as apophytization (section 6.6).

## 6.2 Effects of increasing human impact on species richness

There is much evidence from historical and geographical investigations discussed in section 3 and 4, as well as from general models (e.g. Jacobs, 1975; Grime, 1979; Peet *et al.*, 1983; Trepl, 1983; Crawley, 1986), that vegetation affected by a low degree of disturbance is richer in species than undisturbed vegetation. More intensive impact, however, leads to decreasing species richness, because the pool of species adapted to very high rates of disturbance is small. In order to examine the value of this 'intermediate disturbance hypothesis' (Grime, 1973; Connell, 1979) for urban vegetation affected by varying levels of man-made, not natural, disturbance, the number of species documented in the vegetation relevés, which had been ordinated to the nine levels of hemeroby, was summarized for each degree of hemeroby (fig. 11).

A maximum of species richness is to be found in the mesohemerobic vegetation

<sup>1</sup> This method includes subjective elements because man's impact is assessed and not measured with 'hard' methods. Although some physical effects such as trampling intensity could be measured, the often complex character of human disturbances does not allow a comparable measurement of all effects. (In addition, there is no evidence that the reduction of man's impact to those effects which can be measured is better than a subjective assessment of the sum of all effects.)

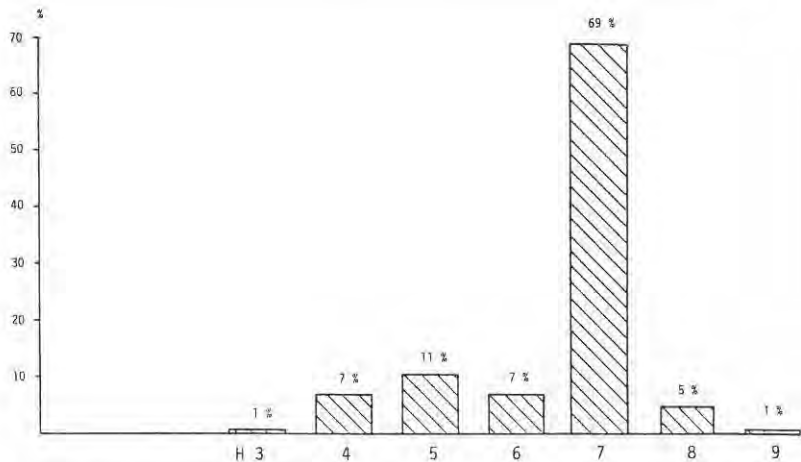


Fig. 8. Hemeroby spectrum of *Euphorbia peplus* as example for a species confined to intensively influenced sites (the human impact increases from H1 to H9; 100% = occurrence in 142 vegetation relevés, mean = 6.6, standard deviation 1.07, hemeroby indicator value = 7).

(hemeroby degree 3, H3), which can be related to a low level of human disturbances; 761 species are growing on these sites instead of 326 in the more or less uninfluenced oligohemerobic vegetation (H1). The pool of species adapted to an extreme level of man-made disturbance is obviously smaller; towards the polyhemerobic vegetation of the most intensively changed sites (H9) the number of species decreases again to 268. In fig. 11, which corresponds well to the general hypothesis, all species are considered *without* regard to their origin.

A differentiation between the patterns of native and alien species reveals distinct

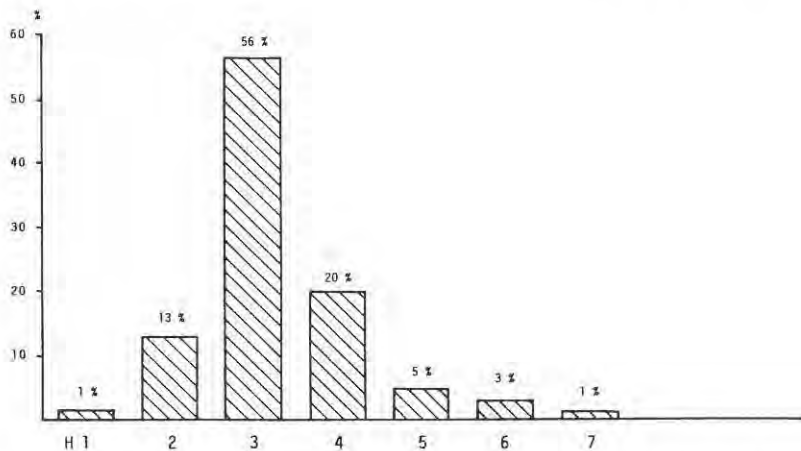


Fig. 9. Hemeroby spectrum of *Prunus serotina* as example for a species confined to weakly influenced sites (the human impact increases from H1 to H9; 100% = occurrence in 436 vegetation relevés, mean = 3.29, standard deviation 0.99, hemeroby indicator value = 3).

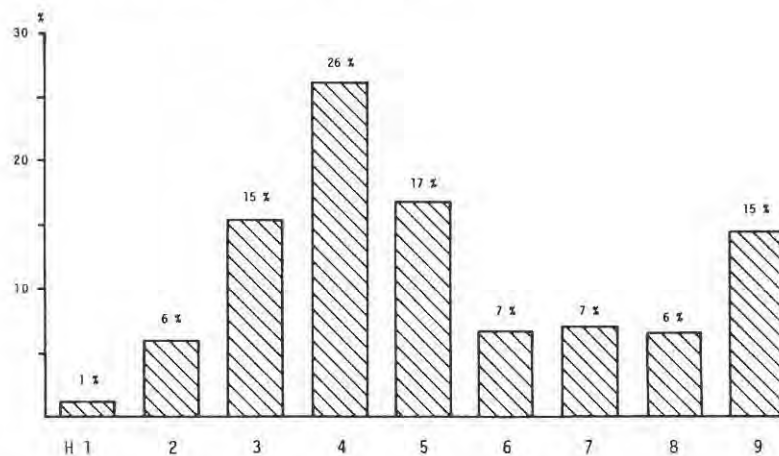


Fig. 10. Hemeroby spectrum of *Poa palustris* as example for a species without confinement to a distinct level of hemeroby (the human impact increases from H1 to H9; 100% = 268 occurrence in 436 vegetation relevés, mean = 5.19, standard deviation 2.20, no set hemeroby indicator value).

differences in the maxima of species richness (fig. 12). Most *native* species are growing in the mesohemerobic vegetation. Their number decreases sharply from 578 to 125 species in the polyhemerobic vegetation. Conversely, *aliens* seem to be encouraged by stronger impact. Their maximal species number is found in  $\alpha$ -euhemerobic vegetation (H7) with 332 species, decreasing again to 143 species in polyhemerobic vegetation. The patterns of archeophytes and neophytes are similar (fig. 13). The proportion between alien and native species is about 1:18 in the oligohemerobic vegetation, changing to 1:3 in the mesohemerobic vegetation. In the strongly influenced  $\alpha$ -euhemerobic and polyhemerobic vegetation there are finally more alien than native species.

Increased species richness on sites affected by more human impact compared with natural sites can be explained as the result of changed competitive relationships among species, e.g. heavy mortality of competitors or an enhancement of the resource base. Thienemann (1920) had already stressed, in his first biocoenotic principle, that an increase in variability of environmental conditions results in a higher number of species. In the mesohemerobic vegetation a high percentage of the species originally from the pristine vegetation can *still* exist, but because of their weakened competitive strength caused by human impact the susceptibility of mesohemerobic vegetation to the invasion of aliens becomes higher, and therefore some aliens can *already* exist. The result of a high number of coexisting native and alien species is maximal species diversity. In contrast, increased human impact finally leads to a decrease in species diversity. Fig. 12, 13 show that increasing human impact improves the conditions for the existence of aliens which obviously profit from man-made site conditions and exclude native species by competition.

It should be pointed out that these explanations cover only one side of the problem: the differences in the response of native and alien species to changed competition relationships and resource bases. But the ratios of native to alien species

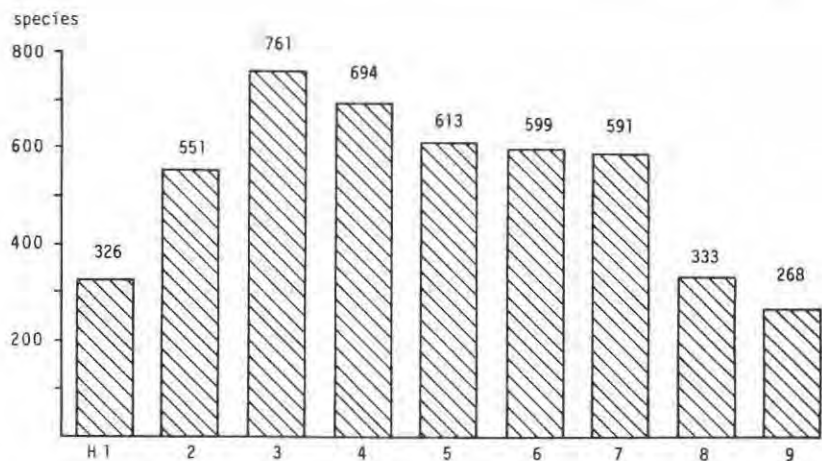


Fig. 11. Number of species occurring on varying levels of hemeroby (the human impact increases from H1 to H9).

in fig. 12, 13 also reflect the result of spreading processes (*i.e.* historical processes) very often beginning on intensively influenced sites such as railway stations, historical parks, or gardens. It can be only a question of time until more or less uninfluenced sites, usually isolated, are invaded by aliens; competition may be involved, but not necessarily (*e.g.* the spread of *Impatiens parviflora* finally invading natural vegetation partly without replacing other vascular species, Trepl, 1984).

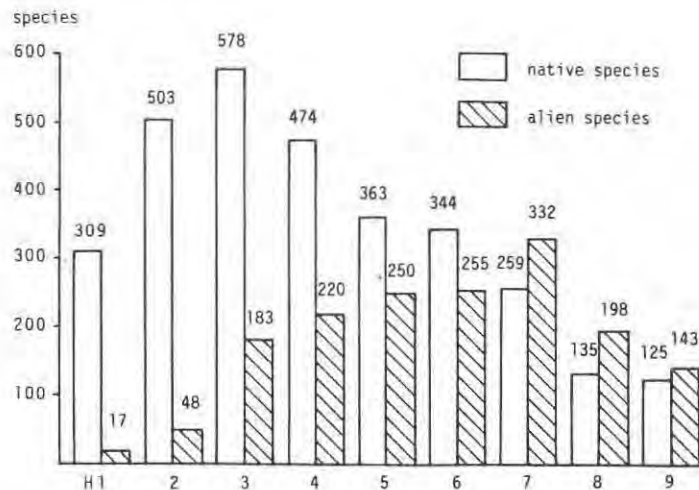


Fig. 12. Number of native and alien species occurring on varying levels of hemeroby (the human impact increases from H1 to H9).

### 6.3 Effects of increasing human impact on abundance patterns

According to Thienemann's second biocoenotic principle not only the number of species but their abundance changes with increasing intensity of an environmental factor. On sites dominated by a single factor fewer species with high numbers of individuals are to be expected. The changes of abundance patterns during the last hundred years, resulting in a higher proportion of rare species (section 3.1), as well as the decline of species richness from mesohemerobic to polyhemerobic vegetation (section 6.2) can be attributed to a higher level of human impact. The objective of this section is to analyse whether increasing human impact really encourages the spread of abundant species.

After having grouped the flora of Berlin (West) into eight abundance classes (class 1: very rare, class 8: very frequent species; see also fig. 3) the proportion of each class was estimated for each of the nine levels of hemeroby (H1–H9). In fig. 14 the proportion of rare species (sum of abundance classes 1 and 2) on H1–H9 is plotted against the proportion of frequent species (sum of abundance classes 6–8). The middle category, abundance classes 3–5, is not represented. There are striking differences in the pattern of native and alien species. The percentage of rare *native* species decreases sharply with increasing human impact, from about 50% in the virtually uninfluenced vegetation (H1, 2) to 14% in the vegetation most affected by human impact (H8, 9). Conversely the percentage of abundant species increases continuously with stronger impact (from 16% to 41%). Obviously the decline in species richness (fig. 12, 13) coincides with an enhancement of a lesser number of strongly competitive and abundant species dominating the vegetation of severely influenced sites.

Most of the *archeophytes* are preadapted to agricultural sites because of their introduction with agriculture. The highest proportion of rare archeophytes, coinciding with species richness (fig. 12, 13), is found in the vegetation subjected to intensive human influences (H6, 7). The high occurrence of rare archeophytes at this level of impact, which is typical for fields, can be related to the confinement of many of these species to traditional agricultural disturbance regimes (their decline results from industrialization of agriculture: e.g. *Consolida regalis*, *Centaurea cyanus*). In contrast, those fewer archeophytes able to invade other vegetation types affected by a lower or stronger impact, respectively, tend to be more frequent (e.g. *Fallopia convolvulus*, *Plantago major*, *Tripleurospermum inodorum*, *Poa annua*).

Most of the *neophytes* still belong to the classes including the more or less rare species – at each level of hemeroby. The changes of the proportion of rare and frequent neophytes in vegetation affected by varying extent of human impact are less significant. This can be explained by the heterogeneous composition of this group regarding the origin and time of introduction, for example, in comparison with native and archeophytic species. But considering the general increase in abundance of neophytes during the last hundred years (see section 3) further changes are to be expected. These patterns contrast with those of the native species. Only the latter correspond exactly with Thienemann's biocoenotic principle, suggesting that concise generalisations without regard to species' history may be misleading.

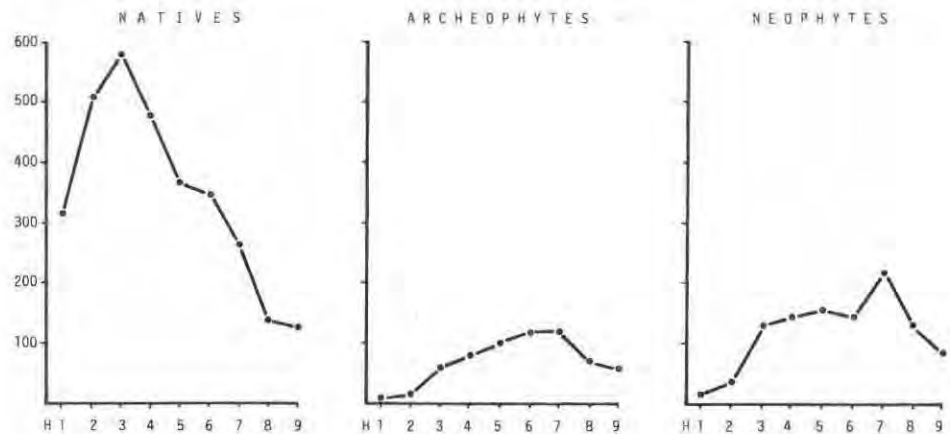


Fig. 13. Number of native, archeophytic, and neophytic species occurring on varying levels of hemeroby (the human impact increases from H1 to H9).

#### 6.4 Hemeroby amplitude and confinement of species to distinct levels of human impact

In order to analyse species' amplitude across varying levels of human impact, I grouped species in a series from steno- to euryhemerobic. Stenohemerobic species, specialized to a distinct level of human impact, have a narrow amplitude occurring only on 1–3 degrees of hemeroby, euryhemerobic species in contrast have a wide amplitude over more than six degrees of hemeroby. Examples for stenohemerobic species growing in intensively influenced vegetation are *Cynodon dactylon* (H9), *Salsola kali* (H8–9), *Amaranthus blitoides* (H7–9), *Consolida regalis* (H7), *Lamium amplexicaule* (H6–8), *Vulpia myuros* (H8–9); stenohemerobic species only affected by a lower level of human impact include *Gladiolus palustris* (H1), *Melampyrum pratense* (H2–4), *Luzula sylvatica* (H3), and *Vinca minor* (H3–5). Euryhemerobic

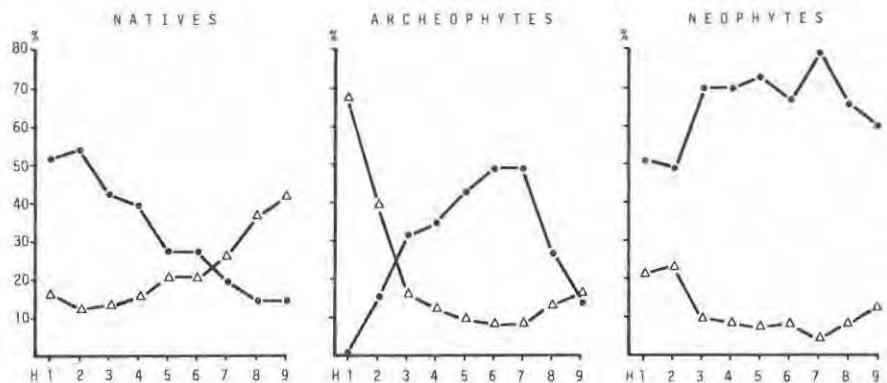


Fig. 14. Proportion of rare (dots) and frequent (triangles) natives, archeophytes and neophytes on varying levels of hemeroby (100 = total number of species according to fig. 13; the human impact increases from H1 to H9).



species are: *Acer platanoides* (H1–9), *Calamagrostis epigeios* (H1–9), *Poa pratensis* (H1–9), *Polygonum persicaria* (H2–9), *Poa annua* (H2–9), *Acer negundo* (H1–9), *Impatiens parviflora* (H1–9), and *Solidago canadensis* (H2–9).

Fig. 15 shows the percentages of stenohemerobic and euryhemerobic species in vegetation samples with varying levels of hemeroby (H1–H9). The middle category (species occurring on 4–6 levels) is not represented. The percentage of stenohemerobic *native* species has a maximum in the virtually uninfluenced vegetation and declines sharply with increasing human impact: from about 45% in the oligo- and mesohemerobic vegetation (H1–3) nearly to zero in the polyhemerobic vegetation (2.4% in H9). Conversely, the percentage of euryhemerobic species increases from about 30% (H1–3) to 85.5% (H9). The euryhemerobic species that predominate in man-influenced vegetation exemplify the apophytes: those native species that are able to invade man-made sites (see also section 6.6).

Again, the patterns of the aliens differ from those of the native species. The euryhemerobic *archeophytes* have a bimodal distribution: they occur mainly in the vegetation affected both by very low or very strong impact; stenohemerobic archeophytes are absent on more or less uninfluenced sites (H1, 2) and virtually so on polyhemerobic sites (H9: 1.8%). The explanation is the same as given above for the abundance patterns: most of the archeophytes, being preadapted to agricultural sites, are not very successful in invading vegetation affected by a disturbance regime differing in intensity (and kind). The pattern of euryhemerobic *neophytes* is similar, although less strongly marked, to that of the archeophytes. But in contrast there is a significant percentage of stenohemerobic neophytes occurring both in weakly and intensively influenced vegetation. This can be related to the heterogeneous character of the group of neophytes, being more diverse both in origin and modes of introduction and including, for example, species preadapted to forest sites (e.g. *Prunus serotina*), as well as to intensively disturbed sites (e.g. *Salsola kali*).

Species' abundance also reflects hemeroby amplitude: the most abundant species (abundance class 6–8) are, without exception, euryhemerobic species; in contrast 3/4 of the rarer species (abundance classes 1–3) are stenohemerobic species. Thus, stenohemeroby is one of the characteristic features of rare species.

To further characterize species' response to varying degrees of human impact, information about the hemeroby amplitude of each species was used to compute an indicator value expressing confinement to a distinct level of hemeroby. From the hemeroby spectra (examples in fig. 8–10) mean values (rounded to integer values) are used as indicator values, when the standard deviation is less than 1.5. For example, in the case of *Euphorbia peplus* (fig. 8) the mean value from the hemeroby spectrum was rounded to the indicator value '7', indicating a coincidence between the occurrence of this species and strong human impact. *Poa palustris* (fig. 10) is an example of an euryhemerobic species with no set indicator value. The hemeroby indicator values derived for 1191 species of the flora of Berlin (West) were checked and partly corrected by specialists. The values listed in Kowarik (1988) indicate the confinement of species to varying levels of human impact and can be used analogously to other ecological indicator values, as set up, for example, by Zolyomi *et al.* (1967) for Hungary, Landolt (1977) for Switzerland, and Ellenberg (1974, 1979) for western Central Europe.

The indicator values for hemeroby can be used for various purposes. Comparisons

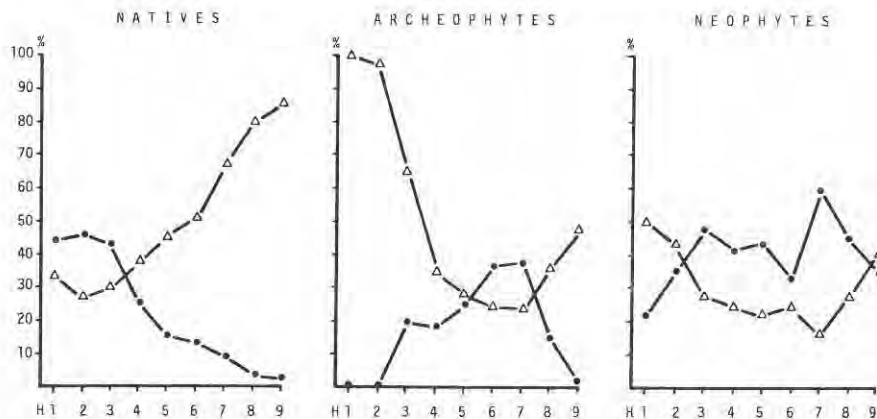


Fig. 15. Proportion of stenohemerobic (dots) and euryhemerobic (triangles) natives, archeophytes and neophytes on varying levels of hemeroby (100% = total number of species according to fig. 13; the human impact increases from H1 to H9).

among species reflect their different reactions to human impact. At the level of communities it is possible to compute average hemeroby indicator values for vegetation units (section 6.5) corresponding to Ellenberg's use of average indicator values for climatic and soil factors. Average values can be useful for the characterization of vegetation units and helpful for nature conservation in urban planning, because they indicate changes due to human impact which might require action by planners.

### 6.5 Response of vegetation units to varying levels of human impact

In this section average hemeroby values (see above) are used to characterize the response of vegetation to varying levels of human impact. Fig. 16, 17 show the results of a case study: investigations of changes in the lawn vegetation of the 'Tiergarten', the largest park in Berlin. Vegetation relevés of lawns recorded 1978 by Trepl (in Sukopp *et al.*, 1979) were repeated in 1986. The difference in average hemeroby values for trampled lawns increased distinctly from 1978 to 1986 (fig. 16), presumably due to recreational activities like playing football, and resulted in far-reaching changes in the floristic composition of the lawns (Kowarik and Jirku, 1988). Species typical of meadows and dry grassland were replaced mainly by euryhemerobic species such as *Poa pratensis*, *Lolium perenne*, and *Poa annua*. Table 5 illustrates the extreme changes of one site recorded in 1978 and 1986 where all species were replaced.

Fig. 17 shows the average hemeroby values computed for lawns of the same park, both for 1978 and 1986, which are fenced in order to develop meadow communities. In most cases the level of hemeroby does not increase as a result of the cessation of trampling (opposite tendencies can be related to varying management methods). Such investigations can be useful in a planning context as well as for successful nature conservation management.

Fig. 18 gives a survey of the response of the whole vegetation of Berlin (West) to varying degrees of human impact. Average hemeroby values computed for 3420



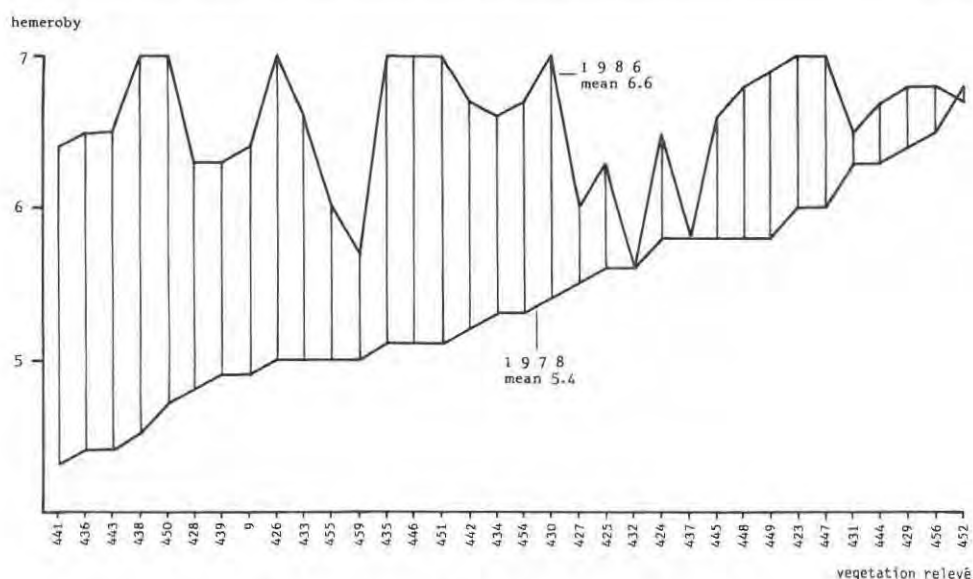


Fig. 16. Average hemeroby indicator values computed for trampled lawns: difference between the vegetation relevés from 1978 and 1987 (the relevés are ranked according to increasing average hemeroby values in 1978).

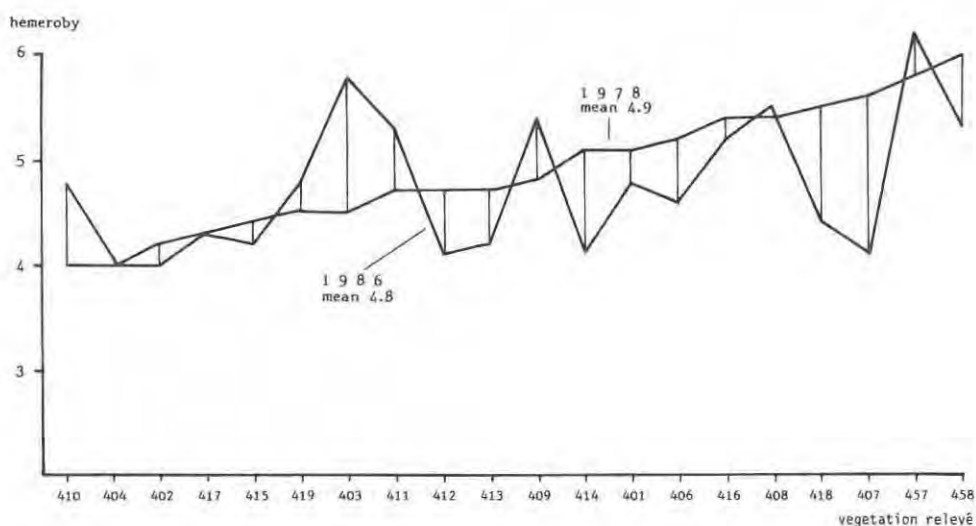


Fig. 17. Average hemeroby indicator values computed for fenced lawns: differences between the vegetation relevés from 1978 and 1987 (the relevés are ranked according to increasing average hemeroby values in 1978).

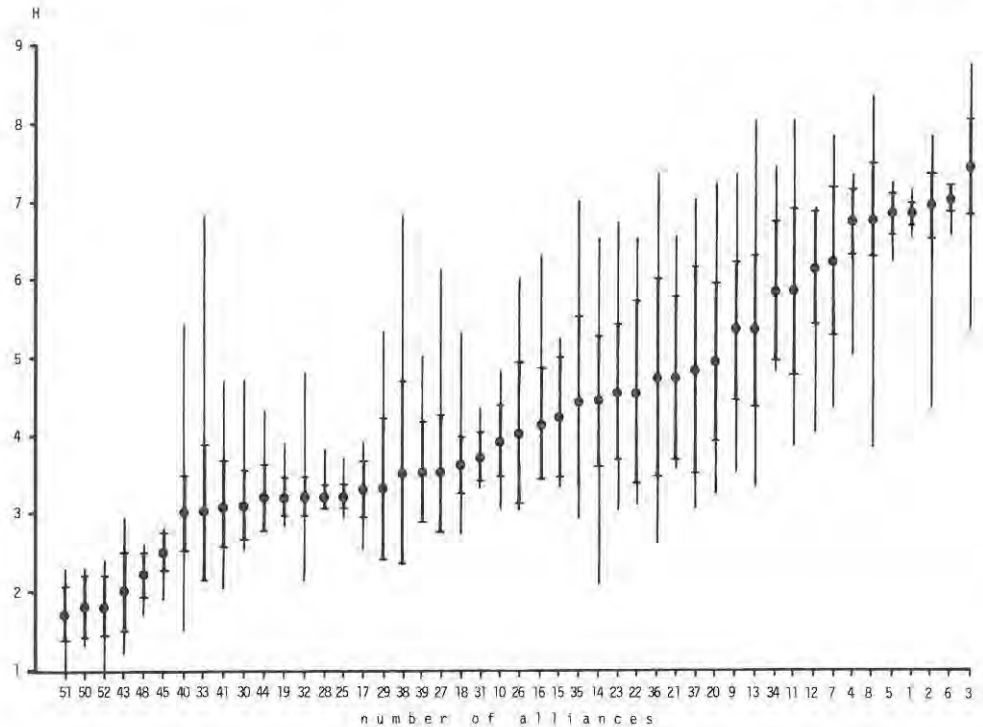


Fig. 18. Survey on the response of vegetation types to varying levels of human impact (H): average hemeroby indicator values summarized for relevés of 52 phytosociological alliances (number of the alliances according to table 1) including range of average values of single relevés and standard deviation. The alliances are ranked according to increasing average hemeroby values.

vegetation relevés are summarized at the level of alliances (the indicated number of alliances is included in table 1). The alliances are ranked according to increasing average hemeroby values. These values as well as the range of average values of single relevés and the standard deviation illustrate the resilience of vegetation types to man-made influences.

#### 6.6 *A balance: apophytization and synanthropization of the flora*

These results reveal that increasing human impact causes a decline of most native species both in number and abundance. One group of native species, however, deviates from the general trend. These species able to invade man-made sites are termed 'apophytes' (Rikli, 1903). Former classifications of apophytes can be traced to Thellung (1918) or Linkola (1916), respectively representing two main approaches. The first, 'qualitative', classifies native species as apophytes (with varying differentiations, e.g. Simmons, 1910; Kopecky, 1985) if they are able to grow on man-made sites. Apophytes (with varying differentiations, e.g. Preuss, 1930; Holub and Jirasek, 1967) according to the second, 'quantitative' approach, include only species which are *more* abundant on man-made than on natural sites. The arguments of

Krause (1929) against Linkola's quantitative classification are still valid for regions with a long and complex history of human influences such as Central Europe: there is not sufficient basis for a comparison between species' abundance on natural and man-made sites. Therefore the classification of apophytes proposed by Kowarik (1988) follows the 'qualitative' tradition.

The native species are divided into three groups according to their present-day occurrence in vegetation affected by more or less strong human impact. Species' hemeroby spectra (see section 6.1) are used as a basis for this classification. 'Proapophytes' are species confined to only weakly influenced sites (H1-3; mainly species of pristine vegetation types such as forests, wetlands and water vegetation). 'Hemiapophytes' as a second group include native species also growing on sites which obviously are subjected to a stronger impact (H4-6; species of man-made heaths, meadows, pastures, intensively managed forests), and finally the third group of 'holoapophytes' are species able to invade intensively influenced sites (H7-9; species of segetal and ruderal vegetation). Hemi- and holoapophytes could be summarized as apophytes in a broader sense.

The process of native species invading man-made sites could be termed 'apophytization', as a parallel to Falinski's 'synanthropization' (see e.g. Falinski, 1987) which includes the effects of establishment of aliens as well as the spread of natives to new sites. Fig. 19 illustrates the far-reaching apophytization of the native flora of Berlin (West). Only about a third of the native species (37%), as proapophytes, remain confined to natural or semi-natural sites (e.g. *Carex* spec. div., *Potamogeton* spec. div., *Andromeda polifolia*, *Drosera anglica*), whereas the rest, that is 63%, have

Table 5. Computing of average hemeroby values for a trampled lawn, recorded 1978 and 1986 (c: cover value according to Braun-Blanquet, 1964; H: hemeroby value; x: no hemeroby value for species without confinement to a distinct level of hemeroby).

1978			1986		
c	species	H	c	species	H
4	<i>Festuca ovina</i>	x	4	<i>Poa annua</i>	7
2	<i>Agrostis tenuis</i>	x	3	<i>Polygonum aviculare</i>	7
2	<i>Bromus hordeaceus</i>	x	3	<i>Trifolium repens</i>	x
2	<i>Capsella bursa-pastoris</i>	7	1	<i>Capsella bursa-pastoris</i>	7
2	<i>Cerastium holosteoides</i>	5	1	<i>Plantago major</i>	7
1	<i>Armeria elongata</i>	4	1	<i>Taraxacum officinale</i>	x
1	<i>Rumex acetosella</i>	x			
+	<i>Arenaria serpyllifolia</i>	x			
+	<i>Arrhenatherum elatius</i>	5			
+	<i>Chenopodium album</i>	7			
+	<i>Crepis capillaris</i>	6			
+	<i>Conyza canadensis</i>	x			
+	<i>Trifolium dubium</i>	5			
+	<i>Veronica arvensis</i>	6			
+	<i>Viola tricolor</i>	7			
r	<i>Potentilla argentea</i>	x			
average hemeroby value		52:9 = 5.8			28:4 = 7.0

NUMBER OF NATIVE SPECIES IN VEGETATION SAMPLES OF VARYING LEVELS OF HEMEROBY		
H 1 - 3	H 4 - 6	H 7 - 9
LEVEL OF APOPHYTIZATION ----->		
low	middle	high
309 (37%) Proapophytes	269 (32%) Hemiapophytes	261 (31%) Holoapophytes
	530 (63%) apophytes s.l.	

Fig. 19. Apophytization of the flora of Berlin (West).

been recorded in biotopes of the urban landscape affected by a stronger human impact. These apophytes *sensu lato* can be divided into hemi- and holoapophytes. Among the 269 hemiapophytes (32%) are *Melampyrum pratense*, *Polygonatum odoratum*, *Veronica officinalis*, *Hieracium sylvaticum*, *Ajuga reptans*, *Alchemilla vulgaris*, *Potentilla verna*; examples of holoapophytes (261 species = 31%) are *Acer platanoides*, *A. pseudoplatanus* (see also Sachse *et al.*, this volume), *Achillea millefolium*, *Agropyron repens*, *Calamagrostis epigeios*, *Cirsium vulgare*, *Dactylis glomerata*, *Equisetum arvense*, *Galium aparine*, *Poa palustris* (fig. 10), *Poa pratensis*, *Saponaria vulgaris*, *Salix alba*, *Scrophularia nodosa*, *Taraxacum officinale*, *Urtica dioica*, and even the orchid *Epipactis helleborine* (see also Dickson, this volume).

The addition of apophytes, archeophytes, and neophytes results in a group of 1123 synanthropic species, or in other words, more than three quarters of the total flora of Berlin (West) are influenced by human impact. A similar dimension of man's impact (66.5% synanthropic species), found by Sudnik-Wojcikowska (1987) in Warsaw, indicates that far-reaching changes in urban floras are a general phenomenon.

## 7. Conclusions

The urban flora and vegetation has responded profoundly to urbanization in both time and space. The dramatic decline of native species during the last hundred years has contrasted with the establishment of aliens and resulted in disruptions of the former patterns of relative abundance. In general, the level of disruption increases from the outskirts to the inner city (city-country gradient). The effects of increasing man-made disturbance (estimated by the application of the hemeroby system) reveal some general responses in species richness, relative abundance, and the confinement of many species to distinct levels of impact. Some of the results conform well to a

general hypothesis (e.g. intermediate disturbance hypothesis), others, however, do not. There are striking differences between the reactions of native and alien species, and between the earlier and later immigrants (archeophytes vs. neophytes), indicating that precise generalisations without regard to a species' history, could be misleading. The hemeroby system seems well-suited for analysing the adaptation of species and vegetation types to man-made disturbance. Such differential sensitivity has obvious implications for both general theory and conservation and management.

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