



## The origin and development of the urban flora of Central Europe

RÜDIGER WITTIG

r.wittig@em.uni-frankfurt.de

*Ökologie und Geobotanik, Botanisches Institut der Johann Wolfgang Goethe-Universität, Siesmayerstraße 70, 60323 Frankfurt, Germany*

**Abstract.** The floras of Central European cities and towns differ largely from the flora of the hinterland. Characteristics of the urban flora (in comparison to that of the hinterland) are: a remarkable decrease in the percentage of indigenous and archeophytic species, in particular of those that have a narrow ecological amplitude and/or are strictly bound to oligotrophic habitats; an increase in the population of a small group of indigenous species resulting from a change from natural to synanthropic habitats (apophytisation, synanthropisation); an immigration of alien species (neophytes), in particular to disturbed habitats; and the development of new ecotypes. The origin and development of the typical features of the Central European urban flora can be divided into four distinctive periods: the time up until the end of the 15th century, the time from the 16th century to the beginning of the industrial age, the industrial age, the post-industrial age.

**Keywords:** apophytes, archeophytes, Central Europe, neophytes, synanthropisation, urban flora

### Introduction

In comparison to natural habitats (forests, grasslands, wetlands, and riparian zones) cities and towns represent very young habitats. We postulate that most species found in urban habitats have expanded their habitat from neighbouring or remote areas, and even from different continents.

In Central Europe numerous authors have dealt with the origin and development of the flora of cities and towns. However, many of the results have not been published in English, so they are not easily available to the whole scientific community. Pyšek (1995a) and Sukopp (2002) have published reviews which address the same subject but have different focal points; here we attempt a review of extant Central European literature.

### Terminology

Apophytes are species represented in the former natural landscape that have meanwhile changed from natural to anthropogenous habitats (Rikli, 1903/04). They are part of the group of the indigenous species which are termed idiochores or idiochorophytes. The original terminology of Thellung (1918/19) was later modified by various authors (Holub and Jirasek, 1967; Kornas, 1968; Schroeder, 1969). As do most German-speaking authors and many authors writing in the romance languages, we here follow Schroeder (1969). Polish authors generally use the more complex terminology of Kornas (1968, 1982), which

considers also the invasive potential of the newcomers (see also Faliński, 1998b). A critical review of the terminology used in plant invasion studies was given by Pyšek (1995b). Sukopp (1998) summarized the history of the study of anthropogenic plant migrations in Europe.

Those species not native in the local natural landscape but present due to human influence are called hemerochorous or anthropochorous species (hemerochores, anthropochores; for more details see Schröder, 1969). In Central European literature this group is divided into two sub-groups: archaeophytes, that arrived from prehistoric up to mediaeval times, and neophytes, which came here more recently. In the non-European literature, these terms are not familiar. Most American and English authors use the terms aliens or invaders (for more details see Richardson et al., 2000). The year 1492 is the line between archaeophytic and neophytic species, because the early voyages of European discovery in the Americas started a very active exchange between the flora of the old and the new worlds.

The arrival of neophytic species is generally documented exactly. But it is often very difficult to differentiate between archaeophytic and indigenous species. That is why archaeophytes and indigenous species are treated together, while the neophytes are dealt with separately.

Besides indigenous species and immigrants there are also some new taxa which have evolved under the influence of humans through isolation, hybridisation, and introgression (e.g. Hurka et al., 2003). These species that have no natural habitat (that we know of) and their present and past distributions are strongly restricted to anthropogenic habitats are called anecophytes or obligatory weeds (Scholz, 1991).

### Indigenous species and archaeophytes

In the neolithic more than 90% of Central Europe was covered by forests (Ellenberg, 1996). That is why most Central European plant species are adapted to shady habitats, to relatively small variations of daily temperatures, and to the absence of frequent disturbances. On the contrary, urban habitats are harsh and variable. They are often fully exposed to sunlight, show great alternations in diurnal temperatures, and are subject to frequent disturbances.

Regardless of the dominance of forests, even in the pre-human landscapes there was an array of natural disturbances that created temporal and spatial variation in particular habitats: riverbanks and seashores, areas cleared by wind, by natural fires, or by avalanches, as well as the dens, wallows, and migratory paths of large mammals. Thus in cities and towns we can find opportunistic and ephemeral indigenous species stemming from such habitats. These species still occur in the natural environment, but often anthropogenous habitats have become their most important habitat (Table 1).

The move from natural to anthropogenous habitats of species (called apophytisation or anthropisation) is an ongoing process. The most recent apophytes are *Humulus lupulus* (Sukopp and Kowarik, 1987) and *Solanum dulcamara* (Wittig, 2002a). For Prague (Praha) Kopecký (1984) describes how *Chaerophyllum aromaticum*, *Ch. bulbosum* and *Anthriscus sylvestris* may have wandered from natural communities (riparian margins, forests, forest edges) via anthropogenous habitats along rivers and streets into nitrophilous communities of settlements.

Table 1. Original habitats<sup>a</sup> of apophytes of the settlements of Central Europe

Original habitats	Examples of species
Woodlands of floodplains and of swamps, tall herb communities of river banks and shallows	<i>Aegopodium podagraria</i> , <i>Calystegia sepium</i> , <i>Galium aparine</i> , <i>Polygonum amphibium</i> , <i>Humulus lupulus</i> , <i>Urtica dioica</i> , <i>Elymus repens</i> , <i>Poa trivialis</i> , <i>Equisetum arvense</i>
Periodically flooded, nutrient enriched mud, sand and gravel surfaces at inland waters	<i>Bidens tripartita</i> , <i>Chenopodium glaucum</i> , <i>Ch. rubrum</i> , <i>Corrigiola litoralis</i> , <i>Plantago major</i> , <i>Polygonum lapathifolium</i> , <i>P. persicaria</i> , <i>Potentilla anserina</i> , <i>P. reptans</i> , <i>Rumex obtusifolius</i>
Strand lines, dunes and rock at seacoasts	<i>Atriplex prostrata</i> , <i>Elymus repens</i> , <i>Sonchus arvensis</i> , <i>Tripleurospermum perforatum</i>
areas of windthrow, clearings	<i>Cirsium arvense</i> , <i>C. vulgare</i> , <i>Verbascum</i> div. spec.
Scree and rubble	<i>Chaenorhinum minus</i> , <i>Galeopsis segetum</i> , <i>Sedum telephium</i> agg., <i>S. acre</i> , <i>Tussilago farfara</i>
Rocks	<i>Asplenium ruta-muraria</i> , <i>A. trichomanes</i> , <i>Sedum album</i> , <i>Bryum capillare</i> , <i>Grimmia pulvinata</i> , <i>Orthotrichum anomalum</i> , <i>Tortula muralis</i> , <i>Caloplaca murorum</i> , <i>Lecanora muralis</i>

<sup>a</sup>According to Oberdorfer (2001).

Many species that occur in cities and towns today date back to settlements in neolithic times. Others are represented in settlements at least from the bronze age onwards (Table 2). Evidence is provided either by pollen analyses or by macrophytic relics (fruits, seeds or vegetative parts) found during archaeological excavations. Willerding (1988) reports *Chenopodium album*, *Fallopia convolvulus*, *Lapsana communis*, *Plantago major*, *Polygonum lapathifolium*, *P. persicaria*, *Rumex acetosella* and *Setaria viridis* from a seven-thousand-year-old settlement in the Leine river valley (Lower Saxony, Germany). The following species, which are very frequent in settlements today, date back to the period of Ribbon Ceramic civilisation settlements (Kreuz, 1994): *Bromus sterilis* (or *tectorum*), *Capsella bursa-pastoris*, *Chenopodium hybridum*, *Echinochloa crus-galli*, *Fallopia convolvulus*, *Nepeta cataria*, *Setaria viridis* (or *verticillata*) and *Solanum nigrum*. The most frequent species of neolithic settlements in Poland are *Chenopodium album*, *Polygonum persicaria*, *P. lapathifolium* and *P. aviculare* (Trzcińska-Tacik and Wasylikowa, 1982).

The status of individual species may be different depending on local, regional, and continental aspects. Many wall plants, e.g. the ferns *Asplenium ruta-muraria* and *A. trichomanes*, are indigenous to Central Europe. However, the North-West European plains that are naturally free of rocks, could not be colonized by these saxicolous plants before humans set up artificial rocks (stone walls, stone houses). In South Germany this took place in Roman times and means that these species are archaeophytes in this region. In Northwest Germany where the Romans did not settle and stone houses were not very common these species did not occur before the beginning of modern times, meaning that the species are neophytes in these regions. Many of the herbaceous plants of old human settlements were used by people for purposes including insect repellent, dyes, medicines, cleaning agents, for fibre production, and of course as food (Table 3).

Table 2. Examples of Central European archaeophytes and the period of their first occurring in Germany

Period <sup>a</sup>	Examples of species <sup>b</sup>
Neolithic time	<i>Arctium lappa</i> *, <i>A. minus</i> *, <i>Bromus sterilis</i> , <i>Capsella bursa-pastoris</i> *, <i>Chenopodium bonus-henricus</i> , <i>Ch. polyspermum</i> , <i>Cirsium vulgare</i> , <i>Convolvulus arvensis</i> *, <i>Lamium album</i> , <i>L. purpureum</i> *, <i>Plantago lanceolata</i> (Ka), <i>Reseda luteola</i> *, <i>Silene alba</i> , <i>Sisymbrium officinale</i> *, <i>Sonchus oleraceus</i> , <i>Veronica arvensis</i> (Kr)
Bronze age	<i>Ballota nigra</i> , <i>Bromus tectorum</i> , <i>Erodium cicutarium</i> , <i>Hordeum murinum</i> , <i>Medicago lupulina</i> , <i>Mercurialis annua</i>
Iron age	<i>Cichorium intybus</i> , <i>Malva neglecta</i> , <i>Taraxacum officinale</i> agg. (KM), <i>Tripleurospermum perforatum</i>
Roman time	<i>Lepidium campestre</i> , <i>L. ruderales</i> , <i>Parietaria officinalis</i> , <i>Portulaca oleracea</i> (KI), <i>Reseda lutea</i>

<sup>a</sup>If not noted differently data are given by Lang (1994), Ka: Kalis and Meurers-Balke (1998), KI: Klotz (1985), KM: Knörzer and Meurers-Balke (1999) and Kr: Kreuz (1990).

<sup>b</sup>Species marked with an asterisk \* are called "old culture companions" by Oberdorfer (2001).

Table 3. Examples of formerly used wild plants in settlements (except of pure ornamental plants and herbs accompanying cereals)<sup>a</sup>

Use	Examples of species
Nutrition	
Vegetable <sup>b</sup>	<i>Aegopodium podagraria</i> , <i>Chenopodium album</i> , <i>Ch. bonus-henricus</i> , <i>Cichorium intybus</i> , <i>Oenothera biennis</i> (R), <i>Saponaria officinalis</i> (R), <i>Sonchus oleraceus</i>
Salad	<i>Sedum telephium</i> agg.
Spice	<i>Artemisia absinthium</i> , <i>A. vulgaris</i> , <i>Pastinaca sativa</i> , <i>Sinapis arvensis</i>
Medicine and hygiene <sup>c</sup>	<i>Aegopodium podagraria</i> , <i>Arctium lappa</i> , <i>Artemisia absinthium</i> , <i>A. vulgaris</i> , <i>Ballota nigra</i> agg., <i>Chelidonium majus</i> , <i>Cichorium intybus</i> , <i>Hyoscyamus niger</i> , <i>Hypericum perforatum</i> , <i>Lamium album</i> , <i>Malva neglecta</i> , <i>Melilotus albus</i> , <i>M. officinalis</i> , <i>Oenothera biennis</i> , <i>Pastinaca sativa</i> , <i>Plantago major</i> , <i>Polygonum aviculare</i> agg., <i>Potentilla anserina</i> , <i>Saponaria officinalis</i> (S), <i>Tanacetum parthenium</i> , <i>T. vulgare</i> , <i>Tussilago farfara</i> , <i>Urtica dioica</i> , <i>Verbascum densiflorum</i> , <i>V. thapsus</i> , <i>Verbena officinalis</i> ,
Other uses	
Moth protection	<i>Anthemis cotula</i> , <i>Melilotus albus</i> , <i>M. officinalis</i> , <i>Tanacetum parthenium</i>
Coloring	<i>Anthemis tinctoria</i>
Fiber plant	<i>Verbascum densiflorum</i>

<sup>a</sup>According to Oberdorfer (2001), supplemented.

<sup>b</sup>R = root vegetable; all others are leaf vegetables.

<sup>c</sup>S = soap; all others are medical plants.

We can assume that these plants were not merely tolerated by the settlers but were valued. They were not only excluded from weeding but some times even protected (and planted?) As the fruits and seeds of many of these plant species are adapted for easy dispersal many were undoubtedly involuntarily carried from old settlements to newly established ones. However, others were intentionally transplanted and sown. In the Middle Ages, such seeding took place regularly in the gardens of monasteries. Such plants are called monuments of natural history (Danish: "naturhistoriske minder") by Hedal (1987) and Østergaard (1957) calls them medieval plants (Danish: "middelalder planter").

### Neophytes

Differentiation between indigenous plants and archeophytes is often difficult because the original habitat range of archeophytes is often obscure and remains "hidden in the darkness of history" (Scholz, 1995). Introduction of alien species in historical times is often clearly documented. Faliński (1971) stated a clear relation between a settlement's size and its number of hemerchorous species. While in smaller settlement the non-indigenous species are merely represented by archeophytes, in large cities the number of neophytes is usually larger than that of archeophytes (Faliński, 1998a). Investigations carried out in Czechia confirm the results from Poland: Pyšek (1989a, b) found that in villages the percentage of archeophytes is relatively high compared to that of the total Czech flora, while there is no significant difference in the amount of neophytes when comparing villages with the total flora of Czechia. In cities and towns, however, the percentage of neophytes is much higher than in the overall Czech flora while there is only a small difference in the percentage of archeophytes (see also Pyšek and Pyšek, 1991; Pyšek, 1998). Berlin, in the centre of which the percentage of archeophytes is higher than in the surrounding villages (Kowarik, 1990a) seems to be an exception. The same differences as between urban flora and village flora have been found in comparisons of recent and old inventories of the flora of towns, e.g. Berlin (Kowarik, 1995), Halle upon Saale (Klotz, 1984a), Posen (Jackowiak, 1990).

Obviously the changes in environmental factors in human altered sites provide specific niches which may be colonized by aliens better than by native species. Comparatively higher temperatures, and more limited soil moisture are characteristic factors on rural to urban gradients. As many alien species in temperate zones originate from warmer areas (Scholz, 1960; Saarisalo-Taubert, 1963), they may be preadaptated to urban conditions. Therefore it is no wonder that the number of neophytes in villages runs parallel to the degree of urbanisation (German: *Verstädterung*). With urbanisation the number of archeophytes in villages decreases (Pyšek and Mandák, 1997).

The correlation between the number of neophytes and the size of the city (indicated by the number of inhabitants) is very well documented for Berlin: in 1787 there were 20 neophytes naturalized, in 1884 their number reached 51 and in 1959 as many as 79 naturalized neophytes were recorded (Scholz, 1960). In the same period the number of human inhabitants rose from 200,000 to 3 million. But it has to be considered that in this period the exchange of goods and materials between countries and continents increased. And due to these increases the possibilities for the invasion of alien species also grew.

Most of these species are not able to colonize intact native communities, but found space where the native flora was reduced, i.e. disturbed habitats. Strictly speaking it is not the increase in the human population, but that of bulk trade (especially in grains) and of the intensity of anthropogenous disturbances (hemerobie) that causes the rise in the number of hemerochorous species. Kowarik (1988) observed a close relation of the hemerobie of the habitat and the increase or decrease on the number of hemerochores: while in the least disturbed habitats only 2% of the species are hemerochores, on highly disturbed areas the hemerochores are 50% of the total. In all habitats of Berlin the number of neophytes is higher than that of archaeophytes.

The increase in the number of neophytes is related to the decrease in the number of indigenous species and archaeophytes. At the beginning of the 1980s in Halle upon Saale (Sachsen Anhalt, Germany), the number of indigenous species represented only 57%, and the number of archaeophytes 78% of the number present in 1848 (Klotz, 1984a). The number of neophytic species, however, increased to 295% of that of 1848. The reasons for metropolitan richness in neophytes which have been discussed by various authors (e.g. Pyšek, 1989b, 2001; Wittig, 1991; Kowarik, 1995) are summarised by Wittig (2002a):

- the high number of highly disturbed anthropogenous habitats
- the characteristics of the urban climate (heat island) which favours species originating from warmer and drier areas;
- cultivation of an uncountable number of foreign species beside roads, in parks and gardens, which form a source for neophyte colonization;
- the functioning of cities as centres of trade and traffic resulting in numerous immigration gates (Table 4) and migration paths.

Those places where goods and waste, particularly from agriculture or forestry, are loaded or unloaded, stored, distributed and/or processed, i.e. railway stations, ports and harbours, markets, dumping grounds, oil mills and wool processing factories, are common immigration gates for plants. Gardens and parks, too, have often functioned as sources for neophytes and bird feeders should also not be underestimated as immigration gates. Most of the neophytes that have successfully escaped from culture in Central Europe are listed in Table 5. In the Czech Republic 74.3% of the successful escapers were introduced as ornamental plants (Pyšek et al., 2002).

Some alien species have started to spread into Central European cities, more recently, e.g. *Inula graveolens* (Gödde, 1984; Reidl, 1984), *Iva xanthifolia* (Sudnik-Wójcikowska, 1987a) and *Chenopodium pumilo* (Kramer, 1991). Very well documented is the spread of *Senecio inaequidens*, originating from South Africa but now present in almost every Central European city (e.g. Adema and Mennema, 1978; Lebeau et al., 1978; Asmus, 1988; Borkamm and Prasse, 1999; Werner et al., 1999). These new invasions show that the formation of the urban flora is still an ongoing dynamic process (Sudnik-Wójcikowska, 1987b; Gutte, 1990, 1996; Jackowiak, 1998). However the number of new species arriving has decreased remarkably in recent times. Jäger (1977) attributes this to the fact that most species able to adapt to Central European urban habitat conditions have had enough time

*Table 4.* Starting points (immigration gates) for the expansion of neophytes within settlements

Immigration gate	Exemplary publication	Place/area
(Freight-)stations	Hupke (1933) <sup>a</sup>	Cologne
	Jauch (1938)	Karlsruhe
	Kreh (1960)	Stuttgart (and generally)
	Meyer (1930, 1932 <sup>b</sup> )	Breslau
	Scheuermann (1930, 1934, 1940)	Rhein.-Westf. industrial region
Harbours	Baumgartner (1973, 1975)	Basel
	Brandes (1989)	Lower Saxony (inland)
	Hamann and Koslowski (1988)	Gelsenkirchen
	Jehlík (1981)	Hamburg
	Jehlík (1984)	Czechoslovakia
	Jehlík and Hejný (1974)	Czechoslovakia
	Klotz (1984b)	Halle-Trotha
	Mißkampff and Züghart (2000)	Bremen
	Runge (1965, 1972)	Münster
	Saarisalo-Taubert (1963)	sea ports of Finland
	Stieglitz (1981)	Neuß
	Stricker (1962)	Leipzig
	Szotkowski (1978)	Upper Oder
Markets	Fiedler (1937)	Central market hall in Leipzig
Garbage depots	Hetzel and Meierott (1998)	Franconia
	Hetzel and Ullmann (1995)	Northern Bavaria
	Scheuermann (1928)	Rhein.-Westf. industrial region
Mills (grain, oil)	Jehlik (1988)	Czech Republic
Gardens, green belts,	Adolphi (1995, 1997)	Rheinland
Parks, and ornamental	Kosmale (1981)	Ore Mountains foreland
Lawns	Kunick (1991)	Germany
	Pedersen (1983)	Denmark (villages)
Bird feeders	Scheuermann and Wein (1937–39)	Nordhausen

<sup>a</sup>Also harbour areas.

<sup>b</sup>Particularly the transshipment places of tropical fruit situated at freight stations.

to conquer these habitats, meaning that almost all species fitting the conditions are already present.

For the migration from one city to another, newly invaded species lacking effective mechanisms for dispersal over long distances (e.g. flight capable diaspores) do need linear structures as “Wanderwege” (migration routes) (s. also Jehlík and Hejný, 1975; Adolphi, 1998; Büscher, 1999). As neophytes in non-disturbed habitats are generally unable to compete with indigenous species, linear structures can only be used as migration routes when they contain areas of reduced competition, i.e. areas of periodical disturbance. Taking the

Table 5. Examples of neophytes of the flora of Central European settlements originally introduced as ornamental plants

Species	Origin <sup>a</sup>	Occurrence <sup>b</sup>	Remarks
<i>Acer negundo</i>	N-America	Railway territory	
<i>Ailanthus altissima</i>	China	In large cities everywhere	Gutte et al. (1987), Kowarik (1983), Kowarik and Böcker (1984), Kramer (1995)
<i>Antirrhinum majus</i>	Mediterranean, W-Asia	Walls	
<i>Aster lanceolatus</i> / <i>A. tradescantii</i>	N-America	Railway and industrial areas	According to Adolphi (1995) frequently confounded with one another
<i>Aster novae-angliae</i>	N-America	Railway areas	Main occurrence on river banks
<i>Aster novi-belgii</i> agg.	N-America	Debris places, railway- and industrial areas	Members of this aggregate are <i>A. novi-belgii</i> , <i>A. x salignus</i> , <i>A. laevis</i> , <i>A. x versicolor</i>
<i>Buddleja davidii</i>	China	In particular railway- and industrial areas	Kreh (1952), Kunick (1970), Wittig (2002b)
<i>Cotoneaster horizontalis</i>	W-China	Walls, crushed stones in track areas	Also outside of settlements at rocky locations
<i>Cymbalaria muralis</i>	Adriatic region to Switzerland	Walls	
<i>Duchessna indica</i>	S- and SO-Asia	Green belts, cemeteries, front yards	
<i>Euphorbia lathyris</i>	Mediterranean, W-Asia	Villages	
<i>Geranium phaeum</i>	Southern Central Europe	In most of Central Europe outside settlements only	But identified as a settlement plant in Denmark (Jensen, 1989)
<i>Heracleum mantegazzianum</i>	SW-Asia	Rarely mowed areas along large roads, e.g. on centre strips	Main occurrence along brooks outside of settlements
<i>Hieracium aurantiacum</i>	Mountains of N- u. M-Europe	Lawns	
<i>Iberis umbellata</i>	Mediterranean	Railway- and industrial areas, rubbish tips, debris places	Often together with <i>Lobularia maritima</i>
<i>Impatiens parviflora</i>	M-Asia	Park forests, hedge seams	Emphasis on forests outside settlements

(Continued on next page.)



Table 5. (Continued).

Species	Origin <sup>a</sup>	Occurrence <sup>b</sup>	Remarks
<i>Lobularia maritima</i>	Mediterranean	Rarely trodden plaster cracks, stony ways	Preferred at trodden areas with possibility of avoidance of tread (plaster cracks, pavement edges)
<i>Lunaria annua</i>	Italy, SO-Europe	Hedges, bushes, especially in villages	
<i>Lysimachia punctata</i>	Asia Minor, SO-Europe, Italy	Road ditches, mountain villages	Also outside settlements
<i>Mahonia aquifolium</i>	N-America	Parks, cemeteries, hedges	
<i>Mentha spicata</i>	West. Mediterranean	Debris places	
<i>Oenothera glazioviana</i>	N-America	Railway- and industrial areas, road edges	Wittig and Tokhtar (2003), Wittig et al. (1999)
<i>Onopordum acanthium</i>	Mediterranean	debris places, dams; also villages	
<i>Oxalis corniculata</i>	Mediterranean	Stone-covered paths, plaster cracks, gardens, lawns	
<i>Parthenocissus inserta</i>	N-America	Railway- and industrial areas, abandoned garden areas	Many literature data for the naturalisation of <i>P. quinquefolia</i> are probably based on the confusion with <i>P. inserta</i>
<i>Paulownia tomentosa</i>	China	Railway and industrial areas, city centres	So far only in few, very large cities, Richter and Böcker (2001); s.a. Nowack (1987)
<i>Platanus hybrida</i>	Origin unknown	In the proximity of planted trees on road flanks and at walls	Brennenstuhl (1990), Kowarik (1984)
<i>Pseudofumaria lutea</i>	S-Alps	Walls	
<i>Reynoutria japonica</i>	O-Asia	Railway and industrial areas, debris places	More frequently outside of settlements than within, emphasis on river bank seams
<i>Robinia pseudacacia</i>	USA	Railway slopes, former rubble sites	Klauck (1988), Kohler and Sukopp (1964), Kowarik (1990b)
<i>Sedum spurium</i>	N-Iran, Caucasus, Armenia, Kurdistan	Walls, stony slopes in mountain villages	

(continued on next page.)

Table 5. (Continued).

Species	Origin <sup>a</sup>	Occurrence <sup>b</sup>	Remarks
<i>Solidago canadensis</i>	Atlant. N-America	Moderately influenced ruderal habitats, seams at traffic routes, abandoned garden areas	also frequently outside settlements in the meadow area of rivers (s. Višňák 1991, Wittig, 1978)
<i>Solidago gigantea</i>	N-America	Similar to <i>S. canadensis</i>	
<i>Symphytum asperum</i> agg.	Caucasus	Abandoned garden areas in villages	Amongst others <i>S. peregrinum</i> and <i>S. x uplandicum</i>
<i>Veronica filiformis</i>	Caucasus, Asia Minor	Lawns	Müller and Sukopp (1993)

<sup>a</sup>Generally according to Adolphi (1995); if not mentioned there, after Oberdorfer (2001);

<sup>b</sup>Author.

necessary disturbance into consideration we can determine the following suitable migration routes:

- streets (e.g. Kopecký, 1988; Nowack, 1993; Radkowitzsch, 1996; Griese, 1998);
- railway tracks (e.g. Dürer 1886; Koster, 1985; Wittig et al., 1985);
- waterways (rivers and channels) (e.g. Sukopp and Scholz, 1965; Pyšek and Prach, 1993).

### Anecophytes

There are several species coexisting with humans since prehistoric times, of which we do not know their natural habitats. We therefore must assume that these species are obligatory weeds (Scholz, 1991) in anthropogenous habitats. Examples are *Bromus hordeaceus*, *Capsella bursa-pastoris*, *Chenopodium album*, *Ch. hybridum*, *Cynodon dactylon*, *Hordeum murinum* s.str., *Poa annua*, *Senecio vulgaris*, and *Stellaria media* (Sukopp and Scholz, 1997). Due to the lack of extant natural habitat these species are called anecophytes. A well-known example is represented by the genus *Oenothera* L., which contains many species that originated in Europe from North American ancestors. Scholz (1993) estimates that the European *Solidago canadensis* is on the way to become a new species, because many of its morphological traits differ from those of the American type.

The development of anecophytes can be caused by:

- former selection as useful plant and later escaping from cultivation (e.g. *Pastinaca sativa*);
- unintentional selection due to agricultural measurements (e.g. *Bromus secalinus*);
- hybridization (e.g. *Poa annua* is supposed to be a hybrid of the mediterranean *Poa infirma* and the Central European montane *P. supina*);
- accelerated speciation as a result of the “founder effect” (e.g. genus *Oenothera*).

### Trends and dynamics

The trends and dynamics in the development of the flora of cities reported in this chapter have been detected by the following methods:

- comparison of the recent urban flora with the flora of the city environment;
- comparison of the flora of cities with the flora of neighbouring villages,
- comparison of the recent city flora (results of recent documentation) with the former flora (results of older documentation)
- observation of the reaction of the flora of villages to urbanisation,
- determination of plants and pollen reported from archaeological research.

Until the 15th century the flora of settlements per definition contains only indigenous species and archeophytes. As cities were much smaller than today, one may assume that the difference between the flora of cities and rural settlements was even smaller. The general composition of some plant communities in cities in Roman times was already very similar to that of today. Knörzer (1987) testified for Cologne (Germany) that trampling communities with *Plantago major* and *Polygonum aviculare* agg., annual ruderal communities with *Bromus sterilis*, *Chenopodium album*, *Ch. murale*, *Sisymbrium officinale* and *Urtica urens*, and perennial ruderal communities with *Arctium* spec., *Artemisia vulgaris*, *Ballota nigra*, *Lamium album* and *Onopordum acanthium*, which are still present, existed already during the Roman period.

The rediscovery of America in 1492 led to an increase of trade and traffic and thus caused the first occurrences of neophytes. However, the neophytes probably remained more or less restricted to sea ports and a few inland centres of trade (capitals and residential cities). The general character of the average city flora did not change.

A great increase in traffic and trade resulted from the introduction of railways and steam vessels at the beginning of the 19th century. The consequence for the urban flora was a great increase in the number of species arriving from foreign countries and continents, especially weed seeds present in ships ballast. However, there is often a time lag between the first record of a new species and its spreading. Therefore it was not until the end of the 19th century that a remarkable increase in the number of neophytes was registered. In those times the establishing of neophytes was promoted by an enormous growth of the cities, which provided large areas of high disturbance suitable to the naturalisation of neophytes. According to Jäger (1988) and Zajac et al. (1998) the greatest influx of neophyta to Europe occurred in the second half of the 19th century. Sudnik-Wojcikowska (1987b), however, demonstrates by the example of Warsaw that the greatest increase in the distribution of neophytic species accompanied by a decrease in indigenous species and archeophytes was observed during the two world wars and in the first decade after the 2nd world war. At present the average flora of cities in Central Europe consists of 60% of native species, 15% of archeophytes, and 25% of neophytes (Pyšek, 1998). The ongoing increase in global temperature may lead to a new increase in the number of neophytes in cities. However, it is always very difficult to differentiate between temperature increase and other causes which favour neophytes (Sukopp and Wurzel, 1995). It also should be carefully observed whether

genetically modified plants bear any synanthropic potential (c.f. Sukopp and Sukopp, 1993a, b).

During the last two decades not only changes in the species composition but also in the habitat conditions have taken place in urban areas. Many of these changes favour the survival and spreading of the spontaneous urban flora. E.g., many lawns in parks and public gardens are no longer weeded intensively and no longer protected from trampling, but used as dog latrines, which results in new species combinations (Wittig, 2001). Vast areas of former industrial and railway terrain have changed to brown fields, now housing a rich ruderal flora and vegetation (Dettmar, 1986, 1992; Rebele and Dettmar, 1996). The use of herbicides in railway stations and along tracks was drastically reduced, so that these areas now have been colonised by new vegetation (Wittig, 2002c; Wittig and Lienenbecker, 2002, 2003, 2004). Finally the weeding intensity in housing areas is often remarkably reduced, due to changes in the population structure and in the attitude towards ruderal vegetation (see Hard, 1998; Hard and Kruckemeyer, 1990). Thus today the number of individuals of neophyta in cities and towns of Central Europe is much higher than it was some decades ago.

When summarising the results concerning the development of the spontaneous flora of Central European cities and towns the following trends become obvious (Kowarik, 1992):

- Remarkable decrease in the percentage of indigenous and archeophytic species, in particular of those that have a narrow ecological amplitude and/or are strictly bound to oligotrophic habitats;
- increase in the population of a small group of indigenous species resulting from a change from natural to synanthropic habitats (apophytisation, synanthropisation);
- immigration of alien species (neophytes), in particular to disturbed habitats;
- development of new ecotypes, subspecies and species.

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