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Biological flora of Central Europe: *Ailanthus altissima* (Mill.) Swingle

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Abstract

Ailanthus altissima (tree of heaven), Simaroubaceae, is an early successional tree, native to China and North Vietnam, which has become invasive in Europe and on all other continents except Antarctica. It is most abundant in urban habitats and along transportation corridors, but can also invade natural habitats. This paper reviews the literature on the morphology, distribution, ecology, habitat requirements, population biology, genetics, physiology, impacts, management and uses of this species.

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Keywords: Dispersal; Plant invasion; Plant trait; Plasticity; Species biology; Temperature change

Taxonomy and morphology

Taxonomy

According to Nooteboom (1962), *Ailanthus altissima* (Mill.) Swingle 1916 (Simaroubaceae) is one of five species within the genus *Ailanthus* Desf. (Mém. Phys. Math. Acad. Sci. Paris 1786, 265, tab 8 1788) nom. cons. Different from *A. altissima,* its congeners *A. excelsa* Roxb., *A. integrifolia* Lam. (incl. *A. calycina* Pierre), *A. triphysa* (Dennst.) Alston, *A. fordii* Nooteboom (in Fu and Hong (2001) affiliated to *A. triphysa*) show a subtropical range. Other authors differentiated more species within the genus *Ailanthus*, e.g. 15 in Engler (1931).

Synonyms *of A. altissima* (tree of heaven, Götterbaum, ailanto, ailante) are *Ailanthus glandulosa* Desf. 1786, *A. procera* Salisb. 1796, *A. giraldii* Dode 1907, *A. vilmoriniana* Dode 1904, *A. peregrina* (Buc'hoz) F.A. Barkley 1937, *A. cacodendron* (Ehrh.) Schinz & Thell. in Thell. 1912, *A. procera* Salisb. 1796, nom. illeg., *A. rhodoptera* F. Mueller 1863, *A. sutchuensis* Dode 1907, *Albonia peregrina* Buc'hoz nom. illeg. 1783 sine descr., *Pongelion cacodendron* (Ehrh.) Degen, *P. glandulosum* (Desf.) Pierre, *Rhus cacodendron* Ehrh. 1783, *R. hypselodendron* Mönch, *R. sinense* Ellis 1757, *R. peregrina* (Buc'hoz) Stapf 1929, *Toxicodendron altissimum* Mill. 1768. Fu and Hong (2001) treat *A. vilmoriniana* and, conditionally, *A. giraldii* as distinct species. The same specimen grown from Chinese seeds in France had been described in 1904 as *A. vilmoriniana* Dode and as *A. glandulosa* Desf. var. *spinosa* M. Vilm. & Bois. The spiny character of young branches disappeared at the still living specimen, and as fruit and leaf traits broadly overlap in trees assigned to *A. vilmoriniana* or *A. altissima*, Geerinck (1990) treated both species as the same.

The name of the genus is thought to derive from the common Moluccan name 'Aylanto' referring to the native *Ailanthus integrifolia* and meaning "tree reaching for the sky" (Engler, 1931; Hu, 1979). From China,

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written names for *Ailanthus altissima* can be found dating back at least to 100 BC. The Chinese name 'ch'un-shu' means spring tree (Hu, 1979).

Within the native Chinese range, *A. altissima* var. *sutchuensis* (Dode) Rehd. & Wilson is differentiated from var. *altissima* (see below). For Taiwan, the var. *tanakei* (Hayata) Kanehira et Sasaki has been described (Huang and Editorial Committee of the Flora of Taiwan, 1977). Several cultivars have been horticulturally selected including 'Aucubaefolia', 'Erythrocarpa', 'Hongye', 'Pendulifolia', 'Purple Dragon', 'Thousand Leaders', and 'Tricolor' (Krüssmann, 1976; Zhang and Dirr, 2004). Plants with red fruits have been combined as *A. altissima* f. *rubra* (Dippel) Geerinck comb. nov. (Geerinck, 2002).

Throughout the paper, information on *Ailanthus altissima* (henceforth mentioned only by its genus name) refers to the variety *altissima* if not differentiated otherwise.

Morphology

Stems and branches

Ailanthus is a medium-sized tree which attains maximum heights of 27–30 m in the temperate zone (Hegi, 1906; Lauche, 1936) and 18–20 m in the (sub-)meridional zone (Hunter, 2000; Arnaboldi et al., 2003). The tallest tree known grew in a park near Bonn (Plittersdorfer Aue), Germany; at the age of 130 years, it had a height of 30 m and a stem diameter of 1.27 m (Lauche, 1936). Ehlert (pers. comm.) reported another tree from Bonn with a DBH of 1.18 m. *Ailanthus* produces shorter spur-like stems on older trees that terminate in compound inflorescences, and longer stems in younger, rapidly growing trees that continue to elongate throughout the growing season (Davies, 1937; Davies and Theiss, 1937).

Renewal shoot growth starts from lateral buds, while terminal buds always obliterate. *Ailanthus* shows acrotonic branching in trunk formation and growth in height is sympodial-modular. The modules are initially equal and all apparently branches, but later a vigorous one becomes prominent functioning as sympodially formed trunk and leading to a forked, sparse and irregular crown shape. Inflorescences are terminal (see below). This habit fits the crown architecture model of Koriba (Hallé et al., 1978). Secondary change in branch orientation is an important feature of this model. After 10–15 years, branching changes to dichasial or monochasial patterns while the prolongation of the lowest branches follows an acroton-hypotonical pattern.

Leaf-bearing branches are green with short hairs. Older branches are reddish-brown and have large heart-shaped leaf scars with a roundish bud at the top. Stems have gray bark and show shallow diamond-shaped fissures with age (Hu, 1979; Hunter, 2000). The heartwood is yellowish with dark streaks, while the sapwood has a cream color. The wood is ring porous with wide rays. At 54.5%, the share made up of pulp exceeds that of aspen at 42% (Adamik, 1955). Further wood characteristics are described by Moussalli (1939), Moslemi and Bhagwat (1970), Grosser (1977) and Arnaboldi et al. (2003).

Initially, branching is rare in *Ailanthus* as young saplings invested most tissue in the development of the main stem axis and leaves (Table 1). Two-year-old saplings in Berlin allocated a high percentage of biomass to roots, and developed 1.2 ± 0.5 shoots from stems from the preceding year (I. Säumel and I. Kowarik unpubl. data), older trees in North America between 2.2 ± 0.2 and 2.3 ± 0.1 shoots (Davies and Theiss, 1937). Branching in 2-year-old saplings of *Acer platanoides* and *A. negundo,* cultivated under the same conditions*,* exceeded that of same-aged plants of *Ailanthus* by a factor ranging between 3.3 and 5.0 (I. Säumel and I. Kowarik unpubl. data). Studying the biomass allocation in five older *Ailanthus* trees, Singh et al. (1992) found most biomass was allocated to stems, followed by the root system, leaves and branches (Table 1).

Leaves

Large, odd-pinnately compound, pubescent or nearly glabrous, with terete petioles, enlarged at the base and often tinged above. The leaflets are ovate-lanceolate with two to four glandular teeth at the rounded base (Hu, 1979). They may be arranged symmetrically or asymmetrically at the petiole (Troll, 1939). The terminal leaflet may have 1–2 enlarged lobes and may differentiate an additional single leaflet, pretending a 'double' terminal leaflet (Heidenhain, 1932). Leaves are extipulate, while short-lived awl-shaped basal leaflets, as pseudostipules, may pretend stipules (Weberling and Leenhouts, 1965). Seedlings have trifoliate leaves above two rounded epigeal cotyledons. Leaves from emerging root sprouts are yellowish-green at first and vary in the number of divisions from unifoliate to pinnately compound (Hu, 1979).

Leaf size and number of leaflets are highly variable. Most authors reported maximum leaf lengths between 0.6 and 1.0 m (e.g. Hegi, 1906; Hunter, 2000). Root sprouts, however, especially when subject to physical disturbance, can produce much larger leaves. The largest leaf known thus far is from a repeatedly cut plant from an urban site in Berlin, which produced a 3.0-m current-year shoot. The leaf had a length of 1.67 m, a maximum width of 0.46 m, 43 leaflets and a leaf area of 30.6 dm^2 (Kowarik and Säumel, 2006a). Comparing leaf characteristics of central European and Mediterranean populations shows that *Ailanthus* can develop similarly shaped leaves in different climate zones (Table 2). With its large leaves and relatively low intensity of branching

Table 1. Biomass allocation of *Ailanthus altissima* in (A) 1-year-old seedlings ($n = 7$), (B) 2-year-old saplings ($n = 5$), both from Berlin, Germany (I. Säumel and I. Kowarik, unpubl. data), and (C) older trees from the western Himalayas ($n = 5$, calculated from data of Singh et al., 1992)

Range			Biomass allocation (%)			
	BD$^{\#}$ or DBH‡ (cm)	Total biomass per plant (kg)	Stem	Branches	Leaves	Roots
A$^{\#}$	0.6–0.69	0.015–0.025	38.9 ± 3.0	0.0 ± 0.0	45.5 ± 5.1	15.5 ± 6.1
B$^{\#}$	12.9–15.5	67.2–78.4	32.2 ± 1.4	0.0 ± 0.0	28.4 ± 2.4	39.4 ± 3.3
C‡	16.2–47.3	47.7–115.6	39.1 ± 3.9	16.3 ± 2.4	18.5 ± 2.3	25.7 ± 2.7

BD, basal diameter; DBH, diameter at breast height.

Table 2. Morphological characteristics of *Ailanthus* leaves from roadside populations in Berlin, Germany, and southern France (Département Gard)

	Berlin ($n = 12$)			Southern France ($n = 10$)		
	Mean ± SD	Min	Max	Mean ± SD	Min	Max
Shoot						
Max. current-year shoot height (cm)	140 ± 64^{a}	55	245	107 ± 27^{a}	60	151
DBH (cm)	13.4 ± 41.4^{a}	9.3	22.9	15.2 ± 1.8^{a}	12.5	18.0
Total leaf number per shoot	21.6 ± 4.3^{a}	14	27	18.2 ± 4.1^{a}	12	24
Largest leaf of a ramet						
Position from the top (leaf #)	6.3 ± 2.2^{a}	4	12	5.6 ± 2.3^{a}	4	9
Length (cm)	91.3 ± 20.2^{a}	61.0	121.0	83.3 ± 13.9^{a}	61.0	98.5
Width (cm)	30.2 ± 4.6^{a}	24.0	38.5	28.9 ± 4.4^{a}	24.0	33.5
Length: width	3.0 ± 0.3^{a}	5.5	4.0	2.9 ± 0.2^{a}	5.5	3.0
Number of leaflets	27.9 ± 4.4^{a}	21	33	30.9 ± 3.0^{a}	21	35
Basal diameter of rachis (mm)	6.4 ± 1.4^{a}	4.2	9.2	13.4 ± 2.8^{b}	4.2	16.3
Largest leaflet						
Length (cm)	15.3 ± 2.3^{a}	12.0	19.0	15.3 ± 2.2^{a}	10.4	17.4
Width (cm)	4.9 ± 0.7^{a}	4.0	6.0	4.8 ± 0.7^{a}	3.5	5.7
Length: width	3.1 ± 0.1^{a}	2.9	3.4	3.2 ± 0.2^{a}	3.0	3.5

The age of the analyzed ramets varied between 1 and 3 years and the height was between 0.6 and 3.4 m. Values within the same row are significantly different (Tukey Test, $P<0.05$) if means are followed by different letters.

(see above), *Ailanthus* appears to be a good example for Corner's rule that postulates a negative correlation between branching density and leaf size (Corner, 1949). Long and tall rachises are hypothesized to fulfill the space-exploring function of branches (White, 1983).

Leaves are spirally arranged at the stem, either in a clockwise (52%) or counter-clockwise (48%) direction. The mean angle of divergence of the leaves is approximately 138°, ranging from 113° to 165°. After 1.5 revolutions in a usually eight-ranked, or octostichous, leaf arrangement, the fifth leaf is opposite to the first, and after the third revolution, the ninth leaf is in position with the first one. Abnormal leaf arrangement and corresponding branching (fasciation) may occur in rapidly growing young stems (Davies, 1937, 1939; Davies and Bennett, 1929).

Nectaries

Ailanthus has different types of floral and extrafloral nectaries (Fig. 1), which have been intensively studied (Davies, 1943, 1946; Bory and Clair-Maczulajtys, 1978, 1980, 1982, 1986; Clair-Maczulajtys and Bory, 1983). Davies (1943) described two types of leaf glands: simple glands as outgrowths of epidermal cells that are scattered over the surface of young leaflets and more specialized glands along the basal margins of the leaflets. Each leaflet has 1–8 such glands, with an average of 2.6. In expanding leaf buds, marginal glands appear first on the tenth unit (Davies, 1946). Pseudostipules also have nectaries (Fig. 1).

The nectaries excrete different forms of sugar up to October. The duration of nectar production and its chemical composition vary seasonally and among types of nectaries and male, female and non-flowering trees. The ablation of the foliar nectaries leads to a sugar accumulation in the leaf, and slows down the reconstitution of starch reserves in the branch. Bory and Clair-Maczulajtys (1986) interpreted the nectaries' function "as being the elimination of excess sugars." After the opening of the buds, the first leaves have

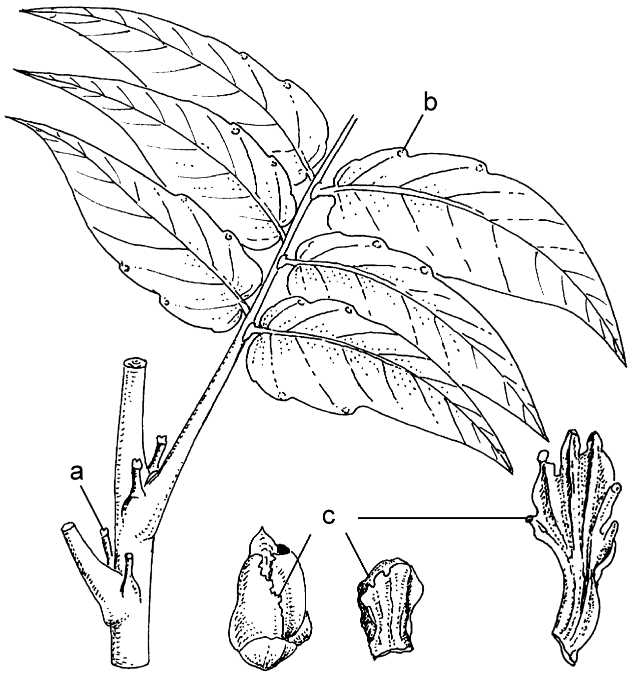

Fig. 1. Localization of different types of extrafloral nectaries in *Ailanthus altissima* occurring at (a) pseudostipules, (b) leaves, and (c) cataphylls (adapted from Bory and Clair-Maczulajtys, 1986).

stalked nectaries with apical pores located at the base of the petioles. Also the adaxial surface of the lamina has stalked nectaries (Clair-Maczulajtys and Bory, 1983). Different types of hairs emerging on cataphylls and young stems after bud burst secrete lipids (Clair-Maczulajtys and Bory, 1985a, b).

Flowers

Ailanthus is a dioecious tree. Female flowers may have stamina, but these do not contain pollen (Nooteboom, 1962). Other authors suggested that flowers might also be bisexual or the trees monoecious, but empirical data on the occurrence and proportion of flower types in populations are missing. Nooteboom (1962, p. 215) and Hu (1979) never observed bisexual flowers. Possibly, some authors address female flowers with sterile stamina as bisexual or 'hermaphrodite'. The yellowish-green inflorescences are arranged in a large double thyrsus at the end of new shoots (Troll, 1964). Male inflorescences are larger and produce more flowers than those on a female plant (Hu, 1979).

According to Hegi (1906, Fig. 1717) and Engler (1931, Fig. 182), a flower has a tiny cupular and 5-lobed calyx, a corolla with five distinct petals and an annular 10-lobed glandular disc. A male flower has ten spreading functional stamina, each with a globular fertile anther and a glandular green disc; carpels are rudimental or missing. A female flower has <10 sterile stamina with abortive anthers, a green glandular disc, a pistil with 5–6 free carpels, styles joined toward the base, free or connate, and a star-like stigma. Male flowers emit an unpleasant odor. Basal and apical parts of the glandular discs have different types of floral nectaries (Davies, 1943; Bory and Clair-Maczulajtys, 1982). The elliptic, tricolporate pollen belongs to the *Rhus*-type and averages 31.5 μm in size (Beug, 2004; Fig. 2e).

Fruits

After flowering, the carpels develop into five (or one to four) samaras (Hu, 1979). The samaras are spirally twisted with one centrally placed seed (Fig. 2). Their color varies from greenish yellow to reddish brown. The embryo lacks an endosperm, but has two large cotyledons with stored oils (Little, 1974). The number of seeds per kilogram averages from 27,000 to 33,000 (Little, 1974). Xiong et al. (1983) found considerable variation in seed color, size, weight and thickness of samaras among trees of 49 provenances from 11 regions of the Yangtze River valley, China. Seed traits also varied widely among populations from southern France (Table 3), while individual and interannual variation in seed shape was small (Bory and Clair-Maczulajtys, 1980). Compared with these data, the range of seed trait variation was smaller in the studied central European populations (Table 3). In North America, samara size ranges from 8 to 12 mm in width and 33 to 48 mm in length (Feret and Bryant, 1974; Feret et al., 1974). From Belgium, Geerinck (1990) reported lengths of 35–60 mm.

Roots

Already as a seedling, *Ailanthus* develops several lateral roots and a taproot, where most carbohydrate and protein reserves are stored (Dubroca and Bory, 1981). Roots at soil depths between 0 and at least 100 cm have several (only in part macroscopically visible) pre-existing primordia or suppressed buds that easily form root suckers. These can emerge from root fragments as small as 1 cm in length and a few millimeters in width (Inverso and Bellani, 1991). Lazarevic et al. (1961) observed root connections between densely sown seedlings.

The spatial extension of the root system is highly variable and often asymmetrical based on the availability of soil water and nutrients (Fig. 3). Kiermeier (1987) reported lateral roots in a subterranean canal at a distance of 27 m from the parent tree. On an urban site in New York, 2-year-old seedlings developed lateral roots up to 2 m. The average root lengths (114.4 cm) were three to four times as long as those of *Acer platanoides* and *Liquidambar styraciflua*. In contrast to these species, lateral roots in *Ailanthus* were coarse, unbranched and widely spread, thus exploiting a much greater soil volume (Pan and Bassuk, 1986). Studying the root system of five trees with DBH ranging from 16 to 46 cm, Singh et al. (1992) found a maximum tap-root

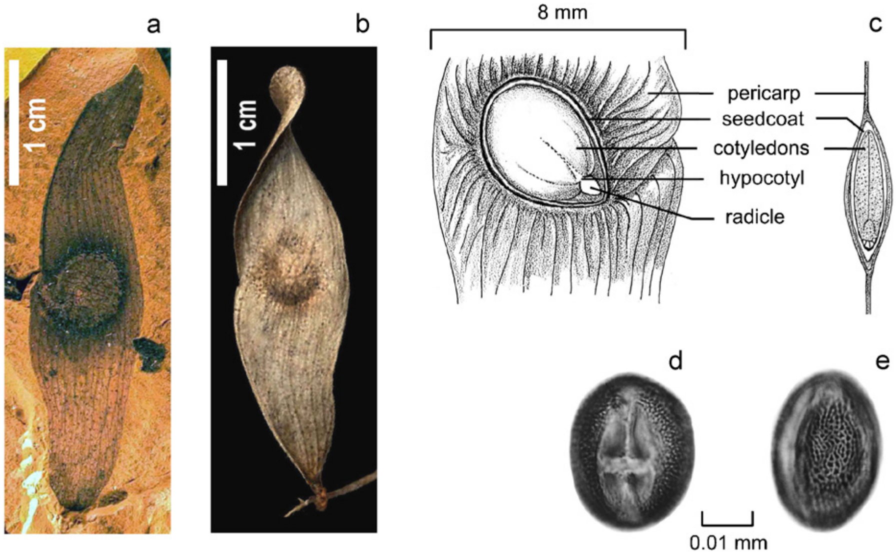

Fig. 2. (a) Fossil samara of *Ailanthus confucii* Unger from North America (adapted from Corbett and Manchester, 2004, Int. J. Plant. Sci., © by The University of Chicago); (b) samara of *Ailanthus altissima*, (c) longitudinal sections through a samara (adapted from Little, 1974); (d, e) pollen of *A. altissima* (from Beug, 2004).

Table 3. Dimensions of samaras and seed grains (southern France: calculated from data in Bory and Clair-Maczulajtys, 1980; Bioflor: Klotz et al., 2002; Berlin: I. Säumel and I. Kowarik unpubl. data; –, no data)

	Southern France ($n = 21$)			Bioflor			Berlin ($n = 50$)		
	Min	Max	Mean±SD	Min	Max	Mean	Min	Max	Mean±SD
Dimensions of samaras									
Weight (mg)	8.5	44.1	29.9±8.1	24.3	38.7	33.6	20.0	37.0	30.4±3.4
Length (mm)	18.5	50.6	42.8±7.6	30.0	50.0	39.1	42.0	52.0	47.2±2.3
Width (mm)	5.7	13.8	10.4±1.9	8.0	12.0	9.9	8.2	11.4	9.4±0.6
Surface (cm^2)	0.61	4.55	3.4±1.0	–	–	–	–	–	–
Thickness (mm)	–	–	–	1.5	2.5	2.0	0.8	1.9	1.5±0.2
Dimensions of seed grains									
Length (mm)	–	–	–	3.0	5.8	4.6	–	–	–
Width (mm)	–	–	–	3.0	5.0	4.2	–	–	–
Weight (mg)	3.1	17.3	11.0±2.9	–	–	14.9	13.0	21.0	17.2±1.9

length of 2.05 m. The number of lateral roots varied from six to nine with an average length of 0.57–2.16 m per tree. One-year-old *Ailanthus* saplings, cultivated under optimal conditions allocated most biomass in the vertical axis, while *Acer platanoides* and *A. negundo* invested more in the root system (von der Lippe et al., 2005). Compared with these species, biomass allocation in *Ailanthus* is more effective due to a greater stem height gain per biomass invested.

Genetic variation

Ailanthus is a tetraploid species with $2n = 80$ chromosomes (Fedorov, 1969). Slavík (1997) reported 80 and 64 chromosomes. Genetic differences among populations have been investigated by analysis of isoenzyme frequency for the secondary range and correlated to significant differences in seed and height characteristics within North American populations (Feret et al., 1974). Seed width and biomass are correlated with latitude, with northern populations having the widest, heaviest seeds. Trees from California grow taller than eastern populations. The observed differences were not related to climatic or edaphic features. A comparison between North American and Chinese populations revealed significant differences in 11 of 14 growth traits (Feret and Bryant, 1974). Populations within the secondary range were taller, allocated relatively less biomass to roots than to stems, and had greater leaf areas than

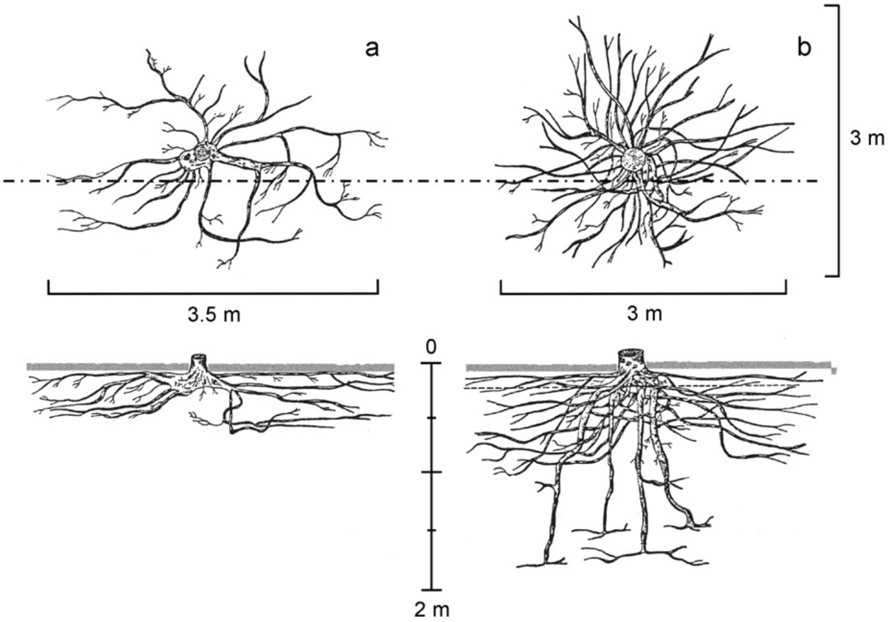

Fig. 3. Variable architecture of the root system in different soil types in Hungary: (a) 21-year-old tree and (b) 25-year-old tree (adapted from Faragó, 1964).

Chinese plants. Although they are likely descended from only a few introductions, trees of the North American provenances showed no tendency toward inbreeding depression nor a significant difference in total genetic diversity compared to Chinese plants. The same isoenzyme frequency was found in both provenances, indicating that the gene pool in *Ailanthus* in North America is as diverse as in the native range. Feret and Bryant (1974) suggested that significant alterations of genetic content have occurred in the 200 years since the first introduction, possibly influenced by selection of plants with the best growth performance for propagation. A 10-year seed source trial revealed a broad variance in mortality and growth characteristics among provenances (Feret, 1985).

First steps for investigations of genetic and genotypic diversity in European populations were recently done by Dallas et al. (2005) who developed nine DNA markers from Mediterranean populations.

Distribution and habitat requirements

Geographical and altitudinal distribution

Fossil records show *Ailanthus* taxa, subsumed under the name *Ailanthus confucii* Unger, in the northern hemisphere Tertiary (Corbett and Manchester, 2004; Fig. 2a). Records cover the Paleocene to Pleistocene in East Asia, the Paleo- to Pliocene in North America, the Eo- to Pliocene in Europe (with the oldest known occurrence in Messel, Germany) and in Western Siberia and Kazakhstan (Mai, 1995; Corbett and Manchester, 2004).

The native range of recent *Ailanthus altissima* covers large parts of China, where the species grows as a natural component of broadleaf forests (Fig. 4). It occurs in a range from Liaoning and Hebei Province in the north to Guangxi and Fujian Province in the South, and from Zhejiang and Shandong in the East to Gansu Province in the West. With a partly overlapping range in China the variety *sutchuensis* (Dode) Rehd. & Wilson can be differentiated from the variety *altissima*. The Chinese range as shown in Fig. 4 may however include a human-induced range expansion because *Ailanthus* had been cultivated since early times (Hu, 1979).

Ailanthus has developed a secondary range on all other continents except Antarctica with a broad latitudinal range from the temperate to meridional zones. It is most frequent in the meridional and submeridional zones (Fig. 5). Both, the native and secondary ranges match well climatic conditions characterized by a long and warm growing season, regular winter frost and annual precipitation of mostly >500 mm. The current distribution corresponds extensively to the *Staphylea* type described by Meusel and Jäger (1992). The potential, climatically determined range seems to be colonized, but global warming may enhance further range expansion (E.J. Jäger, pers. comm.).

In North America, it grows across a broad range of climatic conditions from Florida, to the arid Southwest and the temperate Northeast (Miller, 1990) at elevations <1600 m in the Denver region (Feret, 1985) and <2100 m in New Mexico (Howard, 2004). In the temperate Himalayas, *Ailanthus* grows at 1500–1800 m (Singh et al., 1992), and <500 m on the Azores (Schäfer,

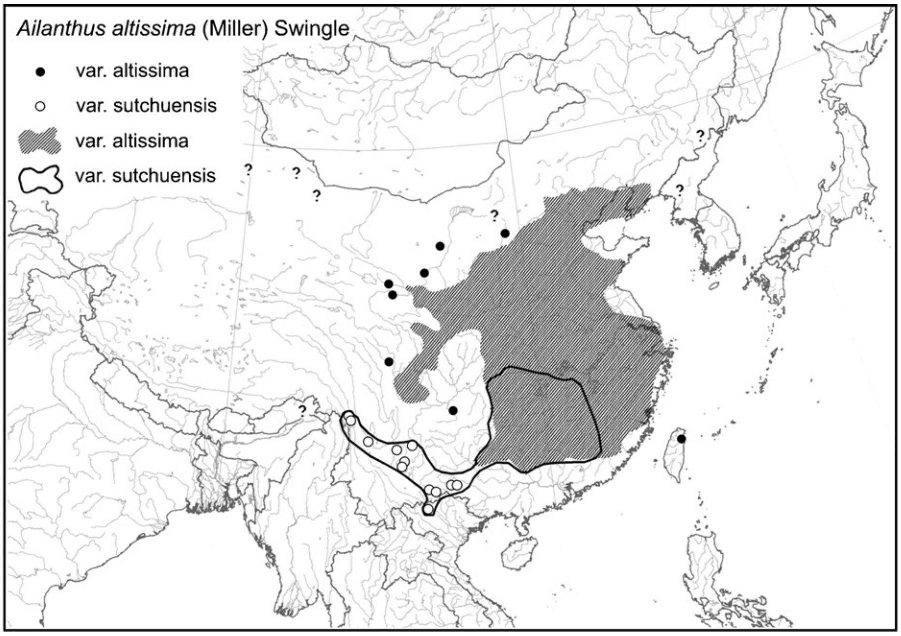

Fig. 4. Native range of *Ailanthus altissima* in China and North Vietnam, with a differentiation of the ranges of the varieties *altissima* and *sutchuensis* (distribution data compiled and mapped by E. J. Jäger & E. Welk, AG Chorology, Institute for Biology Halle/Saale). Herbaria records of possibly synanthropic occurrences are given by question marks.

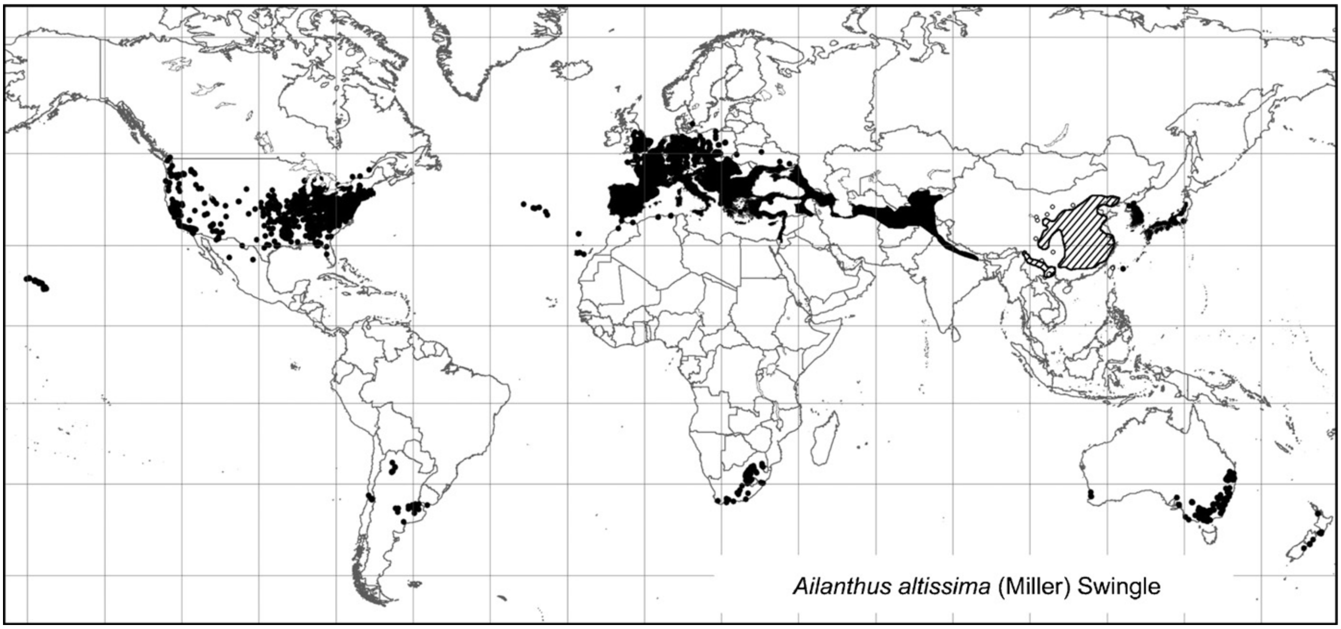

Fig. 5. Range of *Ailanthus altissima,* with a differentiation of the native Chinese range (hatched; including possible early range expansions within China), and of the secondary world-wide distribution (black) resulting from the range expansion since the introduction of *Ailanthus* to Europe in the 1740s (distribution data compiled and mapped by E. J. Jäger & E. Welk, AG Chorology, Institute for Biology Halle/Saale).

2003). In temperate Europe, *Ailanthus* is virtually confined to the lowlands and to low mountain ranges with more favorable climates, such as the Rhine valley. In the Mediterranean, *Ailanthus* occurs <1000 m, e.g. at 1012 m in Vytina, Greece (T. Mavromatis, pers. comm.), 800 m in Korfu on the northern slope of the Pancratos (H. Kuhbier, pers. comm.), and up to 800 m in Montenegro's Lovcen Mountains (I. Säumel, pers. observ.). In China, var. *sutchuensis* occurs between 700 and 2500 m (E.J. Jäger, pers. comm.).

In Europe, *Ailanthus* shows a closed distribution area in the Mediterranean. Along a gradient from the meridional to the temperate zone, its occurrences are increasingly confined to cities at northern outposts of its range. This had been mostly attributed to the effects of urban climate, assumed to provide a longer vegetation period, compensating for missing heat sums, and to curb frost intensity and duration towards the northern limits of its range (Kowarik and Böcker, 1984; Gutte et al., 1987; Sudnik-Wojcikowska, 1998).

The North American distribution pattern and habitat preferences diverge distinctly from the European. Within temperate North America, *Ailanthus* colonizes a broad habitat range in the zone of eastern hardwood forests (Table 5). In contrast to Central Europe, it is not confined to cities although it is usually most abundant in urban habitats. Because winters are usually harsher in temperate North America than in Central Europe, other ecological factors than low winter temperatures appear to drive the divergent distribution patterns. Schenck (1939, p. 58) suggested that length of (and temperature during) the vegetation period function as decisive factors. Wilhelmi (1958) reported frost injury as less severe when occurring subsequent to long, warm summers. As shown below, *Ailanthus* is more sensitive to cold temperatures in juvenile stages than in older stages, and at the same time, responds positively in many growth traits to increased temperatures during the vegetation period.

Until the 1980s, *Ailanthus* preferentially colonized parts of Central Europe with warm summers, i.e. those subject to subcontinental or sub-Mediterranean climate conditions. This held true even for the cities that were northern outposts of the range, as cities subject to an oceanic climate were virtually free of *Ailanthus* (see distribution maps in Kowarik and Böcker, 1984; Gutte et al., 1987). Since the 1980s, distribution has also occurred in coastal cities as well as in those that are exposed to a colder regional climate such as Zurich (Landolt, 2001) or Polish cities (Sudnik-Wojcikowska, 1998; Tokarska-Guzik, 2005). This recent range extension coincides with a period of several successive years of mild climate (IPPC, 2001), which are generally believed to facilitate seedling establishment even in colder regions (Miller, 1990).

Ailanthus has thus far colonized mostly urbanized areas in Germany (Kowarik and Böcker, 1984; Gutte et al., 1987; map available at http://www.floraweb.de), Poland (Tokarska-Guzik, 2005) and the British Isles (Preston et al., 2003). Within cities, distribution patterns mostly show a confinement to inner-city areas and a decreasing frequency along urban–rural gradients. In the 1980s, 92.2% of inner-city grid units in Berlin had *Ailanthus,* but only 3.2% of the urban-fringe grid units, and the distribution pattern reflected the impact of the urban climate (Kowarik and Böcker, 1984; Fig. 6b). Distribution maps exist for Augsburg (Müller, 1987), Berlin (Böcker and Kowarik, 1982; Kowarik and Böcker, 1984), Frankfurt, Gießen and Mainz (Kramer, 1995), Halle and Leipzig (Gutte et al., 1987), London (Burton, 1983), Vienna (Punz et al., 2004), Warsaw (Sudnik-Wojcikowska, 1998), Zurich (Landolt, 2001) and Rome (Celesti-Grapow, 1995; Fig. 6c).

In warmer regions of Europe, in the transition between the temperate and meridional zones, and in the Mediterranean, *Ailanthus* is common in cities, but also colonizes a broad range of rural sites. It is the most frequent non-native tree species in Thessaloniki (Krigas and Kokkini, 2004) and also among the most frequent nonnative species of Italian cities (Celesti-Grapow and Blasi, 1998). In Rome, for example, 180 of 190 mapping units from Celesti-Grapow et al. (2001) had *Ailanthus*. Its distribution map however shows no confinement to the inner city (Fig. 6c). The same holds for the Korean city of Cheon-ju, which is under subtropical climatic influence (Choi, 2004).

History of introduction and uses

The superior range expansion of *Ailanthus* on all continents except Antarctica has been facilitated by a world-wide human-mediated transfer of seeds over the last 250 years and subsequent cultivation for a broad array of uses. *Ailanthus* was first introduced to France by the French missionary Pierre d'Incarville in the 1740s who sent seeds from Nanking to Paris (Hu, 1979). From there, *Ailanthus,* often confounded with the varnish tree *Rhus verniciflua,* was brought early to London (1751) and to other parts of Europe (Hu, 1979; Kramer, 1995). It was first introduced from European seed sources to North America via Philadelphia in 1784 (Shah, 1997). In the late 19th century, Chinese immigrants are believed to have introduced *Ailanthus* to the West Coast because of its cultural significance (Feret, 1985; Hoshovsky, 1988).

In its native Chinese range, *Ailanthus* has traditionally been used since early times in folk medicine (see below), as a timber and fuelwood tree and as forage for silk worms (Hu, 1979). It was planted soon after its introduction to Europe as an ornamental in landscape parks (e.g. since 1780 in Potsdam; Bolle, 1887). Around 1850, it became fashionable as a promenade tree in European and North American cities because of its resistance to herbivory and its tolerance of urban conditions. Due to the unpleasant odor of male flowers, it was later eradicated at many locations (e.g. Engelhardt, 1901; Moussalli, 1939; Shah, 1997). Its use as an ornamental and shade tree however continues today. In the 1950s, plantations for shelterbelts of up to 160 ha year^{-1} were established in southeastern Austria (Burgenland; Adamik, 1955). *Ailanthus* was planted for similar reasons in southeastern Europe and in arid regions of the former Soviet Union (Buchholz and von Maydell, 1965). Further uses include plantations for erosion control on slopes, verges of traffic lanes (Hegi, 1906; Singh et al., 1992) and dunes on the coast of the

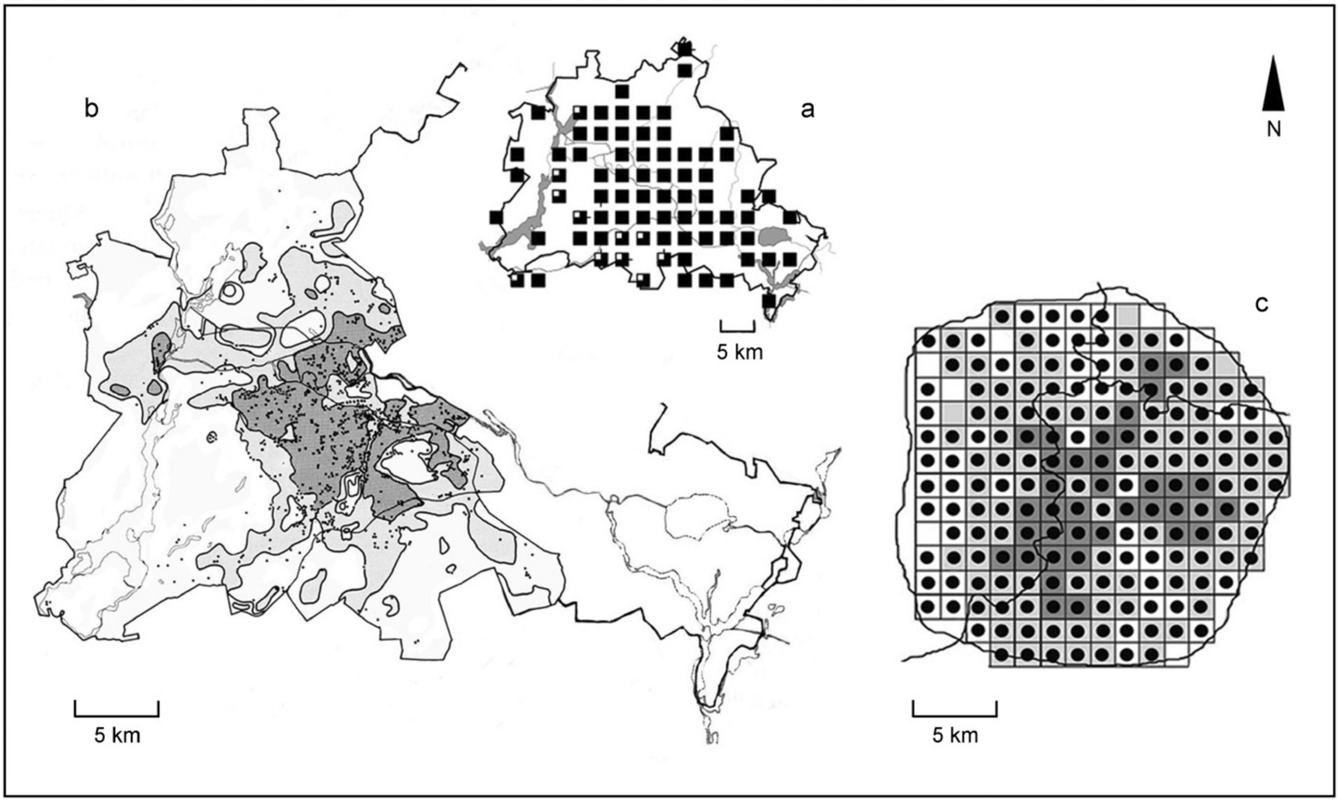

Fig. 6. Concentric distribution of *Ailanthus altissima* in a Central European city (a), Berlin; adapted from Regionalstelle, 2006; (b), relationship between location of trees (dots) and different temperature zones in the western part of Berlin: the warmest zone is in darkest shade; adapted from Kowarik and Böcker, 1984) and area-wide distribution in Rome as an example of a Mediterranean city (c, adapted from Celesti-Grapow, 1995).

Black Sea (Moussalli, 1939); for afforestation or reforestation in Hungary and Czechia (Udvardy, 1998; Křivánek et al., 2006), southeastern Europe, the Middle East, South America and New Zealand (Cozzo, 1972; Hu, 1979; Howard, 2004); and rarely for the reclamation of landfill sites (Witte, 1952) and mine spoils (Gutte et al., 1987). In the late 19th century, *Ailanthus* was cultivated in France as forage for the Chinese silk-producing caterpillar *Samia cynthia* (Rebel, 1925; Moussalli, 1939). In addition, *Ailanthus* functions as food for honeybees; the honey is tasty but initially bad smelling (Melville, 1944; Dalby, 2000).

Medical uses

Ailanthus is traditionally used in Chinese folk medicine as an astringent, antispasmodic, anthelmintic, parasiticide and narcotic (Moussalli, 1939; Hu, 1979). Howard (2004) summarizes further uses of plant parts or extracts: fresh stem bark to treat diarrhea and dysentery; root bark for heat ailments, epilepsy, and asthma; fruits as an emmenagogue and to treat ophthalmic diseases; and leaves as astringent used in lotions for seborrhoea and scabies. Recent pharmacological studies indicate a broad array of possible uses of quassinoids, for example to treat malaria (Okunade et al., 2003), Epstein–Barr-virus infection (Tamura et al., 2003), and HIV infection (Chang and Woo, 2003). In addition, *Ailanthus* is used for homoeopathic remedies (Boericke, 1991).

Habitats

Ailanthus grows on a broad range of anthropogenic to natural sites, from stony and sterile soils to rich alluvial bottoms. Most are subject to a higher level of natural or human disturbance such as urban habitats and transportation corridors.

Urban

All over the temperate to meridional zones, *Ailanthus* colonizes a broad array of urban habitats ranging from walls, fence rows, cracks of sidewalks, and road and railroad embankments to abandoned lots and urban parks (Hu, 1979; Kowarik, 1983; Kowarik and Böcker, 1984; Pan and Bassuk, 1986; Wei, 1989). In Italy, it is among the most common alien species occurring in the urban flora of different phytoclimatic regions (Celesti-Grapow and Blasi, 1998). Hegi (1906) reported first spontaneous occurrences for Germany from derelict urban sites (Mannheim, Freiburg, 1906). In many

Central European cities, as well as in London (Burton, 1983), an abundant colonization began on sites that were opened up by bombing in World War II (Kreh, 1956; Kohler and Sukopp, 1964; Forstner and Hübl, 1971). In Berlin and Vienna, *Ailanthus* today is closely associated with built-up areas, green spaces and railway areas (Table 4).

An analysis of micro-sites in Ithaca, New York, showed that within a city block *Ailanthus* was relatively more frequent on sites with limited topsoil than in open habitats (Pan and Bassuk, 1986). In Basel, 20% of mapped individuals had colonized cracks and crevices; 40% were found in private and public green spaces (Lenzin et al., 2001). In Vienna, *Ailanthus* is most abundant on derelict railway areas (Punz et al., 2004), while in Berlin, it primarily grows in residential areas, mostly close to buildings and within associated courtyards and gardens (Kowarik and Böcker, 1984).

Table 4. Occurrences of *Ailanthus altissima* in different land use types in the cities of Berlin and Vienna

	Berlin		Vienna	
	N	%	*N*	%
Built-up areas[a]	355	56.2	60	24.9
Roadsides	43	6.8	–[b]	
Public green spaces[c]	122	19.3	86	35.7
Railway areas	56	8.9	62	25.7
Water courses Table 5 (channels, rivers)	33	5.2	–[d]	
Urban wastelands	21	3.3	33	13.7
Forests	2	0.3	0	0
Total	632	127	241	100

Adapted from Kowarik and Böcker (1984) and from Punz et al. (2004) data for Berlin refer to the western part of the city, data for Vienna refer to a transect from the center to the southeastern outskirts; –, no data.

[a] Including courtyards, walls, fences, paved areas, crevices in concrete or asphalt, gardens associated with buildings.

[b] In Vienna, roadsides were assigned to the built-up areas.

[c] Parks, graveyards, playgrounds.

[d] Not present in the study area.

In Mediterranean cities, *Ailanthus* is often reported as growing out of walls, in crevices of sidewalks and along roadsides (e.g. Danin, 2000). Although *Ailanthus* is not confined to urban habitats in temperate North America, a study from West Virginia showed a higher frequency in urbanized compared to less urbanized counties (Huebner, 2003; Table 5). It also spreads on landfill sites (Kim et al., 2004) and mine spoils (Gutte et al., 1987). In Beijing, *Ailanthus*, together with *Ulmus pumila*, is the most frequent spontaneously growing tree species that colonizes a broad range of habitats, whereas most other tree species are restricted to green spaces (Wei, 1989).

Transportation corridors

Outside of cities, *Ailanthus* preferentially colonizes transportation corridors, and among these mostly road and railroad verges and medians of motorways (e.g. Adolphi, 1995 for the Rhineland). Mainly starting from roadside verges, *Ailanthus* can invade borders of agricultural fields, meadows, vineyards and old fields (Kowarik, 1983; Facelli and Pickett, 1991; Huebner, 2003). In the studied part of southern France, the majority of populations within the rural landscape grew along roads, and from there also encroached into agricultural fields and near-natural shrub communities by clonal growth (Kowarik, 1983; Table 5). *Ailanthus* is common on Mediterranean islands (Lloret et al., 2004; Vila et al., 2006), and on Crete, its distribution is linked to the main transport network of major roads (Hulme, 2004).

Studies from eastern North America show similar patterns. In southwestern Virginia, 30% of the mileage along the interstate highways was colonized by *Ailanthus* (Burch and Zedaker, 2003). It also colonizes other types of linear habitats, such as railroad verges and stream banks, forest edges and skid trails in forests (Call and Nilsen, 2003; Huebner, 2003; McDonald and Urban, 2006; Table 5). In North Carolina, it colonizes primarily major highways, but is even more associated with railroad rights-of-way (Merriam, 2003). Abundant roadside populations have also been reported in the

Table 5. Range of habitats colonized by *Ailanthus altissima* outside of settlements in the Département Gard, southern France (adapted from Kowarik, 1983), and West Virginia, United States (adapted from Huebner, 2003)

Southern France	%	West Virginia	%
Roadsides	57.7	Roadsides	43.1
From roadsides			
Encroaching into agricultural fields and vineyards	16.7	Railroads	11.8
Encroaching into near-natural evergreen shrub communities	19.2	Trails	5.9
Water courses	5.1	Water courses	17.6
Forests	1.3	Forests	5.9
		Other	15.7

western Himalayas (Singh et al., 1992). In South America (Santiago de Chile, Buenos Aires and Mendoza Province) *Ailanthus* grows in cities, on abandoned land and along railway embankments, road verges, small rivers and creeks.

Forests

In Europe, *Ailanthus* invades riparian forests as well as some mesic and xeric woodlands, preferentially in the submeridional to meridional zones (see below). The species can (co-)dominate pioneer forests on urban sites. In temperate North America, hemlock, oak-hickory and maple-birch forests are also subject to invasions, mostly subsequent to disturbances (Miller, 1990; Huebner, 2003; Table 5). These may be human-induced, such as timber harvests (Call and Nilsen, 2003) or management of other non-natives species (Webb et al., 2001), or can result from natural gap openings due to heavy storms (Knapp and Canham, 2000) or insect herbivory on native species (Orwig and Foster, 1998). Knapp and Canham (2000) characterize *Ailanthus* as a gap-obligate species. It also colonizes slopes, rocky outcrops and debris avalanches (Hull and Scott, 1982; Arnaboldi et al., 2002).

Invasions of forests and river banks have been reported in floodplains of the Danube (Gutte et al., 1987; Drescher et al., 2005), and along streams and riverbeds in the Insubrian region of southern Switzerland (Arnaboldi et al., 2002), in southwestern France (Tabacchi and Planty-Tabacchi, 2003), the Mediterranean (Kowarik, 1983; Lepart and Debussche, 1991), Japan (Müller and Okuda, 1998), and North America. In the western United States, *Ailanthus* colonizes riparian zones including the banks of the Rio Grande (Howard, 2004) and riverbeds in mid-lower elevations of California (Hunter, 2000). It also colonizes river and stream habitats (Huebner, 2003; Merriam, 2003) of eastern North America and there grows well in tidal estuaries in the vicinity of the mean high water level (Kiviat, 2004). In arid regions of Central Asia, *Ailanthus* is increasingly confined to wet habitats (Gutte et al., 1987).

Communities

In the temperate zone, *Ailanthus* occurs in all stages of succession on urban sites from annual pioneer communities (Sisymbrietea, Chenopodietea), to stages dominated by perennial herbs and grasses (Convolvulo-Agropyretea, Artemisietea), to shrub communities (Urtico-Sambucetea; Gutte et al., 1987). On wastelands, it may form pioneer forests, often associated with *Robinia pseudoacacia* or *Acer* species (Kowarik and Böcker, 1984; Gutte et al., 1987). In North American hardwood forests, *Ailanthus* also co-occurs with *Robinia* and *Acer platanoides* (Call and Nilsen, 2003, 2005). In addition, it is a frequent, and often only pioneer on urban sites (Pan and Bassuk, 1986). Rarely in temperate Europe, does *Ailanthus* invade natural shrub communities such as the Pruno-Ligustretum on rocky outcrops of the Rhine valley (Lohmeyer, 1976).

In floodplain forests, e.g. those of the Danube, *Ailanthus* is associated with *Populus alba, P. nigra* and *Fraxinus excelsior* (Gutte et al., 1987). In southern Switzerland, Arnaboldi et al. (2002) reported *Ailanthus* from riparian woodlands with *Alnus incana* and *Fraxinus excelsior,* in Berberidion shrub communities, in *Castanea sativa* coppice forests, in ruderal meadows (Arrhenatheretalia), on acidic rocky sites co-occurring with *Calluna vulgaris* and on natural debris avalanches. In Hungary, it invades calcareous and acidophilous grasslands including steppe vegetation of protected areas (Udvardy, 1999). The Hungarian biotope survey, based on 70% of the country, showed *Ailanthus* occurring in about 3% of all riverine shrub- and woodlands, in 7% of all mesic decidous woodlands, in 14–22% of all closed, and open, dry *Quercus* woodlands, in 34% of all steppe woodlands, in 13% of all dry and semi-dry grasslands, in 29% of open sandy, and 35% of open rocky grasslands (unpubl. data from the MÉTA Database 1.0. Institute of Ecology and Botany, HAS, Vácrátót; see http://www.novenyzetiterkep.hu/meta/en/). It is also frequently associated to *Robinia*-forests that were not covered by this survey (Z. Botta-Dukat, pers. comm.).

In the transition to the submeridional zone, as in Slovakia and in the warmest parts of Hungary and Austria, *Ailanthus* is associated with near-natural and natural shrub and forest communities (Crataego-Prunetea, Quercetea pubescenti-petraeae). It often co-occurs with *Robinia pseudoacacia*, with *Acer negundo* on loess, and with *Prunus mahaleb* on limestone (Udvardy, 1998). In Austria, Mucina and Kolbek (1993) described an *Ailanthus altissima*-(Lamio albi-Chenopodietalia) community. On south-exposed slopes, it may form shrubs with *Syringa vulgaris*. In Georgia, *Ailanthus* forms shrub communities on slopes with *Carpinus orientalis* and *Cotinus coggygria* (Gutte et al., 1987). In the Mediterranean, *Ailanthus* may also invade evergreen shrub communities (garrigue, Quercetum cocciferae), mostly encroaching from disturbed road verges. Only rarely, it is associated with *Quercus ilex* forests (Quercetalia ilicis; Kowarik, 1983).

Response to abiotic factors

Temperature

Ailanthus tolerates a broad amplitude of climatic conditions, but seasonal variation in temperature strongly affects survival, growth and spreading. Climate chamber experiments revealed a high plasticity in growth patterns in response to thermal changes (I. Säumel and I. Kowarik, unpubl. data). As the overview in Table 6 shows, most architectural and growth traits responded positively to the warmest variant, while the performance of the saplings was significantly curbed in the coldest chamber compared to the control. Compared with *Acer negundo* and *A. platanoides*, two frequently co-occurring tree species in urban habitats, *Ailanthus* appears to be much better adapted to warming and strongly handicapped by chilling. Saplings survived in the coldest chamber, although with reduced growth, but 1.5-month-old seedlings that were exposed to the same temperature regimes in a parallel experiment did not (Hildebrand, 2006). This clearly emphasizes the greater susceptibility of early ontogenetic stages to low temperatures.

In the saplings, higher temperatures induced a shift of biomass investment from transpiring tissue to water-accessing tissue (Table 6). *Ailanthus* invested significantly more biomass in roots and less in leaves in the warmer compared to the colder and control chambers. This was associated with a markedly enhanced rooting depth, achieved by an increased main root elongation and volume increment, and with an increased lateral soil exploration by a higher number of secondary roots. As higher temperatures often coincide with drought stress, *Ailanthus* benefits from a reduced allocation to transpiring tissue coinciding with an enhanced relative growth rate of belowground biomass, an increased root elongation and a shift to fine and coarse roots within the root system. Increased temperatures also led to an earlier bud break, but the temperature sum from day of exposure to the day of the first bud break remained constant in all three climate chambers (I. Säumel and I. Kowarik, unpubl. data). Increasing temperature also enhanced allelopathic effects (Lawrence et al., 1991).

Table 6. Significant changes in architectural character and growth traits in *Ailanthus altissima* saplings after exposure to different day/night temperate regimes in climate chambers

	LT	ET
Non-photosynthetic tissue		
Stems		
Total stem height	− −	+ + + +
Basal diameter	−	+ +
Stem volume	−	+ + + +
Slenderness ratio	− − − −	+ + +
Internode number	+/−	+ + + +
Internode length	− − −	+ +
Stem basal area (SBA)	−	+ + + +
Stem tip area	− − −	+ + + +
Stem elongation rate	− −	+ + + +
Circumferential growth rate	− −	+ + + +
Stem mass fraction	+ + + +	+/−
Specific stem mass	+ +	+ + + +
Specific stem height	+ + +	− −
Branches		
Branch number per sapling	+/−	+/−
Branch dry weight	+/−	+/−
Single branch weight	+/−	+/−
Branch mass fraction	− − − −	+/−
Roots		
Main root elongation rate	− −	+ + + +
Main root dry weight	− −	+ + + +
Fine and coarse root dry weight	−	+ + + +
Fine and coarse root mass to root mass ratio	− −	+ + + +
Specific root mass	− − − −	+/−
Main root length increment	− −	+ + + +
Number of secondary roots	− − −	+ + + +
Main root volume	− −	+ + + +
Specific root length	+ + + +	−
Photosynthetic tissue		
Leaves		
Time from exposure to first bud break	+ + + +	− −
Leaf longevity	+/−	− − − −
Leaf number	− −	+
Leaves on branches	+/−	+/−
Total leaf area (LA)	−	+ + + +
Foliar biomass	−	+ + + +
Single leaf size	−	+ + + +
Single leaf weight	−	+ + + +
Specific leaf area	+ + + +	+/−
Pinna number	− − −	+ + + +
LA:SBA	− −	+/−
Leaf mass fraction	− − − −	− −
Leaf area ratio	− − − −	− − − −
Specific leaf mass	+/−	+ + + +
Relative growth rate		
Above- and belowground	− − − −	+ + +
Aboveground	− − − −	+ + + +
Belowground	− − − −	+ + +

The symbols illustrate the effect of lower temperature (LT, 10/05 °C) and elevated temperature (ET, 20/15 °C) compared to the control chamber with a day/night temperate regime of 15/10 °C). The control was oriented towards the daily average temperature of 13.8±5 °C during the growing season in Berlin from March until October. Original data were analyzed for amount and direction of parameter change due to elevated or decreased temperature compared to control. The greatest response in each trait was set as 100%, given as (+ + + +) or (− − − −) for increase or decrease, respectively. The number of symbols illustrates the relative response to the different temperature regimes. The symbol +/− indicates that changes were not significant (after Säumel, 2007).

Frost

Cold injury varies with plant age. In early life stages, *Ailanthus* is most susceptible to frost. In an exposure experiment across an urban–rural gradient in Berlin, 1-year-old saplings suffered from 100% mortality, while *Acer negundo* and *A. platanoides* survived at all sites. This strong die-back in *Ailanthus* was related to the rapid temperature drop with low temperatures between −10 and −16 °C across the urban–rural gradient at the beginning of December following a mild November (von der Lippe et al., 2005). In another exposure experiment across an urban–rural gradient in Hannover, seedlings showed no significant differences in stem height after the first vegetation period (Fig. 7a), but after the second vegetation period, stem height was negatively related to the increasing frost damage during the preceding winter which varied significantly across the urban–rural gradient (Fig. 7b–c). In southern Bavaria, which has a cold-humid climate, regeneration from seeds occurred only rarely (Kiermeier, 1969).

Due to immaturity, winter killing of the upper part of the shoots is common. In the stems studied by Davies and Theiss (1937), stem development started in two successive years from bud position 4.4±0.1 and 9.2±0.7 from the top. In 1-year-old root and stem sprouts from a Central European population, the die-back in shoots from the preceding year averaged 20.5±7.1 cm (I. Kowarik and I. Säumel, unpubl. data). Die-back in the top of shoots also occurs, albeit to a lesser extent, in Mediterranean populations (Blauzac, Département Gard, France): In 2006, it averaged 1.2±1.9 cm in 1–6-year-old ramets and 7.7±3.5 cm in the 14-year-old parent tree (I. Kowarik and I. Säumel, unpubl. data).

Frost injury to young plants as well as to the upper shoot parts of older plants can be related to a long growth period that coincides with a delayed hard frost. Field experiments in Berlin showed that *Ailanthus* had a significantly longer growth period than *A. platanoides* and *A. negundo* and accumulated freeze-protecting soluble sugars later than these species (I. Säumel and I. Kowarik unpubl. data). Hence, early autumnal frost events might be necessary for frost injury to occur.

Older plants may survive cold winters. Temperatures below −15 to −20 °C led to a sharp dieback in shoots that was partly compensated for in the following vegetation period (Scheerer, 1956; Kühn, 1957). As Fig. 7 shows, the amount of die-back in shoots however may negatively influence the height gain in the following vegetation period compared to less injured plants. Experiences from very cold winters show that adult individuals do endure deep frost, e.g. in 1928/1929 up to −33 °C in Bavaria, although with severe damage (Schaaf, 1930). In Russia, 6-year-old trees have survived winters of −33 °C accompanied by high winds (Zelenin, 1976). Von Bartossagh (1841) reported that late frost in spring induced the loss of all leaves, which was however compensated for in the same year.

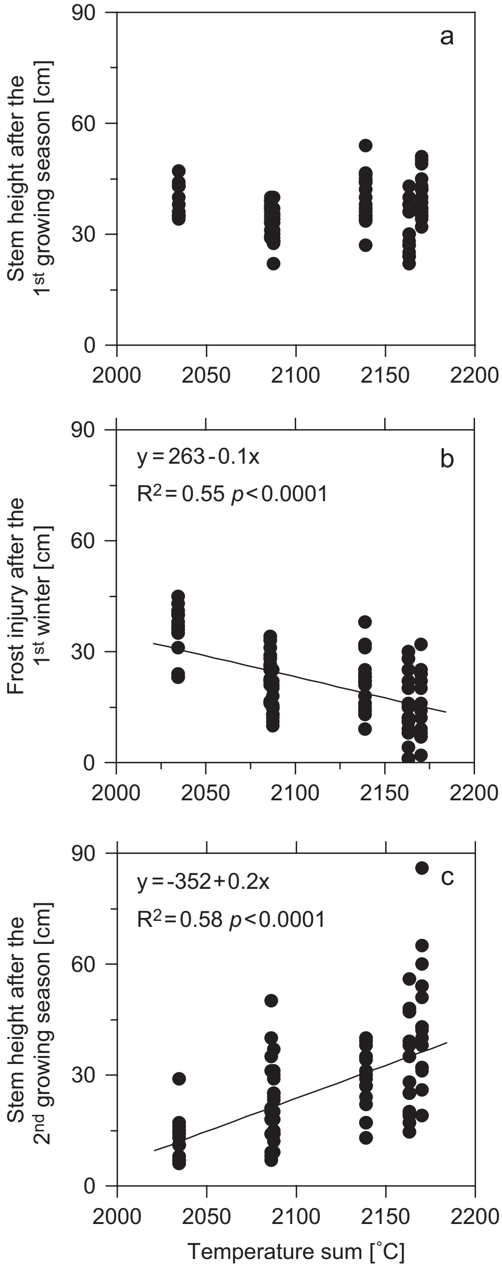

Fig. 7. Response of *Ailanthus altissima* seedlings during the 1994 vegetative period to varying temperature sums ranging from 2035 to 2170 °C across an urban–rural gradient in Hannover, Germany (adapted from Kowarik, 2003). (a) Stem height after the first growing period; (b) frost injury after the following winter, expressed as length of shoot die-back; and (c) stem height after the second growing period.

Ice load

In contrast to most other species, *Ailanthus* showed little damage during an exceptionally heavy load of ice after a winter storm (Croxton, 1939).

Drought

Ailanthus often grows in habitats where limited water availability coincides with high air temperatures, fostering the loss of water through transpiration. *Ailanthus* adapts to drought stress by combining morphological plasticity with some physiological adaptations. It explores water by a root system that is more extended than in other tree species (see above). Elevated temperatures induce a switch in biomass allocation from aboveground plant parts to the root system as well as an increased stem volume (Table 6). This suggests an enhanced uptake of water from soil and vascular movement due to a larger cross-sectional area. The ring-porous structure of water-conducting tissue permits rapid transfer of water from the roots to the leaves at up to $22\,\mathrm{m\,h^{-1}}$ at noontime (Meyer, 1982). As a response to increasing drought stress, stomata are progressively closed to reduce water loss by leaves and to maintain homeostasis in leaf water potential above the turgor loss point. As an additional water-saving mechanism, hydric stress also leads to reduced root hydraulic conductance (Trifilò et al., 2004). Graves et al. (1991) found that roots grown at 34 °C had lower hydraulic conductivity coefficients than roots grown at 24 °C.

Under drought stress, carbohydrates and protein reserves that are mainly localized in the taproot of seedlings were shown to be quickly hydrolyzed (Dubroca and Bory, 1981; Clair-Maczulajtys et al., 1993). Despite water deficiency, starch synthesis increased in leaves and stems during the first stages of stress. Stems showed increased cambial activity and protein content. Later, with the abscission of the terminal bud at the end of the experiment, carbohydrate, lipid and protein contents markedly decreased in stem and taproot while the level of soluble sugar, starch synthesis, stability of proteins and lipid accumulation were enhanced in the lateral roots. Clair-Maczulajtys et al. (1993) emphasized that facing drought stress, *Ailanthus* may quickly mobilize its reserves, then strengthen its cambial growth, and under continuing stress finally reallocate its reserves to the lateral roots from which new ramets can emerge after the loss of the primary shoot.

Shade

Ailanthus is classified as a shade-intolerant, early successional species (Knapp and Canham, 2000) with highly efficient photosynthesis on open sites (Marek, 1988). High levels of net photosynthesis were reported for *Ailanthus* (PN about $20\,\mu\mathrm{mol\text{-}CO_2\,m^{-2}\,s^{-1}}$; Marek, 1988). Hamerlynck (2001) highlighted the uniqueness of *Ailanthus* for its capacity to couple high, shade-plant-like photosynthetic efficiency with high photosynthetic capacity in high irradiance. In shade, stomatal attributes that optimize water-use efficiency are maintained. These features may also facilitate the colonization of natural habitats with more limited photosynthetic photon flux densities compared to open urban habitats (Hamerlynck, 2001).

In contrast to shade-tolerant species, *Ailanthus* leaves that developed in shade had higher compensation points, lower rates of photosynthesis per unit area and lower relative rates of apparent photosynthesis in weak light (Bourdeau and Laverick, 1958). Consistently, seedlings were able to germinate, but not to establish new individuals under a closed forest canopy (Grime and Jeffrey, 1965; Kowarik, 1995; Knapp and Canham, 2000). Bory and Clair-Maczulajtys (1977) found an enhanced height growth of cotyledons with increasing light intensities. The mean extension rate of saplings in gaps was about three times higher compared to forested areas (Kim, 1990). By colonizing open gaps, *Ailanthus* may reach the canopy faster than co-occurring native tree species (Knapp and Canham, 2000) and may then develop clonal ramets even in the shady sub-canopy (Kowarik, 1995). At forest edges or in old-field succession, ramets may be found in shady conditions when other parts of the population receive full sunlight (I. Kowarik, pers. observ.).

Soils

Ailanthus grows on a broad range of natural and human-modified soils ranging from barren rocky substrates to sandy or clayey loams to calcareous dry and shallow soils and artificial depositions of gravel, sand and other materials, tolerating also saline and alkaline soils (Kowarik and Böcker, 1984; Miller, 1990; Singh et al., 1992). In Hungary, for example, *Ailanthus* colonizes soils originating from sand, loess, dolomite and limestone (Udvardy, 1998). It also grows in tidal estuaries on sandy and loamy soils that are moderately well drained, seasonally wet and slow to dry out, with a maximum salt content of about 0.5 ppt; on the coast, roots can be submerged in sea water (Kiviat, 2004). Reclamation studies yielded better results on acid mine spoils than on calcareous spoils (Miller, 1990). *Ailanthus* tolerates pH$<$4.1, soluble salt concentrations up to $0.25\,\mathrm{mS\,cm^{-1}}$, and phosphorus levels as low as 1.8 ppm (Plass, 1975). A soil with NaCl content up to 0.20% ($6.50\,\mathrm{mS\,cm^{-1}}$) did not reduce the germination rate (Bicknell and Smith, 1975). *Ailanthus* is recommended as a salt-tolerant tree (Dirr, 1976).

Growth is best on nutrient-rich, loamy soils, but *Ailanthus* also tolerates nutrient-poor soils (Miller, 1990). Consistently, Pan and Bassuk (1985) found a better seedling growth in sandy loam compared to sand (cf. Rabe and Bassuk, 1984). A fertilization trial (Soják and Löffler, 1988) revealed a positive response to increased availability of nutrients: Two years after applying NPK fertilizer (N, $60\,\mathrm{kg\,ha^{-1}}$; P, $43\,\mathrm{kg\,ha^{-1}}$; K, $81\,\mathrm{kg\,ha^{-1}}$) average height and diameter growth were 3.0 m and 49.3 mm, compared to 1.9 m and 31.7 mm for control plants. In a greenhouse experiment, growth was better on an anthropogenic rubble soil and on a sandy soil than on a peaty substrate (Bachmann, 2005).

Soil compaction

Pan and Bassuk (1985) compared the root development of *Ailanthus* seedlings in compacted and non-compacted sand and sandy loam. Compaction in both soil types reduced the plant dry weights to about 50% and also affected the relation between lateral and taproots. In non-compacted soils, *Ailanthus* produced a thick taproot and 2–3 large lateral roots. Lateral roots accounted for 23.7% of the total root dry weight in sand and 34% in loam. After 146 days of growth, the lateral root length averaged 41.6 and 48.8 cm in sand and in loam, respectively. In both substrates, compaction decreased lateral root length to 23.6–32.3 cm. While compaction curtailed the taproot growth in both soil types, the lateral root dry weights partially compensated for this loss and, after 76 days of growth, exceeded the lateral root weights in the non-compacted soils. In compacted sand, lateral roots accounted for 50% of the total root dry weight and 74% in compacted loam (Pan and Bassuk, 1985).

Ellenberg indicator values

Ellenberg et al. (1991) reported the following indicator values for *Ailanthus*: light, 8 (for seedlings); temperature, 8; continentality, 2; moisture, 5; soil pH, 7; fertility, 8; salinity, 0. Considering the information reviewed in this section, we propose to change the indicator values for continentality to 3, for moisture to 4 and for soil pH and fertility to x (indifferent), and for salinity to 1.

Air pollution

In areas subject to high levels of pollution, *Ailanthus* is among the most tolerant tree species (Kovacs et al., 1982). It is highly resistant to SO_2 (Ranft and Dässler, 1970) and other main components of air pollution. This is supported by the high antioxidative capacity of its leaves associated with a lower level of oxidative lipid breakdown and a higher capacity for detoxification of H_2O_2 in leaves compared to other common urban tree species from the genera *Betula*, *Tilia* and *Platanus*. In contrast to these species, *Ailanthus* was able to react to elevated concentrations of air pollutants with increased activity of ascorbate-specific peroxidase (Rank, 1997). Exposure for 2 weeks to SO_2 concentrations of 0.1 and 0.2 ppm reduced the extension growth and biomass accumulation in 2- and 3-week-old seedlings (Marshall and Furnier, 1981).

Ailanthus is sensitive to ozone. In Italy, severe defoliation and foliar symptoms have been observed since 1985. At a site subject to ozone concentrations up to 128 $\mathrm{nl\,l^{-1}}$ and to acidic drizzle and dew (down to pH 1.4), diffuse yellowing, apical, marginal and spot-like necrosis and interveinal bronzing and stippling occurred as well as defoliation (Gravano et al., 1999). Plants on sites exposed to different ozone concentrations showed foliar symptoms when exposure values reached 5 $\mathrm{ppm\,h^{-1}}$ (Gravano et al., 2003).

Abundance

In general, Nooteboom (1962) reported low abundance in the native range. Species abundance varies strongly across habitats within the secondary range. Mainly in urban environments and along transport corridors, *Ailanthus* may occur abundantly due to both efficient sexual reproduction and clonal growth. In a densely built-up inner-city area of Berlin, *Ailanthus*, with 146.2 stems $\mathrm{ha^{-1}}$ in the field layer, was less common than *Acer* species, but proved to be the most common spontaneously occurring tree in the shrub and tree layers with 30.0 and 7.4 stems $\mathrm{ha^{-1}}$ (Mücke and Kliese, 1991). Punz et al. (1998) reported *Ailanthus* consistently as the most frequent tree in the tree layer of urban wastelands of Vienna. Control measures usually enhance the number of stems within a population. Punz et al. (2004) report 5902 stems $\mathrm{ha^{-1}}$ for a population at a disused railway area in Vienna, which was subject to cut-back of trees. The disturbance of a Mediterranean population induced a shift from 19,660 to 128,650 ramets $\mathrm{ha^{-1}}$ within 4 months (all size classes; I. Kowarik and I. Säumel, unpubl. data). Hull and Scott (1982) reported densities between 671 and 1667 stems $\mathrm{ha^{-1}}$ resulting from the colonization of a debris avalanche over a period of 10 years.

Life cycle and biology

Ailanthus is a short-lived early successional tree that can attain a life span of >100 years. Old trees from Germany were reported by Lauche (1936; 130 years), von Schwerin (1933; 121 years), and Wilhelmi (1958; 113 years). By producing clonal offspring, the genetic individuals are nearly immortal. Sprouts from the first tree introduced in 1784 to America, for example, still exist today (Howard, 2004).

Germination and seedling establishment

Information on germination rates varies broadly in literature. Direct sowing of seeds extracted from samaras in November yielded a germination rate of 98% at a constant temperature of 25 °C (Bory and Clair-Maczulajtys, 1977). Seeds collected in December germinated at rates of 86% and 83% in March and May, respectively, but only 64% germinated in September

(Singh et al., 1992). Little (1974) reported a germination rate of 75% after 1 year of storage. Hildebrand (2006) found 60% of seeds were still able to germinate after being stored for 2 years at room temperature. Germination occurs without stratification but is enhanced by it. After a stay for 0, 4 and 12 days in humid sand, germination increased from 70% to 77% and 96%, respectively (Graves, 1990).

Field experiments showed increasing germination percentages with increasing light (PAR). The proportion of germinated seeds differed not among maternal source trees (Kota et al., 2007). Contact with water significantly influenced the start, duration and rate of germination (Kowarik and Säumel, 2006b): A short 3-day floating period of samaras improved the subsequent germination rate of seeds that had been collected in January (87%) while a 20-day stay at the water surface curbed germination to 32% compared to a rate of 53% in the control. Start and velocity of germination were enhanced by a short and medium stay in water and delayed by a long stay in water. In all variants, number of emerging seedlings and germination kinetics decreased in previously submerged, compared to floating, seeds. In a 20-day floating trial, 10% of seeds directly germinated on the water surface.

In a greenhouse experiment, the germination rate was lower in sand (55%) than in rubble (69%) and peat (71%) substrates (Hildebrand, 2006). In a sowing experiment in the field at altitudes ranging from 400 to 1000 m, germination rate decreased with altitude (Mihulka, 1998).

Seed banking

Although *Ailanthus* does not form a long-term seed bank, it is able to establish temporary soil seed banks. Studies from deciduous forests in New York show it emerging from the seed bank at depth fractions of both 0–5 and 5–10 cm. Seedling number was not related to the importance values of adult trees (Kostel-Hughes et al., 1998). Seeds remained viable on soil (Hildebrand, 2006) and in soil (Kota et al., 2007) for at least 1 year.

Seedling establishment

Facelli and Pickett (1991) and Facelli (1994) studied the combined effects of litter, competition by herbs and insect herbivory on the establishment of *Ailanthus* seedlings in old fields. Without competition by herbs, litter delayed germination, but did not affect the biomass of emerged seedlings. Herb competition reduced seedling growth, but the presence of litter counteracted this negative effect. Litter however also showed negative effects on seedling performance as it fostered damage by enhancing herbivory.

Germination occurs on bare soil as well as under leaf litter. Kostel-Hughes et al. (2005) found no significant differences in the emergence of seedlings on bare soil and under leaf-litter layers of 1–2 and 5 cm deep. However, seedling aboveground and root biomass were about 25 and 70% lower under deep litter than on bare soil. Root-to-shoot ratio and seedling robustness (aboveground biomass divided by seedling height) both decreased with increased litter depth.

Exposure of seeds to water for up to 10 days did not affect the stem increment of seedlings, which was however curbed when seeds stayed for 20 days in water (I. Kowarik and I. Säumel unpubl. data). By testing root and shoot development of seedlings under soil temperatures ranging from 15 to 31 °C, Heninger and White (1974) found best growth at a soil temperature of 19 °C.

Transition to later life stages

Urban populations in Ithaca, New York, were dominated by plants of the smallest size class (70–74%), and a large decline in the next size class suggests a high mortality rate in seedlings (Pan and Bassuk, 1986). Lee and Lee (2006) reported a corresponding size distribution from Seoul. In a neglected inner-city quarter of Berlin, *Ailanthus* was less common in the field layer than *Acer platanoides* and *A. pseudoplatanus*. The transition probability from the field to the shrub and tree layers was however conspicuously higher in *Ailanthus* at 20.5% and 24.7%, respectively, compared to 4.6–5.4% for the shrub layer and 17.9–20.0% for the tree layer in both maple species (data calculated from Mücke and Kliese, 1991).

Stem growth

With a rapid stem elongation, *Ailanthus* is believed to be the fastest-growing tree in North America (Knapp and Canham, 2000; Howard, 2004) and Britain (Mabberley, 1997). Height increment as well as diameter growth are highest in trees between 5 and 10 years old and continue under favorable conditions to an age of 10–20 years, and then begin decreasing (Speranzini, 1937). From Italy, Speranzini (1937) reported a diameter growth in 5–10-year-old trees of 5–10 mm per year, decreasing to 3–4 mm in 50-year-old trees. With an annual radial growth of 2–4 mm, *Ailanthus* showed a significantly higher growth rate than native trees during regeneration in tree-fall gaps in eastern North America (Knapp and Canham, 2000).

One-year-old seedlings can grow to be 1–2 m tall (Hu, 1979). On an urban site, 2-year-old seedlings developed shoots up to 1.72 m with an average shoot length of 0.82 m, which clearly exceeded those of other tree species (Pan and Bassuk, 1986). At forest sites, seedling growth may be much lower (Kota et al., 2007). In trees aged 20–25 years, the mean annual height increment can be less than 8 cm (Illick and Brouse, 1926).

Sprouts from roots, root crowns or stems grow faster than seedlings. Illick and Brouse (1926) reported 0.5 m growth for seedlings, in contrast to 0.8 m for root sprouts and 1.8 m for stem sprouts. Annual shoots can grow up to 3 m (Hegi, 1906; Speranzini, 1937). In a 14-year-old tree in the French Mediterranean, the annual branch extension in the last 3 years ranged from 43.3 to 62.0 cm with a cumulative radial growth between 13.2 and 25.8 mm ($n = 7$). During these 3 years, ramets of the same tree had a vertical extension between 29.4 and 66.1 cm ($n = 32$) per year with a cumulative radial growth between 8.3 and 14.4 mm ($n = 32$). After an experimental basal cut back, the ramets showed a four-months vertical extension from 20 to 119 cm (48.5 ± 26.1 cm, $n = 15$) and a cumulative radial growth between 8.8 and 44.2 mm (15.1 ± 9.2 mm, $n = 15$; I. Kowarik and I. Säumel, unpubl. data).

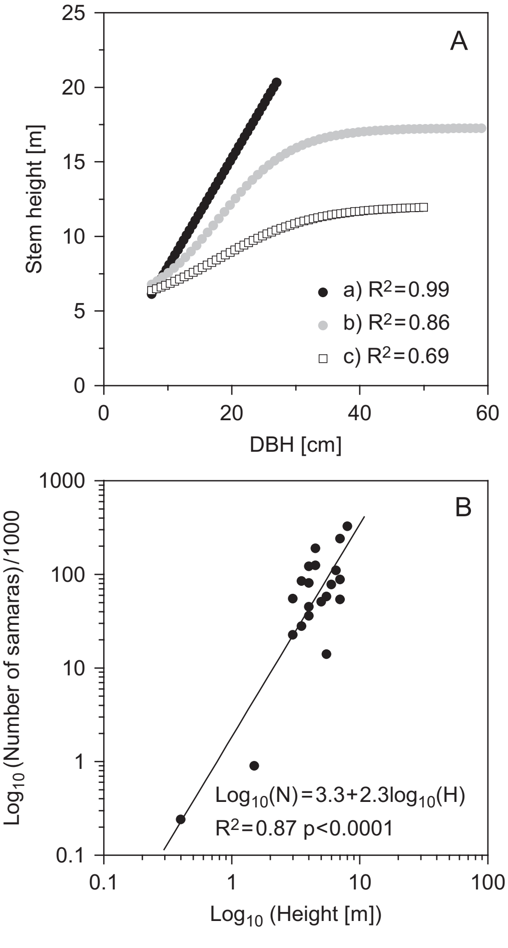

Fig. 8. Height development versus diameter at breast height of *Ailanthus altissima* on different site types (A). Shown are curves of the Boltzmann fit calculated from data from (a) Hungary (Faragó, 1964) and (b, c) Ticino, Switzerland (b: mesic sites; c: xeric sites, Arnaboldi et al., 2003). R^2 of the fit are given. (B) Correlation between tree height [$\log_{10}(H)$] and production of samaras in *Ailanthus altissima* [$\log_{10}(N)$] (calculated using data from Bory and Clair-Maczulajtys, 1980). R^2 and p are given for linear fitting.

Stem growth varies across habitat types and regions. In southern Switzerland, maximum heights on xeric sites were about 2 m less than on mesic sites covered with *Castanea* coppices (Arnaboldi et al., 2003; Fig. 8a). Unfavorable conditions may reduce height increment significantly. On xeric Mediterranean sites, Bory and Clair-Maczulajtys (1980) observed an annual growth rate of 3–5 cm in 5–10-year-old root suckers, which showed less than 1 m of height growth. Mediterranean roadside populations in contact with *Quercus ilex* forests, sometimes subject to cutting during road verge management, however may exhibit growth rates similar to those of Central European populations (Table 2). In the shady understory of a North American oak-sugar maple forest, clonal ramets up to 19 years old, with an average age of 4.7 years and average height of 0.52 m, grew on average only 0.11 m per year (Kowarik, 1995). In climate-chamber experiments, colder conditions curbed stem growth while warmer temperatures increased height development significantly (Table 6).

Reproduction

Ailanthus reproduces abundantly from both seed and root suckers from early life stages. On an urban site, seedlings (42.5%) and root suckers (57.5%) contributed to a total of 1912 excavated established 1-year-old individuals (Pan and Bassuk, 1986).

Sexual reproduction

Ailanthus reaches flowering maturity normally after 3–5 years. Early flowering can occur in 1-year-old seedlings and root suckers (Hegi, 1906). Flowers emerge in seedlings 3 weeks after germination when seedlings are exposed to long photoperiods and high light quantities. The flowers are morphologically abnormal and the developing seeds are not viable (Bory and Clair-Maczulajtys, 1977). Feret (1973) found early flowering 6 weeks after germination. Trees ranging from 12 to 20 years usually show the best seed production (Miller, 1990). *Ailanthus* is pollinated by honeybees, beetles and other nectar- and pollen-feeding insects (Hegi, 1906; Miller, 1990).

Bory and Clair-Maczulajtys (1980) studied seed production in populations from southern France: Seeds grew in fruit clusters with up to 500 samaras per cluster. The number of produced samaras increased exponentially with tree heights ranging from 0.4 to 8 m (Fig. 8b). An 8-m-high tree produced approximately 650 fruit clusters with a total of 325,000 samaras. The percentage of viable seeds varied from 59% to 98% and was lowest in small root suckers. But even these may set fruits, such as a 0.4-m-high shoot that produced four clusters with

240 conspicuously small, but viable, seeds with a mean weight of 8.2 mg. Fruit setting in small root suckers appears to be restricted to xeric Mediterranean sites where growth is often slowed.

Vegetative regeneration

Natural disturbances, such as frost or fire, and human-mediated impacts by cutting, chopping or girdling of stems induce a prolific vegetative regeneration by sprouts that may emerge from the root, the root crown or the stem (von Bartossagh, 1841; Hoshovsky, 1988; Bory et al., 1991). As another pathway to vegetative reproduction, shoot fragments can set adventitious shoots and roots (Kowarik and Säumel, 2006b). Also, undisturbed populations produce root sprouts (Kowarik, 1995).

Vegetative regeneration may originate from pre-existing buds in the hypocotyl, adventitious buds on a cut section, axillary buds of cataphylls present at the base of the new shoots, and from roots (Fig. 9). In an experiment, root suckers emerged from 65.8% of buried root fragments with a length of 22 cm (Singh et al., 1992). Even fragments as small as 1 cm in length and a few millimeters in width can produce root suckers (Inverso and Bellani, 1991). Even seedlings less than 1 year old respond to cutting with a remarkably early development of stump shoots and suckers, increasing in number when subjected to one to three successive cuts within 60 days. Ninety days after each cut, seedlings averaged 1.5, 4.2 and 13.5 adventitious shoots. Most of these were stump sprouts (Bory et al., 1991). In a control experiment in North America, manual cutting 7–15 cm above the ground resulted in an average of 1.6 new sprouts per stem, with 79% of stems resprouting after cutting (Burch and Zedaker, 2003).

The cutting of 21 saplings on an urban site in Hannover, Germany, induced the production of 551 sprouts in the following year, 69% of which were root sprouts and 31% stump sprouts. In the following year, the number of sprouts increased to 722, exceeding the number of cut saplings by a factor of 34.4 (I. Kowarik and I. Säumel, unpubl. data).

Lalhal and Singh (1992) reported on the vegetative regeneration of trees in the Himalayan foothills after a cut back to the root crown. The mean number of root sprouts was 1.0 in the girth class of 0.1–0.2 m and increased to 3.5 in the 0.3–0.4 m class, thereafter again decreasing to 1.0 and 0.5 sprouts in the next two classes. Larger stems produced no sprouts. Shoot length ranged from 0.55 to 0.64 m.

Information on regeneration from stem fragments is contradictory. Singh et al. (1992) reported failing vegetative regeneration from stem cuttings. In an experiment with buried fragments from current-year and second-year stems, 33–75% developed shoots without exposure to water or after a 3–10-day exposure to water. In 10% of all fragments, the emergence of shoots coincided with the setting of adventitious roots, thus indicating a further pathway of asexual propagation (Kowarik and Säumel, 2006b).

Dispersal

Clonal growth

By spacing clonal ramets, genetic individuals can disperse themselves at the local scale. Howard (2004) reported root sprouts appearing as far as 27 m from the parent stem. Under the canopy of a North American oak-sugar maple forest, ramets up to an age of 19 years

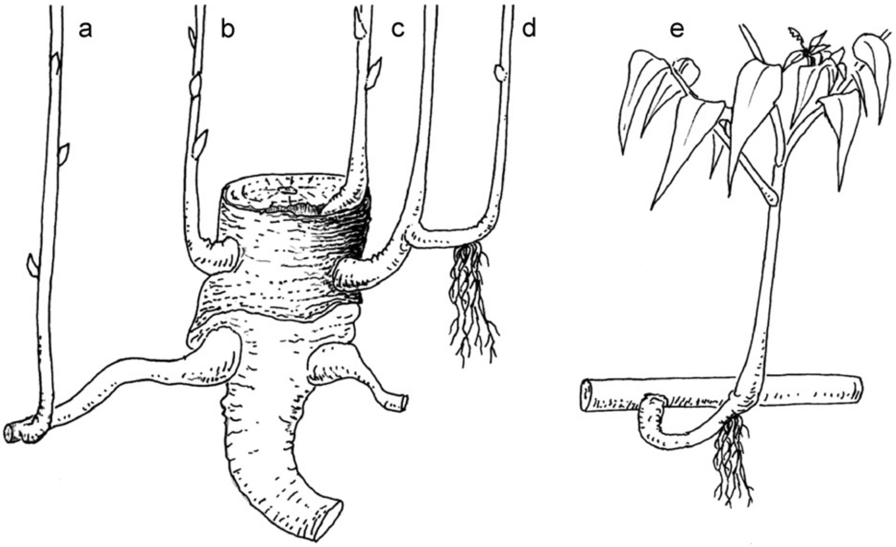

Fig. 9. Vegetative regeneration in *Ailanthus altissima* from (a) roots, (b) pre-existing buds in the hypocotyl, (c) adventitious buds on a cut section, (d) axillary buds of cataphylls present at the base of the new shoots, and (e) from stem fragments (a–d adapted from Bory et al., 1991).

were distributed at a distance of at least 16 m from the parent tree (Kowarik, 1995). In southern France, Kowarik (1983) observed clonal roadside populations up to a length of 120 m. Clonal growth starting on roadsides encroached into evergreen shrub communities out to a distance of 25 m, and arable fields up to 45 m. As clonal populations can be formed by more than one genetic individual, such distances should not necessarily be assigned to a single tree.

Wind

Wind moves samaras both individually as well as aggregated in clusters descending from parts of the panicle. Morphologically, the centrally weighted, spirally twisted, winged samaras of *Ailanthus* are well adapted to wind dispersal (Fig. 2). In addition to their shape, the anatomy of the wings facilitates dispersal by wind as the pericarp has ramified and lignified cells between venation patterns functioning as a kind of empennage covered by the rest of the epiderm and the dry hypoderm (Bory and Clair-Maczulajtys, 1980). Schmidt (1918) reported a rate of descent of samaras of 0.91 m s^{-1} and calculated a medium dispersal distance of 120 m. Matlack (1987) observed a rate of descent of samaras of 0.56 m s^{-1} ($SD = 0.09$). The five longest flights achieved a mean lateral movement of 0.87 m in still air ($SD = 0.1$) after being dropped from a height of 2 m. Using these numbers, a 10 km h^{-1} breeze may result in an estimated lateral transport distance of 112 m when seeds are released from a 20-m tall tree.

As samara morphology varies little within but largely among individuals, considerable variation in seed dispersal can be expected among trees (Bory and Clair-Maczulajtys, 1980). Fig. 10 illustrates the flight types that result from the capacity of samaras to rotate around both their longitudinal axis and their center of gravity, and also to fly without rotation (Fig. 11). As a secondary dispersal vector, wind also moves parts of seed clusters and samaras that have already fallen. In this case, the twisted shape of the samara facilitates lateral transport, which may proceed with or without further rotations along the longitudinal axis (I. Kowarik, pers. observ.).

The long and highly variable period of seed abscission (Fig. 11) enhances the chance that heavy storms will lead to long-distance dispersal. In a field study covering 6 months (Kota, 2005), wind moved samaras at least 200 m over a hay field, with four 18-m high trees as seed sources. As is typical for wind-dispersed trees, seed densities showed a strong decline with increasing distance from seed sources. At urban sites in Korea, Cho and Lee (2002) found 75% of seedlings within 20 m of the parent tree with single seedlings to a distance of about 65 m, and at a restored landfill site in New York, the maximum distance of seedlings from the nearest seed-bearing tree was 70 m (Robinson and Handel, 1993).

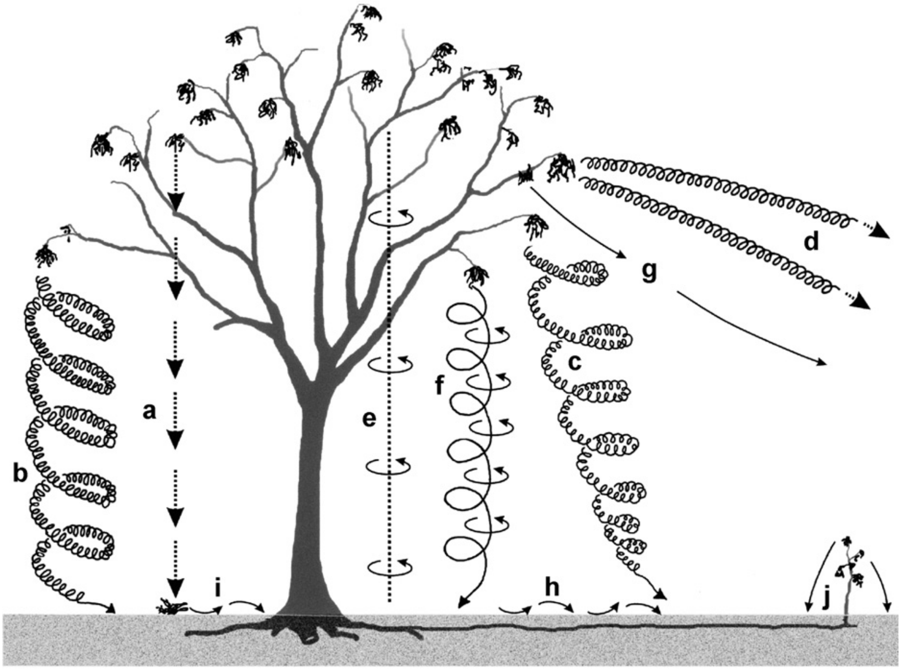

Fig. 10. Different types of transport of samaras of *Ailanthus altissima* (adapted from Bory and Clair-Maczulajtys, 1980). Vertical fall of seed clusters (a), rotation of samaras about their longitudinal axis leads to spirally (b), spirally twisted (c), and straight-lined flights (d). Rotation about the short axis leads to vertical descent flights without spinning in the horizontal plain (e), or to spiral descents in a helical manner (f). Samaras can also fly without rotation (g), and can be moved secondarily over the soil (h). Also seed clusters or parts of them can be moved secondarily by wind (i). In addition, seed release occurs from root suckers (j).

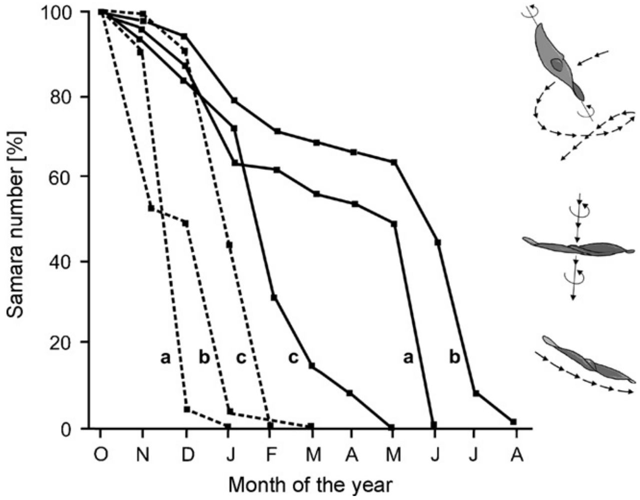

Fig. 11. Seasonal variation in seed abscission in three *Ailanthus* trees (a–c) in two consecutive years (dashed line: 1978–1979; solid line: 1979–1980), and typical flying movements of samaras (adapted from Bory and Clair-Maczulajtys, 1980).

In urban habitats, sealed surfaces of pavements or streets may facilitate secondary dispersal of samaras by wind along linear habitats. After a heavy storm in March 2005, the seed shadow from an isolated, 8-m-high tree extended for 450 m along a sidewalk. Experiments with exposed samaras in the same habitat revealed that wind as a secondary dispersal vector moved fallen samaras over the surface of the pavement to an observed distance of 150 m (Kowarik and von der Lippe, 2006). The dispersal of seed clusters may result in patches of closely related seedlings (Pan and Bassuk, 1986). Merriam (2003) suggested that the reason that *Ailanthus* is most closely associated with railroad rights-of-way in North Carolina is because winds from passing trains carry seeds along the tracks more effectively than in other edge habitats.

Water

Populations in river corridors as well as some anecdotal information suggest hydrochory as a secondary dispersal vector in *Ailanthus* (Lepart and Debussche, 1991; Thébaud and Debussche, 1991; Parsons and Cuthbertson, 1992). This hypothesis finds experimental support: In a study by Kowarik and Säumel (2006b), 81% of exposed samaras were able to drift for at least 20 days on water. Both floating and submerged seeds were able to germinate after differing periods of exposure to water (see above). In addition, 10% of buried stem fragments developed both adventitious shoots and roots after a stay of 3 or 10 days in water. Thus, moving water is believed to move sexual as well as asexual propagules over long distances.

Other dispersal vectors

Rodents may occasionally act as dispersal agents by padding out their dens with collected samaras (Bory and Clair-Maczulajtys, 1980). In Texas, several bird species feed on *Ailanthus* seeds (Miller, 1990). Parsons and Cuthbertson (1992) mention machinery moving seeds.

Spatial distribution of plants within populations

The spatial arrangement of urban populations often shows a distinct clustering of larger sized individuals. Clumping may result both from concentrated patches of seedlings descending from dispersed seed clusters or from older individuals that produce ramets (Pan and Bassuk, 1986). Clonal growth along fences, roads or railway embankments often leads to the linear extension of populations, starting outward from the central stem. In southern France, Kowarik (1983) reported such populations with lengths of up to 120 m, possibly descending from more than one individual. The spatial arrangement on a disused railway area in Vienna showed a combination of clumped and linear patterns, the latter partly tracing the track pattern (Schinninger et al., 2002). In 6–7-year-old regeneration stages of clear-cut forests, Call and Nilsen (2003) found mostly randomly spread individuals which might be due to regeneration from seeds. Gap colonization however can also lead to clumped patterns in forest habitats (Knapp and Canham, 2000). These can develop from single trees that share the upper tree layer and distribute clonal ramets in the field layer (Kowarik, 1995).

In a study of 30 clonal populations throughout Sardinia, there was a clear separation of sexes among clones (Carta, 2005). A third of the 30 clones had plants exclusively with female (‘hermaphrodite’) flowers, 47% showed only masculine flowers, and the remaining clones had not yet developed flowers.

Phenology

Due to high-temperature requirements for bud break, the seasonal development of *Ailanthus* starts later than that of many other tree species, but lasts longer, until late autumn. Climate-chamber experiments revealed that increased temperatures led to an earlier bud break, but the temperature sum from day of exposure to first bud break remained constant at a significantly higher temperature sum than in *Acer platanoides* and *A. negundo* (I. Säumel and I. Kowarik unpubl. data).

Phenological studies in northeastern Germany revealed a south-to-north and an urban-to-rural gradient in leaf emergence. Compared with Berlin which is located in the center of Brandenburg, leaves emerged about 3 days later in southern Brandenburg, and 6 days later in the northern part of this region (Henniges and

Chmielewski, 2006). At a local scale, there was an earlier leaf emergence in the center of Berlin compared to less densely built-up residential areas (I. Säumel, pers. observ.). In the Rhine valley, at Linz (25 km southeast of Bonn), bud break occurred at the end of April (1990–1994), and foliage was completely developed around May 20 (Adolphi, 1995). Depending on latitude, flowers appear in North America from mid-April to July, from the arid south to the temperate north of the United States (Miller, 1990). In the French Mediterranean, flowering starts mid-May (I. Kowarik, pers. observ.), while in Central Europe, July is the main month of flowering (Klotz et al., 2002). In Turkey, the pollen season starts in the last week of May (15th week) and ends in the fourth week of July (30th week) with a peak between the end of May and the third week of June (Bicakci and Akyalcin, 2000).

After ripening in September–October, the abscission of samaras strongly varies in time between individuals and years. In some years, almost all samaras may be released before the end of February, while in other years, about 60% may stay on the tree until the beginning of May, with a subsequent abscission period sometimes lasting even until August (Bory and Clair-Maczulajtys, 1980, Fig. 11).

Response to competition

Interspecific interference was studied between seedlings of *Ailanthus* and *Robinia pseudoacacia* and *Acer negundo*, which often co-occur on open, disturbed sites. Call and Nilsen (2005) studied the interference of seedlings of *Ailanthus* and *Robinia pseudoacacia* planted at different densities and mixtures in a greenhouse. After a period of 4.5 months, each species showed competitive attributes enabling it to dominate. In mixed plantings, *Ailanthus* yielded a relatively larger above- and belowground biomass. The belowground dominance of *Ailanthus* suggests a competitive advantage when root competition from soil resources is intense. The occasional dominant aboveground biomass in *Robinia* and the development of dominant individuals in 40% of mixed pots compared to only 10% in *Ailanthus* suggest a competitive advantage for *Robinia* when competition for light is important. Competition studies in older, established populations are missing, but evidently both species co-occur in pioneer forests on urban wastelands (Kowarik and Böcker, 1984; Gutte et al., 1987) and in regeneration stages after clear-cut (Call and Nilsen, 2003). Faragó (1964) reported a competitive advantage of *Ailanthus* over *Robinia* from mixed stands on sandy soils in the Danube-Theiss region in Hungary. Long-term dynamics of such stands are however unknown.

As *Ailanthus* often co-occurs with *Acer negundo* on urban sites, effects of intra- and interspecific interference on germination and seedling growth were analyzed in a garden experiment that was run with different seed densities and mixtures. *Ailanthus* showed higher germination rates than *Acer negundo*. Interspecific competition enhanced the number of *Ailanthus* seedlings compared to the same density in mono-specific seed mixtures and produced the opposite effect in *A. negundo* (Bachmann, 2005). This may be advantageous when only few propagules are present at a germination site or when the number of *Ailanthus* seeds exceeds that of *A. negundo*.

Studies of natural tree-fall canopy gaps in an old-growth hemlock-hardwood forest in New York suggest that *Ailanthus* can reach the canopy (Knapp and Canham, 2000). *Ailanthus* had an abundance among saplings taller than 30 cm equal to that of all native species combined. The dominant *Ailanthus* saplings were taller and had a greater diameter and extension growth than the tallest native saplings in a given gap. Considering mean annual diameter growth rates between 1.96 and 3.70 mm year^{-1} and the maintenance of highly competitive growth rates for up to 23 years, Knapp and Canham (2000) concluded that *Ailanthus* saplings can successfully compete with native saplings for light and may ultimately reach the canopy. The observed age structure of the population shows a window of opportunity for establishment in open gaps for a limited time span of some years.

A study in West Virginia showed that single individuals can survive in the tree layer and may build a ramet bank of clonal offspring with reduced annual extension growth. This has been described as ‘clonal oscar strategy’ providing a competitive advantage of *Ailanthus* ramets over other species in case of a new gap formation (Kowarik, 1995).

Allelopathy

The root bark, bark of other plant parts, leaves, samaras and wood of *Ailanthus* contain, with decreasing intensity, allelopathic compounds that are toxic to numerous woody and herbaceous species in the laboratory (Mergen, 1959; Heisey, 1990, 1996; Lawrence et al., 1991). The quassinoid compound ailanthone was identified as the most effective phytotoxic component (Lin et al., 1995; Heisey, 1996), with concentrations of 0.7 ml l^{-1} causing 50% inhibition of radicle elongation in a standardized bioassay with garden cress (*Lepidium sativum*) seeds (Heisey, 1996). In greenhouse tests, primarily ailanthone exhibited an inhibitory activity against several weed species, with a more post- than pre-emergent efficiency (Lin et al., 1995; Heisey, 1996). Ailanthone is released into the rhizosphere, but its toxic effects are short-lived, probably due to microbial degradation (Heisey, 1996).

Voigt and Mergen (1962) found a seasonal variation in toxicity of extracts from fresh and dried leaves with less pronounced inhibiting effects in leaves from October compared to younger leaves. In a more detailed analysis, Heisey (1990) revealed toxicity as highest in young leaflets just after emergence and then decreasing with age. Germination experiments (Greer and Aldrich, 2005) showed that toxicity of *Ailanthus* is greater in juveniles up to 2 years old than in older age classes. Increasing aboveground biomass removal induced increased phytotoxin production. This and the allocation of highest allelochemical activity in exterior tissues may also function as a barrier against herbivory. Insecticidal effects of tissues or extracts have been observed, for example, on the gypsy moth (*Lymantria dispar*; Heisey, 1990).

Seeds without pericarp inhibited cress radicle growth in contrast to those that still were covered by a pericarp. This suggests that the pericarp prevents the loss of inhibitory compounds due to leaching by rain during the long period before abscission of samaras (Heisey, 1990).

In field experiments, Lawrence et al. (1991) showed that allelopathic components affected neighboring species. Periods of high rainfall and moderate temperatures decreased the toxic impacts whereas enhanced effects were found during periods of little precipitation and higher temperatures. Plants from populations that co-occurred with *Ailanthus* in the field were less susceptible than plants of the same species from populations that had not been previously exposed to *Ailanthus*. The same effect emerging in plants grown from seeds of both groups suggests an adaptive ability in at least some neighboring species.

Information on autotoxicity is contradictory. Bory and Clair-Maczulajtys (1977) found decreased growth in young *Ailanthus* seedlings watered with extracts of fresh leaves, whereas Heisey (1996) found no detectable injury to seedlings due to the application of ailanthone.

Herbivores and pathogens

Outside of its native range, *Ailanthus* is usually subject to a low herbivore pressure, which has been attributed to the chemical composition of its tissues (Ohmoto and Koike, 1984). Its resistance to the invasive beetle *Anoplophora glabripennis,* for example, is due to toxic effects of α-pinene, β-pinene and α-terpinene in the bark and leaves (Ding et al., 2006). *Ailanthus* is palatable to snails as generalist herbivores, for example, *Cepaea hortensis* (Dormann and King, 2004).

Mammalia

Ailanthus is browsed by large mammals, e.g. white-tailed deer (*Odocoileus virginianus*) in North America, but usually less than other tree species. This is believed to be a competitive advantage in forests with high deer populations (Knapp and Canham, 2000). In Hungarian forests that are dominated by *Robinia pseudoacacia* and *Pinus sylvestris, Ailanthus* is the predominant browse species of red deer (*Cervus elaphus;* Matrai et al., 2004). Ostfeld et al. (1997) studied effects of rodents on the survival of tree seeds and seedlings invading old fields in eastern North America. The mouse *Peromyscus leucopus*, a major seed predator, avoided *Ailanthus* seeds. The vole *Microtus pennsylvanicus*, a major seedling predator, fed on *Ailanthus* seedlings, but preferred native tree species. Bourke (1996) reported that *Ailanthus* was nontoxic for goats.

Insecta

Its broad resistance to insect herbivory as compared to *Tilia* species, for example, was a prominent reason for 19th century plantations of *Ailanthus* along streets and in other urban sites in European and North American cities: "*Ailanthus*, the strong scented foliage of which no insect will attack, is every day becoming a greater metropolitan favorite" (Downing, 1847, cited by Shah, 1997). World-wide, honeybees feed on *Ailanthus* and produce good-tasting honey (Melville, 1944; Dalby, 2000). Mite species visit the extrafloral nectaries (Bory and Clair-Maczulajtys, 1986). Xue and Hong (2006) reported the presence of the eriophyoid mite *Aculus altissimae* from central China.

Ding et al. (2006) reviewed information on herbivorous insects associated with *Ailanthus* in its secondary range and in China. They reported nine herbivorous insects for North America: the Lepidoptera *Atteva punctella*, *Hyphantria cunea, Halisidota tessellaris, Hemerocampa leucostigma, Samia cynthia;* the Homoptera *Dialeurodes citri, Lepidosaphes* spp.; the Coleoptera *Maladera castanea*; and, in Pakistan, the Isoptera *Heterotermes indicola. Atteva punctella* switched from a Simaroubaceae tree, native to Florida (*Simarouba glauca*), to *Ailanthus* and is now called 'Ailanthus webworm' although it is native to North America.

Two insect species also feed on *Ailanthus* in Europe. The mulberry moth *Hyphantria cunea* has been reported in Austria (Schimischek, 1952; Schwarz, 1955). The Ailanthus silk moth (*Samia cynthia* Drury 1773) was introduced in 1856 from China to Turin, Italy, and from there in 1858 to France where trials for silk production with *Ailanthus* as a cultivated fodder plant were run until 1914 (Rebel, 1925; Moussalli, 1939). In 1860, the moth was introduced from France to the United States (Frank, 1986). Today, it is established in some parts of France (Alsace, Paris, Oise, Gironde), southern Switzerland, the northern Italian lakes, northeastern Austria and Vienna, Hungary, the Istrian Peninsula (Croatia), and central Slovenia. The population originally introduced into northeastern Spain (Barcelona) has now died out (Pittaway, 2005). North American occurrences are confined to cities along the East Coast and west to Indiana. Frank (1986) explained the confinement to cities as a result of reduced predatory pressure from birds and the decline of *S. cynthia* in the 20th century as a result of increasing parasitism. Correspondingly the level of herbivory on *Ailanthus* is expected to decrease. Rebel (1925) reported on naturalized populations from Sydney, Australia.

In contrast to native European maple species, seeds of *Ailanthus* were not damaged by carpophagous species (Kelbel, 2000).

Ding et al. (2006) listed 46 phytophagous arthropod species that feed on *Ailanthus* in its Chinese range: 18 Lepidoptera, 16 Coleoptera, seven Homoptera, two Hemiptera, and three Acari. The weevils *Eucryptorrhynchus brandti* and *E. chinensis* are regarded as major pests on *Ailanthus* and appear to be host-specific. In Huaibei, Anhui province of central China, for example, by 1996, more than 80% of trees had been damaged and 37% of them had died. Other important, but not host-specific, herbivores are larvae of several Lepidoptera and the planthopper *Lycorma delicatula* (Ding et al., 2006).

Nematoda

Ailanthus is tolerant or resistant to common root-knot nematodes (Meloidogyne) (Santamour and Riedel, 1993). Khan et al. (1998) found ten genera of stylet bearing nematodes associated with the rhizosphere of *Ailanthus* at eight localities in Pakistan.

Fungi

Ding et al. (2006) reported 65 fungi species that are associated with *Ailanthus* in its secondary range, emphasizing that little detailed information is available on their host specificity and impact. For China, 18 fungi species are known (Ding et al., 2006).

In southern Styria, Austria, fungal infections caused mortality in trees 35 years and younger (Cech, 1998). Symptoms were dieback of branches beginning in the upper crown and bark necroses extending down the stem. Besides *Verticillium* sp., which is regarded as the main cause of the decline, the following microfungi were found in dead bark tissues: *Phomopsis ailanthi, Nectria coccinea, Fusarium* sp., *Botryosphaeria melanops, Cytospora* sp., *Nectria peziza* and *Gibberella moricola* (Cech, 1998). The saprophytic *Schizophyllum commune* was reported by Scholler (1994) and by Arnaboldi et al. (2002). The latter also mentioned *Armillaria* sp. and *Fusarium lateritium* from Ticino. Skarmoutsos and Skarmoutsou (1998) reported wilt disease caused by *Verticillium dahliae* from Greece. Juhásová et al. (2003) identified the phytoparasitic fungi *Cercospora glandulosa* Ell. et Kell. and *C. ailanthi* P. Syd. on *Ailanthus* in Slovakia. Similar to Europe, wilt diseases caused by *Verticillium* spp. are regarded as the most important fungal diseases on *Ailanthus* in North America (Hepting, 1971).

Benkert (2005) reported the ascomycete *Nectria cinnabarina* and some basidiomycetes from trees in Berlin: the saprophytes *Resupinatus trichotis, Pluteus cervinus*; the facultative parasites *Pleurotus ostreatus, Polyporus squamosus, Flammulina velutipes*; and the parasite *Laetiporus sulphureus.* Other species are the parasite *Pholiota aurivella* (Kreisel, 1961).

Viruses

One potyvirus has been reported from the Chinese range (Yao and Liu, 1993).

Mycorrhiza

First results of Huebner et al. (2005) indicate that roots can be colonized by endomycorrhizal fungi.

Biochemical data

The bark contains oleoresin, resin, some mucilage, ceryl alcohol, ailanthin, ‘quassiin’, calcium oxalate crystals, and isoquercetin (quercitin 3-glycoside), tannin, phlobaphene, ceryl palmitate, saponin, quassin and neoquassin. Leaves contain 12% tannin, quercetin, isoquercetin, and the alkaloid linuthine. Seeds contain quassiin (List and Horhammer, 1969–1979; Perry, 1980). Proteins called quassinoids have been intensively studied due to their pharmacological relevance and phytotoxic impacts. Ailanthone was identified as the most effective phytotoxic component (Lin et al., 1995; Heisey, 1996) and may potentially be used as a broad spectrum herbicide (Heisey and Heisey, 2003). Besides ailanthone, which showed the greatest inhibitory activity, De Feo et al. (2003) isolated ailanthinone, chaparrine, and ailanthinol B (quassinoid derivatives); the alkaloid 1-methoxycanthin-6-one was not active. Okunade et al. (2003) isolated the quassinoids ailanthone and 6-alpha-tigloyloxychaparrinone and revealed antiplasmodial activity in these compounds. Other new quassinoids are ailantinol E, F, G, and H

(Tamura et al., 2003, 2006). Hwang et al. (2005) isolated five coumarin derivatives from the bark.

The chemical composition of extrafloral nectar and its seasonal variation have been analyzed by Bory and Clair-Maczulajtys (1986). The authors emphasize a high content of fructose and galactose as typical of *Ailanthus*. In the secretion from glandular trichomes emerging on cataphylls and young stems, Clair-Maczulajtys and Bory (1985a, b) isolated bound lipid (mainly monogalactosyldiacylglycerol) and oleic, palmitic and linoleic acids in the free state.

Impacts and management

Impacts

Detailed data-traced studies on the impacts of *Ailanthus* and an evaluation of the impacts as positive or negative are rare, although *Ailanthus* conspicuously colonizes a broad array of habitats, often with prolific populations. At present, most European populations of *Ailanthus* are confined to disturbed urban and rural habitats, above all along transportation corridors which often have a low conservation value. In cities, conflicts may arise due to the need for increased maintenance in urban green spaces or along road sides because of the high level of vegetative regeneration in *Ailanthus*. Stands along roadsides may create safety hazards by obstructing the views of drivers (Burch and Zedaker, 2003). Roots may break asphalt surfaces (Danin, 2000) and also enter wells and sewage lines (Hu, 1979). Mainly in warmer parts of Europe, *Ailanthus* may damage modern as well as historic buildings with its extensive root system, as reported, for example, for the walls and roof of the cathedral of Coimbra, Portugal (Almeida et al., 1994). In archaeological remains in Italy, *Ailanthus* is considered the most important weed with a high destructive potential (Celesti-Grapow and Blasi, 2004).

In addition to the esthetic value of *Ailanthus*, benefits include a significant contribution to ecosystem services in urban and industrial areas due to its capacity for colonizing strongly altered urban-industrial sites. Its tolerance of a broad range of site conditions and of most pollutants enables further functional uses as an ornamental, for shelterbelts and for erosion control. However, cultivation outside of cities may foster invasions of adjacent near-natural or natural habitats.

Ailanthus is believed to suppress native vegetation by competition and allelopathic effects. The establishment of pure stands implies strong community effects that have however rarely been studied in detail. As an exception, Vila et al. (2006) found a decrease in species richness of 23.8 ± 3.1% in invaded plots on Mediterranean islands compared to nearby non-invaded plots. *Ailanthus* also induced an increase in total N, organic C and soil pH, and a decrease in the C/N ratio.

Ailanthus is classified as a noxious weed, as invasive or as a major invader in many regions (e.g. Hunter, 2000; Weber, 2003; Brunel, 2005; Wittenberg, 2005). Consequences for endangered species are mostly unknown, but evidently, some endangered habitat types are affected, mostly in warmer parts of Europe. These are mainly Pannonian steppe formations, riverbed vegetation, rocky outcrops and coastal zones of Mediterranean islands.

Human health may be affected as well. In Sardinia, 10 of a total of 54 patients showed an allergic reaction to *Ailanthus* pollen and, at the same time, to other allergens (Ballero et al., 2003). The authors thus suggest possible cross-reactions between *Ailanthus* and other pollens. In some cases contact with *Ailanthus* sap may cause dermatitis (Derrick and Darley, 1994) and, in a rare case report, even myocarditis (Bisognano et al., 2005).

Management

The methods used to control *Ailanthus* include manual, mechanical and chemical means, and burning, grazing, and biocontrol (Hoshovsky, 1988; Hunter, 2000). As *Ailanthus* is very difficult to remove once it has established a taproot, all treatments require subsequent monitoring and control of shoots emerging from remaining seeds, roots or stumps.

Hand pulling can be performed on very young seedlings but soon becomes ineffective as seedlings rapidly develop an extended root system. Root suckers emerge from remaining root fragments (see above). It is common to cut and chop stems, but this leads to heavy root and stump sprouting and thus requires extensive follow-up treatment. Girdling the cambial tissue on the stem induces root sprouting as does burning (Hoshovsky, 1988; Hunter, 2000). In the Austrian Danube National Park, incomplete girdling is currently being tested for its ability to curb root sprouting (Drescher and Ließ, 2006).

Thus far, the combination of mechanical and chemical treatment appears to provide the best results. Meloche and Murphy (2006) compared the effects on the number of shoots of four treatments: (a) hand-pulling seedlings with a height of <0.6 m and subsequent mulching; (b) cutting stumps of larger plants, followed by glyphosate application; (c) cutting stumps without further treatments; (d) injecting glyphosate in trees with a DBH >0.05 m. Monitoring of the plots for 2 years showed a clear reduction in the number of shoots after the hand-pull treatment, but in the second year, the plots had about 50% of the initial shoot number. Cutting without other treatments increased the shoot number by a factor of 1.6. Herbicide injection affected the treated adult trees, but not the juvenile growth. Best results followed from the combination of stem cut and herbicide application, leading to a reduction from 11.8 to 1.0 shoots m^{-2}. The root system is most affected when herbicides are applied late in the growing season (Hoshovsky, 1988).

Burch and Zedaker (2003) recommended chemical control with a combined mixture of different herbicides. Best results were achieved with a combination of picloram and triclopyr, which reduced the stem density to 33 stems ha^{-2} 2 years after treatment compared to 2286 stems ha^{-2} after cutting. In a long-term trial on herbicide effectiveness for controlling herbaceous species, however, the application of diuron and simazine triggered the dominance of *Ailanthus* (Tworkoski et al., 2000).

Ailanthus belongs to the top 20 environmental weeds identified as targets of classical biological control in Europe (Sheppard et al., 2006). Surveys in China identified nine specific plant pathogens and four arthropods (Zheng et al., 2004). Of these, two weevils (*Eucryptorrhynchus brandti*, *E. chinensis*), one heteropteran (*Orthopagus lunulifer*), and three fungal pathogens (*Alternaria ailanthi*, *Aecidium ailanthi* and a *Coleosporium* sp.) have been selected for further study (see also Ding et al., 2006). A commercial stump treatment product (Stumpout^{TM}) based on the fungus *Cylindrobasidium laeve* (Pers.) Chamuris has been used in South Africa, killing 80% of treated stumps (Lennox et al., 1999).

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References

Adamik, K., 1955. Der Götterbaum als Faserholz. Centbl. Gesamte Forstwes. 73/74, 85–94.

Adolphi, K., 1995. Neophytische Kultur- und Anbaupflanzen als Kulturflüchtlinge des Rheinlandes. Nardus 2, 1–272.

Almeida, M.T., Mouga, T., Barracosa, P., 1994. The weathering ability of higher plants. The case of *Ailanthus altissima* (Miller) Swingle. Int. Biodeter. Biodegr. 33, 333–343.

Arnaboldi, F., Conedera, M., Maspoli, G., 2002. Distribuzione e potenziale invasivo di *Ailanthus altissima* (Mill.) Swingle nel Ticino centrale. Boll. Soc. Ticin. Sci. Nat. 90, 93–101.

Arnaboldi, F., Conedera, M., Fonti, P., 2003. Caratteristiche anatomiche e auxometriche di *Ailanthus altissima*. Sherwood 91, 1–6.

Bachmann, T., 2005. *Ailanthus altissima* Mill. Swingle und *Acer negundo* L. als typische Neophyten urbaner Pflanzengemeinschaften. Vergleichende Untersuchungen zur inter- und intraspezifischen Konkurrenz. Diploma Thesis, Technical University of Berlin.

Ballero, M., Ariu, A., Falagiani, P., Piu, G., 2003. Allergy to *Ailanthus altissima* (tree of heaven) pollen. Allergy 58, 532–533.

Benkert, D., 2005. Die Pilze des Späth-Aboretums in Berlin-Baumschulenweg. Verh. Bot. Ver. Berlin Brandenburg 138, 47–82.

Beug, H.-J., 2004. Leitfaden zur Pollenbestimmung für Mitteleuropa und angrenzende Gebiete. Verlag Dr. Friedrich Pfeil, München.

Bicakci, A., Akyalcin, H., 2000. Analysis of airborne pollen fall in Balikesir, Turkey, 1996–1997. Ann. Agric. Environ. Med. 7, 5–10.

Bicknell, S.H., Smith, W.H., 1975. Influence of soil salt, at levels characteristic of some roadside environments, on the germination of certain tree seeds. Plant Soil 43, 719–722.

Bisognano, J.D., McGrody, K.S., Spence, A.M., 2005. Myocarditis from the Chinese sumac tree. Ann. Intern. Med. 143, 159–160.

Böcker, R., Kowarik, I., 1982. Der Götterbaum (*Ailanthus altissima*) in Berlin (West). Berl. Naturschutzbl. 26, 4–9.

Boericke, W., 1991. Homöopathische Mittel und ihre Wirkungen, Materia Medica und Repertorium. Grundlagen und Praxis, Leer.

Bolle, C., 1887. Andeutungen über die freiwillige Baum- und Strauchvegetation der Provinz Brandenburg. Verlag des Märkischen Provinzial-Museums, Berlin.

Bory, G., Clair-Maczulajtys, D., 1977. Germination et floraison des plantules chez l'*Ailanthus glandulosa* Desf. (Simarubacées). Rev. Gen. Bot. 84, 201–211.

Bory, G., Clair-Maczulajtys, D., 1978. Morphologie, anatomie et développement des glandes foliaires chez l'*Ailanthus glandulosa* Desf. (Simarubacées). Rev. Gen. Bot. 85, 137–156.

Bory, G., Clair-Maczulajtys, D., 1980. Production, dissémination et polyphormisme des semences d'*Ailanthus altissima* (Mill.) Swingle, Simarubacées. Rev. Gén. Bot. 88, 297–311.

Bory, G., Clair-Maczulajtys, D., 1982. Morphology, structure and ontogeny of *Ailanthus grandulosa* floral nectaries. Can. J. Bot. 60, 818–824.

Bory, G., Clair-Maczulajtys, D., 1986. Composition of the nectar and the role of extrafloral nectars in *Ailanthus glandulosa*. Can. J. Bot. 64, 247–253.

Bory, G., Sidibe, M.D., Clair-Maczulajtys, D., 1991. Effects of cutting back on the carbohydrate and lipid reserves in the tree of heaven (*Ailanthus glandulosa* Desf. Simaroubaceae). Ann. Sci. Forestry 48, 1–13.

Bourdeau, P.F., Laverick, M.L., 1958. Tolerance and photosynthetic adaptability to light intensity in white pine, red pine, hemlock and ailanthus seedlings. For. Sci. 4, 196–207.

Bourke, C.A., 1996. Lack of toxicity of *Ailanthus altissima* (tree-of-heaven) for goats. Aust. Vet. J. 74, 465.

Brunel, S.E., 2005. Invasive plants in Mediterranean type regions of the world. In: Proceedings of the International Workshop, Mèze, France, 25–27 May 2005. Council of Europe Publishing, Strasbourg.

Buchholz, G., von Maydell, H.J., 1965. Aufforstungen in den ariden Gebieten der Sowjetunion. Bericht über russische Erfahrungen seit 1841. Mitt. Bundesforschungsanst. Forst-Holzwirtsch. 59.

Burch, P.L., Zedaker, S.M., 2003. Removing the invasive tree *Ailanthus altissima* and restoring natural cover. J. Arboric. 29, 18–24.

Burton, R.M., 1983. Flora of the London Area. London Natural History Society, London.

Call, L.J., Nilsen, E.T., 2003. Analysis of spatial patterns and spatial association between the invasive tree-of-heaven (*Ailanthus altissima*) and the native black locust (*Robinia pseudoacacia*). Am. Midland Nat. 150, 1–14.

Call, L.J., Nilsen, E.T., 2005. Analysis of interactions between the invasive tree-of-heaven (*Ailanthus altissima*) and the native black locust (*Robinia pseudoacacia*). Plant Ecol. 176, 275–285.

Carta, L., 2005. *Ailanthus altissima* (Miller) Swingle (Simaroubaceae). Strategia riproduttiva e diffusione in Sardegna. Inf. Bot. Ital. 37, 318–319.

Cech, T.L., 1998. Absterben von Götterbäumen (*Ailanthus altissima*) in der Südsteiermark. Forstsch. Aktuell. 22, 16–18.

Celesti-Grapow, L., 1995. Atlante della flora di Roma (Atlas of Rome flora). Argos, Roma.

Celesti-Grapow, L., Blasi, C., 1998. A comparison of the urban flora of different phytoclimatic regions in Italy. Global Ecol. Biogeogr. 7, 367–378.

Celesti-Grapow, L., Blasi, C., 2004. The role of alien and native weeds in the deterioration of archaeological remains in Italy. Weed Technol. 18, 1508–1513.

Celesti-Grapow, L., Di Marzio, P., Blasi, C., 2001. The importance of alien and native species in the urban flora of Rome (Italy). In: Brundu, G., Brock, J., Camarda, I., Child, L., Wade, M. (Eds.), Plant Invasions, Species Ecology and Ecosystem Management. Backhuys Publishers, Leiden, pp. 209–220.

Chang, Y.S., Woo, E.R., 2003. Korean medicinal plants inhibiting to human immunodeficiency virus type 1 (HIV-1) fusion. Phytother. Res. 17, 426–429.

Cho, C.W., Lee, K.J., 2002. Seed dispersion and seedling spatial distribution of the tree of heaven in urban environments. Kor. J. Environ. Ecol. 16, 87–93.

Choi, I., 2004. Vorkommen und Verbreitung von Pflanzenarten in der Stadt Cheon-ju (Südkorea) unter besonderer Berücksichtigung anthropogener Einflüsse. Ph.D. Thesis, Technical University Berlin. 〈http://opus.kobv.de/tuberlin/frontdoor.php?source_opus=1019ss〉.

Clair-Maczulajtys, D., Bory, G., 1983. Pedicellate extrafloral nectaries in *Ailanthus glandulosa*. Can. J. Bot. 61, 683–691.

Clair-Maczulajtys, D., Bory, G., 1985a. Evolution de la composition lipidique des cataphylles chez *l'Ailanthus glandulosa* Desf. au cours de l'ouverture du bourgeon. Physiol. Veg. 23, 275–282.

Clair-Maczulajtys, D., Bory, G., 1985b. Lipids from the glandular trichome of *Ailanthus altissima*. Phytochemistry 24, 1599–1600.

Clair-Maczulajtys, D., Sarthou, C., Haddad, Y., Bory, G., 1993. Effects of drought stress on reserve metabolites and cambial activity of *Ailanthus glandulosa* Desf. (Simarubaceae). Acta Bot. Gallica 140, 449–456.

Corbett, S.L., Manchester, S.R., 2004. Phytogeography and fossil history of *Ailanthus* (Simaroubaceae). Int. J. Plant Sci. 165, 671–690.

Corner, E.J.H., 1949. The durian theory or the origin of the modern tree. Ann. Bot. 13, 367–414.

Cozzo, D., 1972. Comportamiento inicial de *Ailanthus altissima* en una plantacion experimental. Rev. Forest. Argent. 16, 47–52.

Croxton, W.C., 1939. A study of the tolerance of trees to breakage by ice accumulation. Ecology 20, 71–73.

Dalby, R., 2000. Minor bee plants in a major key: tamarisk, ailanthus and theasel. Am. Bee J. 1401, 60–61.

Dallas, J.F., Leitch, M.J.B., Hulme, P.E., 2005. Microsatellites for tree of heaven (*Ailanthus altissima*). Mol. Ecol. Notes 5, 340–342.

Danin, A., 2000. The inclusion of adventive plants in the second edition of Flora Palaestina. Willdenowia 30, 305–314.

Davies, P.A., 1937. Leaf arrangement in *Ailanthus altissima*. Am. J. Bot. 24, 401–407.

Davies, P.A., 1939. Leaf position in *Ailanthus altissima* in relation to the Fibonacci series. Am. J. Bot. 26, 67–74.

Davies, P.A., 1943. Floral glands in *Ailanthus altissima*. Trans. Kentucky Acad. Sci. 11, 12–16.

Davies, P.A., 1946. Leaf glands on *Ailanthus altissima*. Trans. Kentucky Acad. Sci. 12, 31–33.

Davies, P.A., Bennett, D., 1929. Abnormal branching in *Ailanthus*. J. Hered. 20, 348–349.

Davies, P.A., Theiss, F.W., 1937. Factors affecting the method of branching in *Ailanthus altissima*. Bull. Torrey Bot. Club 64, 229–233.

De Feo, V., De Martino, L., Quaranta, E., Pizza, C., 2003. Isolation of phytotoxic compounds from tree-of-heaven (*Ailanthus altissima* Swingle). J. Agric. Food Chem. 51, 1177–1180.

Derrick, E.K., Darley, C.R., 1994. Contact reaction to the tree of heaven. Contact Dermatitis 30, 178.

Ding, J.Q., Wu, Y., Zheng, H., Fu, W.D., Reardon, R., Liu, M., 2006. Assessing potential biological control of the invasive plant, tree-of-heaven, *Ailanthus altissima*. Biocontrol Sci. Technol. 16, 547–566.

Dirr, M., 1976. Selection of trees for tolerances to salt injury. J. Arboricult. 2, 209–216.

Dormann, C.F., King, R., 2004. Comparing the palatability of native and non-native Mediterranean plants. Ecol. Mediterr. 30, 39–46.

Drescher, A., Ließ, N., 2006. Control of alien woody species in the Danube National Park (Austria). The example of *Ailanthus altissima* (Mill.) Swingle. BfN-Skripten 184, 106.

Drescher, A., Fraissl, C., Magnes, M., 2005. Nationalpark Donauauen. In: Umwelt und Wasserwirtschaft (Ed.), Bundesministerium für Land- und Forstwirtschaft, Aliens. Neobiota in Osterreich. Böhlau, Wien, pp. 222–254.

Dubroca, E., Bory, G., 1981. Glucidic and nitrogen compounds and resistance to drought in *Ailanthus altissima*. Biochem. Syst. Ecol. 9, 283–288.

Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W., Paulißen, D., 1991. Indicator values of plants in Central Europe. Scripta Geobot. 18, 1–248.

Engelhardt, R., 1901. *Ailanthus glandulosa* und *Ulmus latifolia* als Strassen- und Alleebäume. Möllers's Dtsch. Gärtner-Z. 16, 324.

Engler, A., 1931. Die Natürlichen Pflanzenfamilien, vol. 19a, second ed. Wilhelm Engelmann, Leipzig.

Facelli, J.M., 1994. Multiple indirect effects of plant litter affect the establishment of woody seedlings in old fields. Ecology 75, 1727–1735.

Facelli, J.M., Pickett, S.T.A., 1991. Indirect effects of litter on woody seedlings subject to herb competition. Oikos 62, 129–138.

Faragó, S., 1964. The tree-of-heaven. Erdész. Kutat. 60, 87–110 (in Hungarian).

Fedorov, A.A., 1969. Chromosome Numbers of Flowering Plants. Komarov Botanical Institute, Academy of Sciences of the USSR, Leningrad.

Feret, P.P., 1973. Early flowering in *Ailanthus*. For. Sci. 19, 237–239.

Feret, P.P., 1985. *Ailanthus*: variation, cultivation and frustration. J. Arboricult. 11, 361–368.

Feret, P.P., Bryant, R.L., 1974. Genetic differences between American and Chinese *Ailanthus* seedlings. Silvae Genet. 23, 144–148.

Feret, P.P., Bryant, R.L., Ramsey, J.A., 1974. Genetic variation among American seed sources of *Ailanthus altissima* (Mill.) Swingle. Sci. Hortic. 2, 405–411.

Forstner, W., Hübl, E., 1971. Ruderal-, Segetal- und Adventivflora von Wien. Notring, Wien.

Frank, K.D., 1986. History of the *Ailanthus* silk moth (Leptidoptera: Saturniidae) in Philadelphia: a case study in urban ecology. Entomol. News 97, 41–51.

Fu, L., Hong, T., 2001. Higher Plants of China, vol. 8, Beijing.

Geerinck, D., 1990. *Ailanthus vilmoriniana* versus *A. altissima* (Simaroubaceae). Belg. J. Bot. 123, 14–18.

Geerinck, D., 2002. Considérations taxonomiques et nomenclaturales sur des arbres et des arbustes cultivés en Belgique III. Taxonomania 7, 2–4.

Gravano, E., Ferretti, M., Bussotti, F., Grossoni, P., 1999. Foliar symptoms and growth reduction of *Ailanthus altissima* Desf. in an area with high ozone and acidic deposition in Italy. Water Air Soil Pollut. 116, 267–272.

Gravano, E., Giulietti, V., Desotgiu, R., Bussotti, F., Grossoni, P., Gerosa, G., Tani, C., 2003. Foliar response of an *Ailanthus altissima* clone in two sites with different levels of ozone-pollution. Environ. Pollut. 121, 137–146.

Graves, W.R., 1990. Stratification not required for tree-of-heaven germination. Tree Planter's Notes 41, 10–12.

Graves, W.R., Joly, R.J., Dana, M.N., 1991. Water use and growth of honey locust and tree-of-heaven at high root-zone temperature. HortScience 26, 1309–1312.

Greer, G., Aldrich, P.R., 2005. Genetics and biochemical variation of US *Ailanthus altissima* populations: A preliminary discussion of a research plan. In: Proceedings of the 16th US Department of Agriculture Interagency Research Forum on Gypsy Moth and other Invasive Species, 2005 GTR-NE-337, pp. 29–30.

Grime, J.P., Jeffrey, D.W., 1965. Seedling establishment in vertical gradients of sunlight. J. Ecol. 53, 621–642.

Grosser, D., 1977. Die Hölzer Mitteleuropas. Ein mikrophotographischer Lehratlas. Springer, Berlin.

Gutte, P., Klotz, S., Lahr, C., Trefflich, A., 1987. *Ailanthus altissima* (Mill.) Swingle. Eine vergleichend pflanzengeographische Studie. Folia Geobot. Phytotax. 22, 241–262.

Hallé, F., Oldeman, R.A.A., Tomlinson, P.B., 1978. Tropical Trees and Forests. An Architectural Analysis. Springer, Berlin.

Hamerlynck, E.P., 2001. Chlorophyll fluorescence and photosynthetic gas exchange responses to irradiance of Tree of Heaven (*Ailanthus altissima*) in contrasting urban environments. Photosynthetica 39, 79–86.

Hegi, G., 1906. Illustrierte Flora von Mitteleuropa, vol. V/1. J.F. Lehmann, München.

Heidenhain, M., 1932. Die Spaltungsgesetze der Blätter. Fischer, Jena.

Heisey, R.M., 1990. Allelopathic and herbicidal effects of extracts from tree of heaven (*Ailanthus altissima*). Am. J. Bot. 77, 662–670.

Heisey, R.M., 1996. Identification of an allelopathic compound from *Ailanthus altissima* (Simaroubaceae) and characterization of its herbicidal activity. Am. J. Bot. 83, 192–200.

Heisey, R.M., Heisey, T.K., 2003. Herbicidal effects under field conditions of *Ailanthus altissima* bark extract, which contains ailanthone. Plant Soil 256, 85–99.

Heninger, R.L., White, D.P., 1974. Tree seedling growth at different soils temperatures. For. Sci. 20, 363–367.

Henniges, Y., Chmielewski, F.-M., 2006. Stadt-Umland-Gradienten phänologischer Phasen im Raum Berlin 2006. Humboldt-Universität, Berlin.

Hepting, G.H., 1971. Diseases of forest and shade trees of the United States. In: US Department of Agriculture, F.S. (Ed.) US Department of Agriculture, Forest Service.

Hildebrand, N., 2006. Temperature and substrate effects on the juvenile establishment of the species *Ailanthus altissima* (Mill.) Swingle and *Acer negundo* L. M.Sc. Thesis, University of Greenwich.

Hoshovsky, M., 1988. Element Stewardship Abstract for *Ailanthus altissima*. The Nature Conservancy, Arlington, VA.

Howard, J.L., 2004. *Ailanthus altissima*. In: Fire Effects Information System, [Online]. US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). 〈http://www.fs.fed.us/database/feis/〉.

Hu, S.Y., 1979. *Ailanthus*. Arnoldia 39, 29–50.

Huang, T.C., Editorial Committee of the Flora of Taiwan (eds.), 1977. Flora of Taiwan, vol. 3. Department of Botany, National Taiwan University, Teipei.

Huebner, C., 2003. Vulnerability of oak-dominated forests in West Virginia to invasive exotic plants: temporal and spatial patterns of nine exotic species using herbarium records and land classification data. Castanea 68, 1–14.

Huebner, C., McQuattie, C., Rebbeck, J., 2005. A preliminary microscopical assessment of mycorrhizal associations in *Ailanthus altissima* from two habitats. Abstract Botanical Society of America, 〈http://www.2005.botanyconference.org/engine/search/index.php?func = detail&aid = 61〉.

Hull, J.C., Scott, R.C., 1982. Plant succession on debris avalanches of Nelson County, Virginia. Castanea 47, 158–176.

Hulme, P.E., 2004. Islands, invasions and impacts: a Mediterranean perspective. In: Fernández-Palacios, J.M., Morici, C. (Eds.), Island Ecology. Asociación Española de Ecología Terrestre (AEET). Cabildo Insular de La Palma, La Palma, pp. 359–383.

Hunter, J., 2000. *Ailanthus altissima* (Miller) Swingle. In: Bossard, C.C., Randall, J.M., Hoshovsky, M.C. (Eds.), Invasive Plants of California's Wildlands. University of California Press, Berkeley, pp. 32–36.

Hwang, S.W., Lee, J.R., Lee, J., Kwon, H.S., Yang, M.S., Park, K.H., 2005. New coumarins from the *Ailanthus altissima*. Heterocycles 65, 1963–1966.

Illick, J.S., Brouse, E.F., 1926. The ailanthus tree in Pennsylvania, Bulletin 38. Harrisburg, PA, Department of Forests and Waters, 29pp.

Inverso, A., Bellani, L., 1991. Origin and development of *Ailanthus glandulosa* Desf. root suckers. Giorn. Bot. Ital. 125, 39–45.

IPPC, 2001. Third Assessment Report: Climate Change 2001. Cambridge University Press, Cambridge.

Juhásová, G., Tkácová, S., Kobza, M., 2003. The results of phytopathological and mykological research of the trees on Sun lakes in Senec. Mitt. Biol. Bundesanst. Land-Forstwirtsch. 394, 35–41.

Kelbel, P., 2000. Monitoring of carpophages of invasive and expansive wood species. J. For. Sci. 46, 485–489.

Khan, A., Shaukat, S.S., Khanzada, A.K., 1998. Survey of stylet bearing nematodes associated with *Ailanthus altissima* (Mill.) Swingle in Mardan district. Sci. Khyber 11, 61–67.

Kiermeier, P., 1969. Über Vorkommen, Eigenschaften und Wuchszonen ausländischer Gehölzarten in Südbayern. Ph.D. Thesis, Technische Hochschule München.

Kiermeier, P., 1987. Ausbreitung von Gehölzen durch Ausläufer. Neue Landsch. 32, 371–377.

Kim, K.D., Lee, E.J., Cho, K.H., 2004. The plant community of Nanjido, a representative nonsanitary landfill in South Korea: implications for restoration alternatives. Water Air Soil Pollut. 154, 167–185.

Kim, P., 1990. Treefall gaps in an old-growth oak-hemlock forest. Occasional Publication of the Institute of Ecosystem Studies 4, 18–23.

Kiviat, E., 2004. Occurrence of *Ailanthus altissima* in a Maryland freshwater tidal estuary. Castanea 69, 139–142.

Klotz, S., Kühn, I., Durka, W., 2002. BIOFLOR – Eine Datenbank mit biologisch-ökologischen Merkmalen zur Flora von Deutschland. Schr. Reihe Veg. kd. 38, 1–334.

Knapp, L.B., Canham, C.D., 2000. Invasion of an old-growth forest in New York by *Ailanthus altissima*: sapling growth and recruitment in canopy gaps. J. Torrey Bot. Soc. 127, 307–315.

Kohler, A., Sukopp, H., 1964. Über die Gehölzentwicklung auf Berliner Trümmerstandorten. Ber. Dtsch. Bot. Ges. 76, 389–406.

Kostel-Hughes, F., Young, T.P., McDonnell, M.J., 1998. The soil seed bank and its relationship to the aboveground vegetation in deciduous forests in New York City. Urban Ecosyst. 2, 43–59.

Kostel-Hughes, F., Young, T.P., Wehr, J.D., 2005. Effects of leaf litter depth on the emergence and seedling growth of deciduous forest tree species in relation to seed size. J. Torrey Bot. Soc. 132, 50–61.

Kota, N.L., 2005. Comparative seed dispersal, seedling establishment and growth of exotic, invasive *Ailanthus altissima* (Mill.) Swingle and native *Liriodendron tulipifera* (L.). M.Sc. Thesis, University of Morgantown.

Kota, N.L., Landenberger, R.E., McGraw, J.B., 2007. Germination and early growth of *Ailanthus* and tulip poplar in three levels of forest disturbance. Biol. Invasions 9, 197–211.

Kovacs, M., Opauszky, I., Klincsek, P.K., Podani, J., 1982. The leaves of city trees as accumulation indicators. In: Steubing, L.S., Jäger, H.J. (Eds.), Monitoring of Air Pollutants by Plants. Methods and Problems. Dr. W. Junk, The Hague, pp. 149–153.

Kowarik, I., 1983. Zur Einbürgerung und zum pflanzengeographischen Verhalten des Götterbaumes (*Ailanthus altissima* (Mill.) Swingle) im französischen Mittelmeergebiet (Bas-Languedoc). Phytocoenologia 11, 389–405.

Kowarik, I., 1995. Clonal growth in *Ailanthus altissima* on a natural site in West Virginia. J. Veg. Sci. 6, 853–856.

Kowarik, I., 2003. Biologische Invasionen. Neophyten und Neozoen in Mitteleuropa. Ulmer, Stuttgart.

Kowarik, I., Böcker, R., 1984. Zur Verbreitung, Vergesellschaftung und Einbürgerung des Götterbaumes (*Ailanthus altissima* (Mill.) Swingle) in Mitteleuropa. Tuexenia 4, 9–29.

Kowarik, I., Säumel, I., 2006a. Das größte Blatt des Götterbaumes (*Ailanthus altissima* (Mill.) Swingle). Verh. Bot. Ver. Berlin Brandenburg 139, 31–39.

Kowarik, I., Säumel, I., 2006b. Hydrochory may foster invasions of river corridors by the primarily wind-dispersed tree *Ailanthus altissima*. BfN-Skripten 184, 176.

Kowarik, I., von der Lippe, M., 2006. Long-distance dispersal of *Ailanthus altissima* along road corridors through secondary dispersal by wind. BfN-Skripten 184, 177.

Kramer, H., 1995. Über den Götterbaum. Nat. Mus. 125, 101–121.

Kreh, W., 1956. Götterbaumhaine auf deutschem Boden. Kosmos 52, 235–238.

Kreisel, H., 1961. Die phytopathogenen Großpilze Deutschlands. (Basidiomycetes mit Ausschluß der Rost- und Brandpilze). Fischer, Jena.

Krigas, N., Kokkini, S., 2004. A survey of the alien vascular flora of the urban and suburban area of Thessaloniki, N Greece. Willdenowia 34, 81–99.

Křivánek, M., Pyšek, P., Jarosik, V., 2006. Planting history and propagule pressure as predictors of invasion by woody species in a temperate region. Conserv. Biol. 20, 1487–1498.

Krüssmann, G., 1976. Handbuch der Laubgehölze. Paul Parey, Berlin.

Kühn, R., 1957. Gehölz-Winterschäden und ihre Auswirkungen. Gartenamt 10, 201–202.

Lalhal, J.S., Singh, O., 1992. Sucker development in *Ailanthus glandulosa* Desf. Van Vigyan 30, 179–180 (cited after Howard 2004).

Landolt, E., 2001. Flora der Stadt Zürich. Birkhäuser, Basel.

Lauche, R., 1936. Dendrologisches aus Bonn und Umgebung. Mitt. Dtsch. Dendr. Ges. 48, 143–145.

Lawrence, J.G., Colwell, A., Sexton, O.J., 1991. The ecological impact of allelopathy in *Ailanthus altissima* (Simaroubaceae). Am. J. Bot. 78, 948–958.

Lazarevic, Z., Korac, M., Gajic, M., 1961. Observations on sowing methods in *Ailanthus glandulosa* Desf. Sumarstvo 14 January–February 1961, 15–23 [in Serbo-Croatian].

Lee, H.-W., Lee, C.S., 2006. Environmental factors affecting establishment and expansion of the invasive alien species of tree of heaven (*Ailanthus altissima*) in Seoripool Park, Seoul. Integr. Biosci. 10, 27–40.

Lennox, C.L., Morris, M.J., Wood, A.R., 1999. Stumpout^{TM} – commercial production of a fungal inoculant to prevent regrowth of cut wattle stumps in South Africa. In: Spencer, N.R. (Ed.), X International Symposium on Biological Control of Weeds. Montana State University, Bozeman, Montana, pp. 169–172.

Lenzin, H., Kohl, J., Muehlethaler, R., Odiet, M., Baumann, N., Nagel, P., 2001. Verbreitung, Abundanz und Standorte ausgewählter Neophyten in der Stadt Basel (Schweiz). Bauhinia 15, 39–56.

Lepart, J., Debussche, M., 1991. Invasion processes as related to succession and disturbance. In: Groves, R.H., Di Castri, F. (Eds.), Biogeography of Mediterranean Invasions. Cambridge University Press, Cambridge, pp. 159–177.

Lin, L.J., Peiser, G., Ying, B.P., Mathias, K., Karasina, F., Wang, Z., Itatani, J., Green, L., Hwang, Y.S., 1995. Identification of plant growth inhibitory principles in *Ailanthus altissima* and *Castela tortuosa*. J. Agric. Food Chem. 43, 1708–1711.

List, P.H., Horhammer, L., 1969–1979. Hager's Handbuch der Pharmazeutischen Praxis, vols. 2–6. Springer, Berlin.

Little, S., 1974. *Ailanthus altissima* (Mill.) Swingle. *Ailanthus*. In: Schopmeyer, C.S. (Ed.), Seeds of Woody Plants in the United States. US Department of Agriculture, Forest Service, Washington, pp. 201–202.

Lloret, F., Médail, F., Brundu, G., Hulme, P.E., 2004. Local and regional abundance of exotic plant species on Mediterranean islands: are species traits important? Glob. Ecol. Biogeogr. 13, 37–45.

Lohmeyer, W., 1976. Verwilderte Zier- und Nutzgehölze als Neuheimische (Agriophyten) unter besonderer Berücksichtigung ihrer Vorkommen am Mittelrhein. Nat. Landsch. 51, 275–283.

Mabberley, D.J., 1997. The Plant Book: a Portable Dictionary of the Vascular Plants, second ed. Cambridge University Press, Cambridge.

Mai, D.H., 1995. Tertiäre Vegetationsgeschichte Europas. Fischer, Jena.

Marek, M., 1988. Photosynthetic characteristics of *Ailanthus* leaves. Photosynthetica 22, 179–183.

Marshall, P.E., Furnier, G.R., 1981. Growth responses of *Ailanthus altissima* seedlings to SO_2. Environ. Pollut. 25, 149–153.

Matlack, G.R., 1987. Diaspore size, shape, and fall behavior in wind-dispersed plant species. Am. J. Bot. 74, 1150–1160.

Matrai, K., Szemethy, L., Toth, P., Katona, K., Szekely, J., 2004. Resource use by red deer in lowland nonnative forests, Hungary. J. Wildl. Manage. 68, 879–888.

McDonald, R.I., Urban, D.L., 2006. Edge effects on species composition and exotic species abundance in the North Carolina Piedmont. Biol. Invasions 8, 1049–1060.

Meloche, C., Murphy, S.D., 2006. Managing tree-of-heaven (*Ailanthus altissima*) in parks and protected areas: a case study of Rondeau Provincial Park (Ontario, Canada). Environ. Manage. 37, 764–772.

Melville, R., 1944. *Ailanthus*, source of peculiar London honey. Nature 154, 640.

Mergen, F., 1959. A toxic principle in the leaves of *Ailanthus*. Bot. Gaz. 121, 32–36.

Merriam, R.W., 2003. The abundance, distribution and edge associations of six non-indigenous, harmful plants across North Carolina. J. Torrey Bot. Soc. 130, 283–291.

Meusel, H., Jäger, E.J., 1992. Vergleichende Chorologie der zentraleuropäischen Flora, vol. 3. Fischer, Jena.

Meyer, F.H., 1982. Bäume in der Stadt. Ulmer, Stuttgart.

Mihulka, S., 1998. The effect of altitude on the pattern of plant invasions: a field test. In: Starfinger, U., Edwards, K., Kowarik, I., Williamson, M. (Eds.), Plant Invasions. Ecological Mechanisms and Human Responses. Backhuys, Leiden, pp. 313–320.

Miller, J., 1990. *Ailanthus altissima* (Mill.) Swingle. Ailanthus. In: Burns, R.M., Honkala, B.H. (Eds.), Silvics of North America, vol. 2: Hardwoods. US Department of Agriculture, Forest Service, Washington, pp. 101–104.

Moslemi, A.A., Bhagwat, S.G., 1970. Physical and mechanical properties of the wood of tree-of-heaven. Wood Fiber 1, 319–323.

Moussalli, V., 1939. Etude générale des Simarubacées et en particulier, des espèces ayant une utilisation médicinale, alimentaire ou industrielle. Editions la Médicale, Paris.

Mucina, L., Kolbek, J., 1993. *Ailanthus altissima* – (Lamio albi-Chenopodietalia) – Gesellschaft. In: Mucina, L., Grabherr, G., Ellnauer, T. (Eds.), Die Pflanzengesellschaften Österreichs. Teil 1. Gustav Fischer, Jena, p. 228.

Mücke, M., Kliese, R., 1991. Floristische und gehölzdemographische Untersuchungen des Scheunenviertels in Berlin-Mitte. Diploma Thesis, Technical University of Berlin.

Müller, N., 1987. *Ailanthus altissima* (Mill.) Swingle und *Buddleja davidii* Franchet – zwei adventive Gehölze in Augsburg. Bayer. Bot. Ges. 58, 105–107.

Müller, N., Okuda, S., 1998. Invasions of alien plants in floodplains: a comparison of Europe and Japan. In: Starfinger, U., Edwards, K., Kowarik, I., Williamson, M. (Eds.), Plant Invasions. Ecological Mechanisms and Human Responses. Backhuys, Leiden, pp. 321–332.

Nooteboom, H.P., 1962. Simaroubaceae. Flora Malesiana, Ser. 1.6, 193–226.

Ohmoto, T., Koike, K., 1984. Studies on the constituents of *Ailanthus altissima* Swingle, 3: the alkaloidal constituents. Chem. Pharm. Bull. 32, 170–173.

Okunade, A.L., Bikoff, R.E., Casper, S.J., Oksman, A., Goldberg, D.E., Lewis, W.H., 2003. Antiplasmodial activity of extracts and quassinoids isolated from seedlings of *Ailanthus altissima* (Simaroubaceae). Phytother. Res. 17, 675–677.

Orwig, D.A., Foster, D.R., 1998. Forest response to the introduced hemlock woolly adelgid in southern New England, USA. J. Torrey Bot. Soc. 125, 60–73.

Ostfeld, R.S., Manson, R.H., Canham, C.D., 1997. Effects of rodents on survival of tree seeds and seedlings invading old fields. Ecology 78, 1531–1542.

Pan, E., Bassuk, N., 1985. Effects of soil type and compaction on the growth of *Ailanthus altissima* seedlings. J. Environ. Hortic. 3, 158–162.

Pan, E., Bassuk, N., 1986. Establishment and distribution of *Ailanthus altissima* in the urban environment. J. Environ. Hortic. 41, 1–4.

Parsons, W.T., Cuthbertson, E.G., 1992. Noxious Weeds of Australia. Indata Press, Melbourne.

Perry, L.M., 1980. Medicinal Plants of East and Southeast Asia. MIT Press, Cambridge.

Pittaway, R.A., 2005. Saturniidae of Europe 〈http://tpittaway.tripod.com/silk/satlist.htm〉.

Plass, W.T., 1975. An evaluation of trees and shrubs for planting surface-mine spoils. Research Paper NE-317. US Department of Agriculture, Forest Service, Northeastern Forest Experimental Station, Upper Darby, PA (cited after Howard 2004).

Preston, C.D., Pearman, D.A., Dines, T.D., 2003. New Atlas of the British & Irish Flora. Oxford University Press, Oxford.

Punz, W., Aigner, B., Schimpfl, C., Pietsch, G., Schosmeier, Maier, R., 1998. Stadtbrachen in Wien. Verh. Zool.-Bot. Ges. Österreich 135, 171–184.

Punz, W., Kober, M., Armeanu, K., Kugler, R., Engenhardt, M., Schinninger, I., Sieghardt, Maier, R., 2004. Beiträge zur Ökophysiologie von *Ailanthus altissima* im Raum Wien. Verh. Zool.-Bot. Ges. Österreich 141, 1–11.

Rabe, E.P., Bassuk, N., 1984. Adaptation of *Ailanthus altissima* to the urban-environment through analysis of habitat usage and growth response to soil compaction. HortScience 19, 572.

Ranft, H., Dässler, H.G., 1970. Smoke-hardiness test carried out on woods in a SO_2-chamber. Flora 159, 573–588.

Rank, B., 1997. Oxidative stress response and photosystem, 2: efficiency in trees of urban areas. Photosynthetica 33, 467–481.

Rebel, H., 1925. Der Ailanthusseidenspinner, ein heimisch gewordener Großschmetterling, seine Lebensweise und Zucht, Rassen, Verbreitung und Einbürgerung, sowie dessen Bedeutung als Seidenspinner. Fritz Wagner, Wien.

Regionalstelle für die floristische Kartierung Berlins, 2006. Verbreitungsatlas der wildwachsenden Farn- und Blütenpflanzen Berlins (draft version). Berlin.

Robinson, G.R., Handel, S.N., 1993. Forest restoration on a closed landfill: rapid addition of new species by bird dispersal. Conserv. Biol. 7, 271–278.

Santamour, F.S.J., Riedel, L.G.H., 1993. Susceptibility of various landscape trees to root-knot nematodes. J. Arboric. 19, 257–259.

Säumel, I., 2007. Temperature effects on invasive tree species. Architecture, biomass allocation, plasticity and distribution patterns. Ph.D. Thesis, Technical University of Berlin.

Schaaf, G., 1930. Der Winter 1928/29 und seine Einwirkungen auf die Pflanzenwelt. Nat. Wiss. Monatsz. Dtsch. Lehrerver. 43, 34–43.

Schäfer, H., 2003. Chorology and diversity of the Azorean flora. Diss. Bot. 374, 1–130.

Scheerer, O., 1956. Winterschäden 1955/56. Gartenamt 9, 171–175.

Schenck, C.A., 1939. Fremdländische Wald- und Parkbäume. Paul Parey, Berlin.

Schimischek, E., 1952. Probleme des Forstschutzes im Wienerwald, Auwald der Donauauen bei Wien, Marchfeld, den Flugerdeaufforstungen im Wiener Becken und den Wohlfahrtsaufforstungen im Seewinkel des Burgenlandes. Österr. Vierteljahresschr. Forstw. 93, 174–199.

Schinninger, I., Maier, R., Punz, W., 2002. Der stillgelegte Frachtenbahnhof Wien-Nord. Standortbedingungen und ökologische Charakteristik der Gefäßpflanzen einer Bahnbrache. Verh. Zool.-Bot. Ges. Österreich 139, 1–10.

Schmidt, W., 1918. Die Verbreitung von Samen und Blütenstaub durch die Luftbewegung. Österr. Bot. Ztschr. 67, 313–328.

Scholler, M., 1994. Ein Beitrag zur Pilzflora der Bahnanlagen in Berlin. Verh. Bot. Ver. Berlin Brandenburg 127, 45–58.

Schwarz, H., 1955. Die forstliche Bedeutung des Götterbaumes für Österreich. Österr. Vierteljahresschr. Forstw. 96, 133–142.

Shah, B., 1997. The checkered career of *Ailanthus altissima*. Arnoldia 57, 20–27.

Sheppard, A.W., Shaw, R.H., Sforza, R., 2006. Top 20 environmental weeds for classical biological control in Europe: a review of opportunities, regulations and other barriers to adoption. Weed Res. 46, 93–117.

Singh, R.P., Gupta, M.K., Chand, P., 1992. Autecology of *Ailanthus glandulosa* Desf. in Western Himalayas. Indian Forester 118, 917–921.

Skarmoutsos, G., Skarmoutsou, H., 1998. Occurrence of wilt disease caused by *Verticillium dahliae* on *Ailanthus glandulosa* in Greece. Plant Dis. 82, 129.

Slavík, B. (Ed.), 1997. Květena České republiky [Flora of the Czech Republic], vol. 5. Academia, Praha.

Soják, D., Löffler, A., 1988. Effect of fertilizer application on increment and biomass production of *Ailanthus altissima*. Lesnícky Casopis 34, 399–412.

Speranzini, F., 1937. Memoria sulla cultivatione dell'ailanto. Alpe 23, 377–386.

Sudnik-Wojcikowska, B., 1998. The effect of temperature on the spatial diversity of urban flora. Phytocoenosis 10, 97–105.

Tabacchi, E., Planty-Tabacchi, A.M., 2003. Recent changes in riparian vegetation: possible consequences on dead wood processing along rivers. River Res. Appl. 19, 251–263.

Tamura, S., Fukamiya, N., Okano, M., Koyama, J., Koike, K., Tokuda, H., Aoi, W., Takayasu, J., Kuchide, M., Nishino, H., 2003. Three new quassinoids, ailantinol E, F, and G, from *Ailanthus altissima*. Chem. Pharm. Bull. 51, 385–389.

Tamura, S., Fukamiya, N., Okano, M., Koike, K., 2006. A new quassinoid, ailantinol H from *Ailanthus altissima*. Nat. Prod. Res. 20, 1105–1109.

Thébaud, C., Debussche, M., 1991. Rapid invasion of *Fraxinus ornus* L. along the Hérauld river system in Southern France: the importance of seed dispersal by water. J. Biogeogr. 18, 7–12.

Tokarska-Guzik, B., 2005. The Establishment and Spread of Alien Plant Species (Kenophytes) in the Flora of Poland. Wydawnictwo Uniwersytetu Slaskiego, Katowice.

Trifilò, P., Raimondo, F., Nardini, A., Lo Gullo, M.A., Salleo, S., 2004. Drought resistance of *Ailanthus altissima*: root hydraulics and water relations. Tree Physiol. 24, 107–114.

Troll, W., 1939. Vergleichende Morphologie der höheren Pflanzen, vol. 1. Gebrüder Borntraeger, Berlin.

Troll, W., 1964. Die Infloreszenzen, vol. 1. Fischer, Jena.

Tworkoski, T.J., Welker, W.V., Vass, G.D., 2000. Weed community changes following diuron, simazine, or terbacil application. Weed Technol. 14, 197–203.

Udvardy, L., 1998. Spreading and coenological circumstances of the tree of heaven (*Ailanthus altissima*) in Hungary. Acta Bot. Hung. 41, 299–314.

Udvardy, L., 1999. Some remarkable instances of invasion of *Ailanthus altissima* in Hungary. In: Abstracts, Fifth International Conference Ecology of Invasive Alien Plants, 13–16 October 1999, La Maddalena, Sardinia 〈http://www.lboro.ac.uk/research/cens/invasives/5iceap_title.htm〉.

Vila, M., Tessier, M., Suehs, C.M., Brundu, G., Carta, L., Galanidis, A., Lambdon, P., Manca, M., Medail, F., Moragues, E., Traveset, A., Troumbis, A.Y., Hulme, P.E., 2006. Local and regional assessments of the impacts of plant invaders on vegetation structure and soil properties of Mediterranean islands. J. Biogeogr. 33, 853–861.

Voigt, G.K., Mergen, F., 1962. Seasonal variation in toxicity of *Ailanthus* leaves to pine seedlings. Bot. Gaz. 123, 262–265.

Von Bartossagh, J., 1841. Beobachtungen und Erfahrungen über den Götterbaum (*Ailanthus glandulosa* L.). Ofen [Budapest].

Von der Lippe, M., Säumel, I., Kowarik, I., 2005. Cities as drivers of biological invasions. The role of climate changes and traffic. Erde 136, 123–143.

Von Schwerin, F., 1933. Bericht zur Jahresversammlung in Köln. Mitt. Dtsch. Dendr. Ges. 45, 436–504.

Webb, S.L., Pendergast, T.H., Dwyer, M.E., 2001. Response of native and exotic maple seedling banks to removal of the exotic, invasive Norway maple (*Acer platanoides*). J. Torrey Bot. Soc. 128, 141–149.

Weber, E., 2003. Invasive Plant Species of the World: A Reference Guide to Environmental Weeds. CABI International, Wallingford.

Weberling, F., Leenhouts, P.W., 1965. Systematisch-morphologische Studien an Therebinthales-Familien. Abh. Akad. Wiss. Lit. Mainz, Math.-Naturw. Kl. 1965, 10.

Wei, J., 1989. Study on the spontaneous trees in Beijing urban ecosystems. In: Rusong, W. (Ed.), Human Ecology in China. China Science and Technology Press, Beijing, pp. 79–82.

White, P.S., 1983. Corner's rules in eastern deciduous trees: allometry and its implications for the adaptive architecture of trees. Bull. Torrey Bot. Club 110, 203–212.

Wilhelmi, T., 1958. *Ailanthus altissima* Swingle in der Bundesrepublik. Forst-Holzwirt. 13, 71–73.

Witte, F., 1952. Über die Berliner Trümmerberge und ihre Begrünung. Garten Landsch. 62, 8–9.

Wittenberg, R., 2005. An Inventory of Alien Species and their Threat to Biodiversity and Economy in Switzerland. CABI Bioscience Switzerland Centre report to the Swiss Agency for Environment, Forests and Landscape. CABI Bioscience Switzerland Centre, Delémont.

Xiong Ai'ying, Feng, D., Qiwen, S., 1983. Trial test of super *Ailanthus altissima* clones. Shandong For. Sci. Technol. 4, 28–31.

Xue, X.F., Hong, X.Y., 2006. Eriophyoid mite fauna from Henan Province, central China (Acari: Eriophyoidea) with descriptions of five new species. Zootaxa 1204, 1–30.

Yao, J., Liu, Y., 1993. Study on Ailanthus potyvirus. For. Sci. 39, 503–508 (cited after Ding et al., 2006) (in Chinese).

Zelenin, A.V., 1976. Afforestation of saline soils in the Sal'skaya steppes. Lesnoe Khozyaistro 9, 79–81 (cited after Hoshovsky, 1988) (in Russian).

Zhang, D., Dirr, M.A., 2004. Potential new ornamental plants from China. In: SNA Reserach Conference, vol. 49, pp. 607–609. 〈http://www.sna.org/research/04proceedings/04proceedingspdfs/ResProcSec12.pdf〉.

Zheng, H., Wu, Y., Ding, J., Binion, D., Fu, W., Reardon, R., 2004. Invasive Plants of Asian Origin established in the United States and their Natural Enemies. USDA Forest Service, FHTET-2004-05, Washington, DC. 〈http://www.invasive.org/weeds/asian/〉.