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# TIME LAGS IN BIOLOGICAL INVASIONS WITH REGARD TO THE SUCCESS AND FAILURE OF ALIEN SPECIES

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## Abstract

The historical reconstruction of invasion dynamics of woody species alien to Brandenburg, Germany revealed that 210 species began to spread within the period 1780 to 1990. Lag phases between the first release for cultivation and the beginning of spontaneous spread were reconstructed for 184 species. On average, there was a time lag of 147 years between the introduction to Brandenburg and the initiation of invasion (170 years for trees, 131 for shrubs). The first occurrence of a seedling in the area was defined as the start of a biological invasion without regard to the subsequent success or failure of this invasion. Species' success and failure were evaluated in terms of naturalization and frequency of the 3150 woody species introduced to Germany. It was established that successful invaders are not necessarily quicker in starting invasions than less successful species and that less than 10% of the introduced species begin to invade, 2% become established, and 1% may successfully invade the natural vegetation. When applying this 10:2:1 rule to assess the invasion risk, it has to be considered that the ratio between introductions and starting invasions is not constant, but has increased through time: in 1780 only about 3% of the introduced species had invaded, compared to 7.4% in 1990. Consequently, the number of invasions breaking out will still increase, even if no additional species are introduced. The analysis of timing of biological invasions cannot be explained sufficiently by deterministic factors referring to species' life history. As discussed for some species, the successful invasion can be due to an interaction of directional climatic changes (rising temperatures since 1850) and of stochastically induced shifts in the availability and accessibility of safe sites.

## Introduction

There is abundant information on successful invasions by plant species but a fundamental lack of data on unsuccessful or failed introductions (Mooney and Drake 1989). This is particularly true of studies addressing the whole invasion process, including the history of first introduction and subsequent spread. There are some well documented case-studies showing the increased success of invading species over a longer time period (*e.g.*, Wein 1939/40; Jäger 1977, 1986; Trepl 1984; Mack 1986; Guillermin *et al.* 1990; Kornas 1990; Pyšek 1991), but these studies are biased due to the known success of the species studied: they had already spread conspicuously or were suspected of causing trouble in land management or nature conservation.

Lag phases in population growth are recognized preceding the successful invasion of an alien species (Hengeveld 1989), but in comparison to animal invasions, little data exist on selected plant species (*e.g.*, Jäger 1988; Pyšek and Prach 1993). Generalizations on the length of lag phases are necessary for the understanding of the history of population growth (Hengeveld 1987), though even this is not yet possible because most studies are confined to those species which have already spread conspicuously after having overcome their lag phase. The present paper considers the time lags of both successful (in terms of naturalization and frequency) and unsuccessful species.

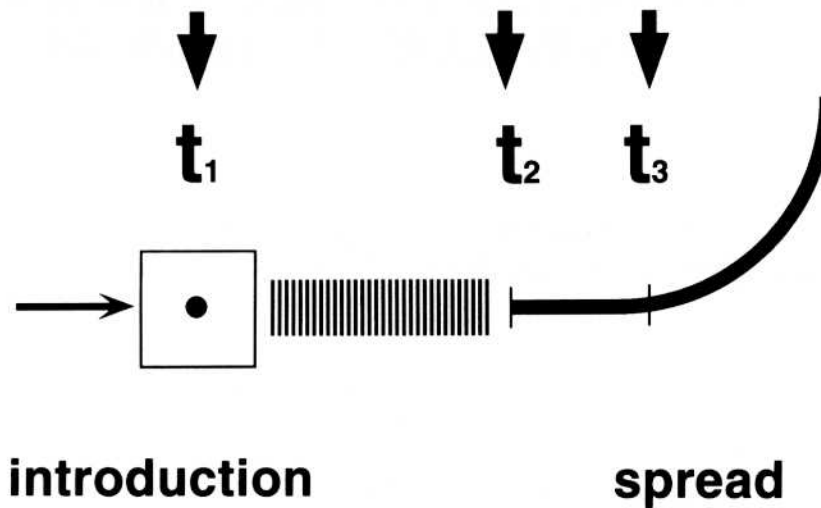


Fig. 1. The process of biological invasions including two kinds of lag phases: (a) the period between the first introduction to an area and the first spread ( $t_2-t_1$ ), (b) the period preceding the switch to a significantly higher rate of population growth ( $t_3-t_2$ ).

Two kinds of lag phases may be distinguished within the process of biological invasion (Fig. 1). After their first spread, most species need time to establish populations before a shift in the population growth rate opens the window to a more expansive phase of invasion ( $t_3 - t_2$  in Fig. 1). Those species however, which had been brought in as ornamentals or crops had already surpassed a previous lag phase: the time between their first release for cultivation and the beginning of spontaneous spread ( $t_2 - t_1$  in Fig. 1). The present paper focuses mainly on this lag phase as the first barrier between the initial introduction as a predisposition, and the first spontaneous spread as a starting point of a potentially successful invasion.

Aiming to provide a more general insight into the early history of success and failure of intentionally introduced species, the following questions are addressed: (1) How many of the deliberately introduced species were able to start an invasion by escaping from cultivation? (2) How long was the time lag between the first introduction and the beginning of spread? (3) Is there a relationship between the failure or success during the invasion process and the ability of a species to spread rapidly after introduction? In the discussion, the known implications of differences in species' life history for a successful invasion are only briefly considered. The focus lies on the role of both directional environmental changes and of stochastic events in order to elucidate the role of chance and timing in biological invasions. The historical reconstruction of invasion dynamics of all woody species which have been reported as escaped from cultivation in Brandenburg, Germany, were used as a suitable data set for this attempt.

## Methods

This paper is based on historical reconstructions of introduction and spreading dynamics of woody species which are not native to Brandenburg, Germany. It covers about the last four hundred years. For several reasons, trees, shrubs, and woody climbers are well suited for such a study: (a) with only few exceptions, alien woody species have been brought in and planted deliberately, and the history of these introductions is well documented compared to unintentionally introduced species; (b)

selecting the species studied by their life form admits a high taxonomic variety in the data set and prevents focusing on taxa which are known to be better pre-adapted than others to successful invasions; (c) the species are selected mainly because of aesthetic or economically useful attributes, that is the first introduction of woody species to a new area is not a result of successful invasion. In contrast, even the first appearance of alien herbs introduced unintentionally with exotic seeds or fruits, for example, can be assumed as a first step to successful invasion.

In this paper, the term 'introduction' refers to the first cultivation of an alien woody species in Brandenburg. 'Aliens' (= non-native, non-indigenous) are species occurring in an area in which they have not evolved since the last Ice Age *and* whose introduction or immigration was supported deliberately or involuntarily by human activities.\* This includes species from other continents as well as species native to neighbouring regions. *Picea abies*, for example, is only indigenous to southern Brandenburg but escaped from cultivation in other parts of this country. The terms 'invasion' and 'spread of alien species' are used synonymously. They refer to the whole process of range extension of alien species, including its very beginning. Consequently, the first occurrence of a seedling is defined as the start of a biological invasion without regard to the subsequent success or failure of this invasion. However, because of the tradition in natural history, most data on the beginning of invasions actually refer to individuals already well established.

Published and unpublished horticultural and floristic data were used to reconstruct both the time of local introductions to Brandenburg and the first spontaneous emergence of species within this area. Beginning with the '*hortus lusatiae*' by J. Franke, the written sources date back to 1594. For those species whose time of introduction to Brandenburg could not be reconstructed, Goeze's (1916) data covering central Europe were used (including some corrections by Wein 1930, 1931). The first record of the spontaneous, *e.g.*, non-cultivated, appearance of a species was defined as the beginning of an invasion. The flora of Willdenow (1787) was used as the first source with safe distinctions between cultivated and spontaneously spreading species.

Some limitations of floristic data for historical reconstructions and ecological analysis, emphasized by Pyšek and Prach (1993), are also valid for this study. The quality of information may depend on the changing interest of botanists in selected species, and there may be a delay between introduction and spread, respectively, and the information thereon. Nevertheless, it can be assumed that the results are far from anecdotal. The gardening tradition in Brandenburg, including Berlin, is extensive and well documented in the horticultural and forest literature since the 16th century. The intensity of floristic research is high (Scholz 1987; Sukopp 1987) and has resulted in temporally and spatially overlying data.

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\*This definition of alien species is in the tradition of Thellung (1912, 1918/19, see also Trepl 1990). It also follows the definition of Roy (1990) but enlarges it by two additions: first, by the reference to the last Ice Age. This is necessary in order to exclude species as natives which had formerly evolved in the area but became extinct during the colder periods. (Some foresters, for example, call taxa such as *Ginkgo biloba* or *Pseudotsuga* native to Europe.) Re-introduced they should be treated as aliens because if they occurred in the area before or during the last Ice Age, it was not under the present conditions as the climate was different from today (Webb 1985). One of the important consequences is the lacking phase of coevolution with native species in the period after the last glaciation. Second, by the connection to the role of humans enabling the introduction or immigration of alien species. This reference is necessary because most native species did not evolve *in situ* either, but arrived during the period since the last Ice Age, as already stated by Egler (1961). In contrast to alien species, however, the immigration of natives has not necessarily been supported by humans (see Pyšek 1995 for a detailed discussion).

Commonly, the success of invasion is expressed by the rate of population growth over time or the gain of area occupied (Elton 1958; Hengeveld 1989). Appropriate to the data character, in this study the invasion success has been evaluated by the central European approach to naturalization. This concept had been promulgated by Thellung (1912, pp. 622ff.) who referred mainly to the classic work of De Candolle (1855). An alien species is naturalized in the sense of Thellung when it “demonstrates all the characteristics of a wild indigenous plant, *i.e.*, growth and reproduction with natural means of reproduction (seeds, bulbs, tubers *etc.*) without the direct assistance of humans, more or less frequent occurrence at suitable sites, and maintenance for a number of years (including years with unusual climatic phenomena)” (translation in Sukopp and Trepl 1987).

In this tradition, those alien species which took at least the first step toward spreading were grouped as: (*a*) species which began to spread without having become established (‘ephemerophytes’; terminology following Schroeder 1969), (*b*) species which are only established in man-made plant communities and which would disappear with the cessation of human activities (‘epikophytes’), (*c*) species which are established in the natural vegetation and which would continue to exist even if human influence ceased (‘agriophytes’). A fourth group includes the species which became extinct after an unsuccessful invasion. As a second parameter of success, the species were ranked according to their frequency. Because of the substantial information available, both frequency and naturalization were evaluated for species spreading in the area of Berlin, which has been studied extensively during the last decades (for an overview see Sukopp 1990). The complete data set, including times of introduction and of first spread for all species, as well as their ranking according to naturalization and frequency, has been published in Kowarik (1992).

## Results

### *Introductions and subsequent invasions*

The exact number of woody species introduced to central Europe is unknown. The data set compiled by Goeze (1916) however, indicates the dimension, listing 2645 species introduced to the nemoral Europe. The temporal stratification of species with different origins reflects the history of voyages and discoveries (Fig. 2). At first, species from other parts of Europe and from the Mediterranean were cultivated, among them some which had already been dispersed by the Romans (*e.g.*, *Juglans regia*, *Castanea sativa*).

At the end of the 18th century, introductions from North America increased evidently. They had been enhanced by both a paradigmatic shift in garden style and the beginnings of sustainable forestry. The modern landscape garden contained more room for trees and shrubs compared to the traditional baroque garden (Kiermeier 1988). Additionally, American species were tested with great expectations as forest trees (*e.g.*, Von Burgsdorf 1787, 1806). In the second half of the last century, the opening of eastern Asia resulted in an exponential growth of introduced species, mainly from China and Japan (Bretschneider 1898). Some of these found limited use in forestry, but have been planted extensively to the present day in parks and gardens (*e.g.*, *Rhododendron* spp., *Cotoneaster* spp.).

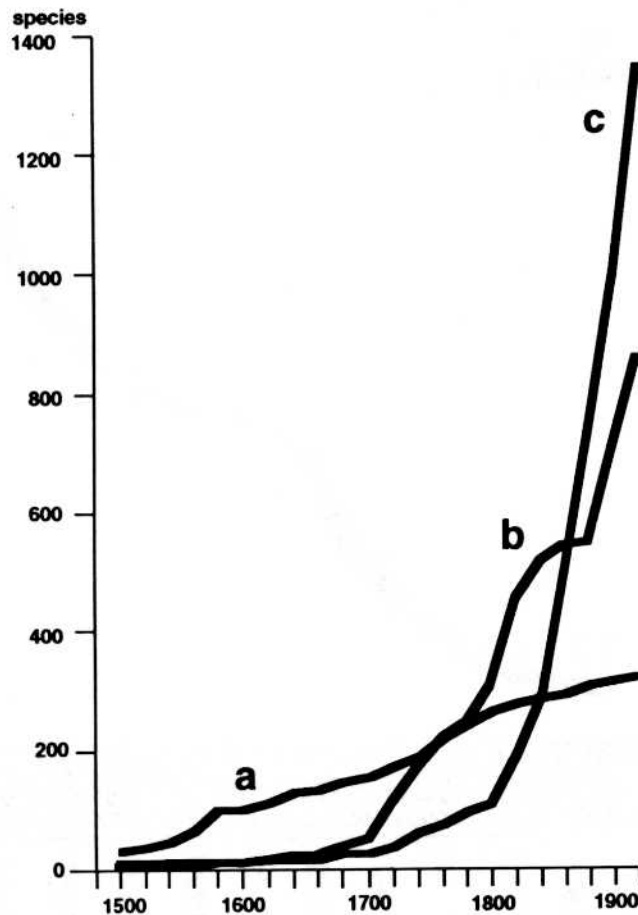


Fig. 2. Introductions of woody species to nemoral Europe during the period between 1500 and 1916. The species are grouped according to their origin in (a) other parts of Europe (including the Mediterranean,  $n = 309$ ), (b) America ( $n = 857$ ), and (c) central and east Asia ( $n = 1351$ ) (cumulative curves; calculated after Goeze 1916; additional 128 species introduced from west Asia and of cultural or unknown origin are not shown).

The historical analysis of floristic data from between 1787 and 1990 revealed that in Brandenburg 210 woody species invaded beyond their original native area. Most of these species were shrubs (132, 62.9%), 70 were trees (33.3%) and 8 were woody climbers (3.8%). 65 species originated in other parts of nemoral and meridional Europe, 63 came from North America, 43 from central and east Asia, the other 39 came from west Asia or were of cultural or unknown origin.

Relating the 210 spreading species to the 2645 introduced species listed by Goeze (1916) or to the 3150 alien woody species currently cultivated in German parks (Kowarik 1992, from the data set of Bartels *et al.* 1981) showed that about 7-8% of these introduced species started spreading in Brandenburg. Assuming that fewer species were cultivated in Brandenburg than had been brought into central Europe, the probability of beginning invasions must be higher.

For 184 of that 210 species the dates of the beginning of invasion were identified (Fig. 3). (Among the 26 species which are not considered in Fig. 3, 10 are native to some parts of Brandenburg, but are invading other parts as aliens, 4 were being already cultivated before 1594, 8 *Rubus*-species were introduced incidentally as weeds instead of having escaped from cultivation, and 4 were doubtful cases.) The number of new species starting to spread has increased to the present day, but the gains are far from regular. Two periods can be distinguished during which higher numbers of newly invading species were reported: the second half of both the 19th and the 20th centuries.

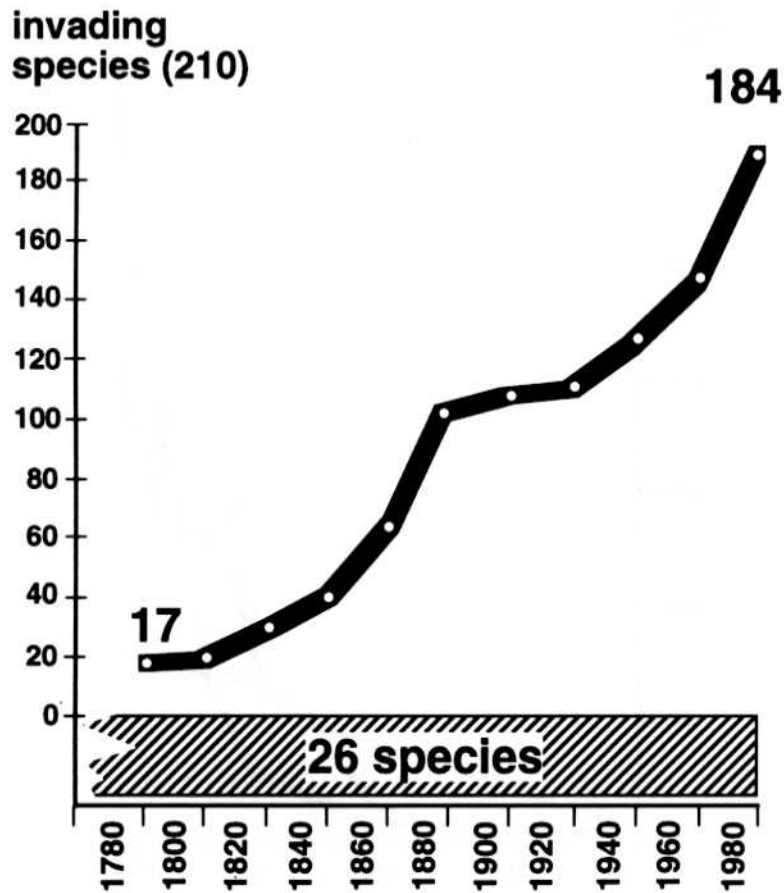


Fig. 3. Reconstruction of the beginning of invasion of woody species introduced to Brandenburg (cumulative curve for 184 of 210 species; 26 species were not differentiated temporally; see text for explanations).

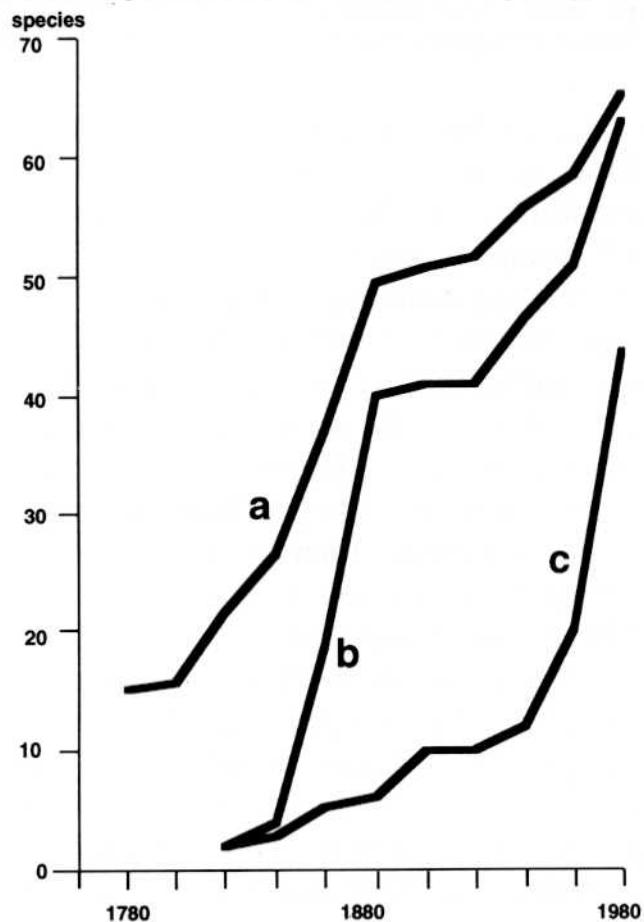


Fig. 4. Reconstruction of the beginning of invasion of woody species (1787-1990, cumulative curves) differentiated according to their origin in (a) other parts of Europe (including the Mediterranean), (b) America, and (c) central and eastern Asia. (Species native to more than one or two areas were counted more than once; species from west Asia and of cultural or unknown origin are not shown.)

## Lag phases preceding invasions

In Fig. 4, three groups of invading species, originating in central or east Asia, North America, or in other parts of Europe (including the Mediterranean), were differentiated according to the time of the beginning of invasion. Comparing this figure with the temporal stratification of the total introductions from these areas (Fig. 2) shows a coincidental temporal pattern. Most of the European species spread earlier than American species, which were introduced later, followed finally by those from east Asia which had been introduced mainly in the 19th century. Obviously, the history of beginning invasions echoes the history of introductions.

For 184 species, time lags were calculated between the first introduction of a species to Brandenburg and the first record announcing its becoming invasive. These time lags have a broad range (Fig. 5a). Only 6% of the 184 species began to spread within 50 years after their first cultivation, 25% lagged up to 100 years, 51% up to 200 years, 14% up to 300 years and 4% invaded only after more than three centuries following their first introduction to Brandenburg. On average, there was a delay in invasion of 147 years after the first release of a species. In Fig. 5b, the species are differentiated by their life forms as trees and shrubs (including woody climbers). The pattern is similar, but shrubs began to spread more quickly ( $\bar{x} = 131$  years) than trees ( $\bar{x} = 170$  years). Through time, the ratio between introductions and beginning invasions was not a constant (Table 1). Calculations for those species which originated in other parts of Europe, North America, or east Asia show that at the end of the 18th century 3.0% of the introduced species began to be invasive. 100 years later this percentage has almost doubled to 5.3%, and, at present, it has increased to 7.4%. Supposing that the number of species introduced in the second half of the 20th century is negligible (Jäger 1988), Goeze's data for 1916 are also taken for the calculations for 1940 and 1990. Differentiating the data according to species' origin reveals obvious differences (Table 1). In the whole period between 1780 and 1990, 21% of

Table 1. Varying ratio (*c*) through time between cumulative number of woody species introductions to central Europe (*a*) and cumulative number of invasions breaking out in Brandenburg (*b*).  $c = b/a \times 100$ . The numbers of introductions have been calculated using the data of Goeze (1916). Supposing that the number of species introduced in the second half of the 20th century is negligible, Goeze's data for 1916 are also taken for the calculations for 1940 and 1990. The data are differentiated according to species' origin. Arranged by I: other parts of Europe (including the Mediterranean), II: North America, III: east Asia. Species from west Asia and those of cultural origin were not considered.

	1580	1680	1780	1820	1860	1900	1940	1990
I. Europe								
a. introductions	93	133	225	267	277	296	309	309
b. invasions	?	?	15	22	37	51	56	65
c. ratio b/a	?	?	6.7	8.2	13.4	17.2	18.1	21.0
II. North America								
a. introductions	7	51	268	449	562	713	857	857
b. invasions	?	?	0	2	18	41	47	93
c. ratio b/a	?	?	0	0.4	3.2	5.8	5.5	10.9
III. East Asia								
a. introductions	11	15	79	193	494	1004	1351	1351
b. invasions	?	?	0	2	6	10	12	43
c. ratio b/a	?	?	0	1.0	1.2	1.0	0.9	3.2
I+II+III								
a. introductions	111	199	572	909	1333	2013	2517	2517
b. invasions	?	?	17	29	65	107	122	185
c. ratio b/a	?	?	3.0	3.2	4.9	5.3	4.8	7.4



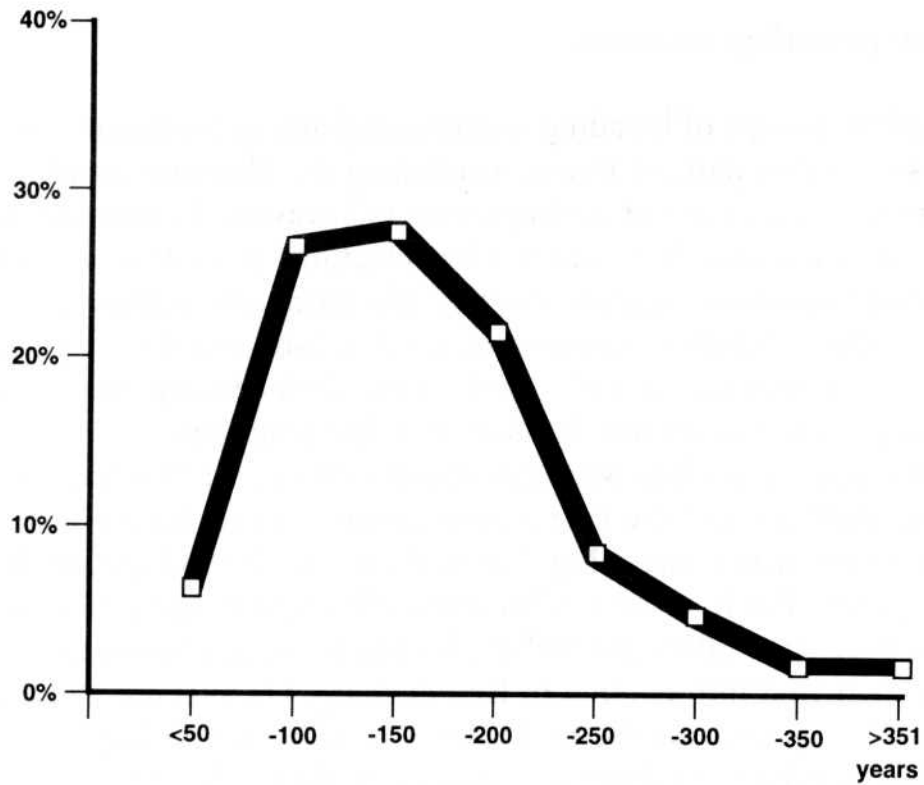


Fig. 5a.

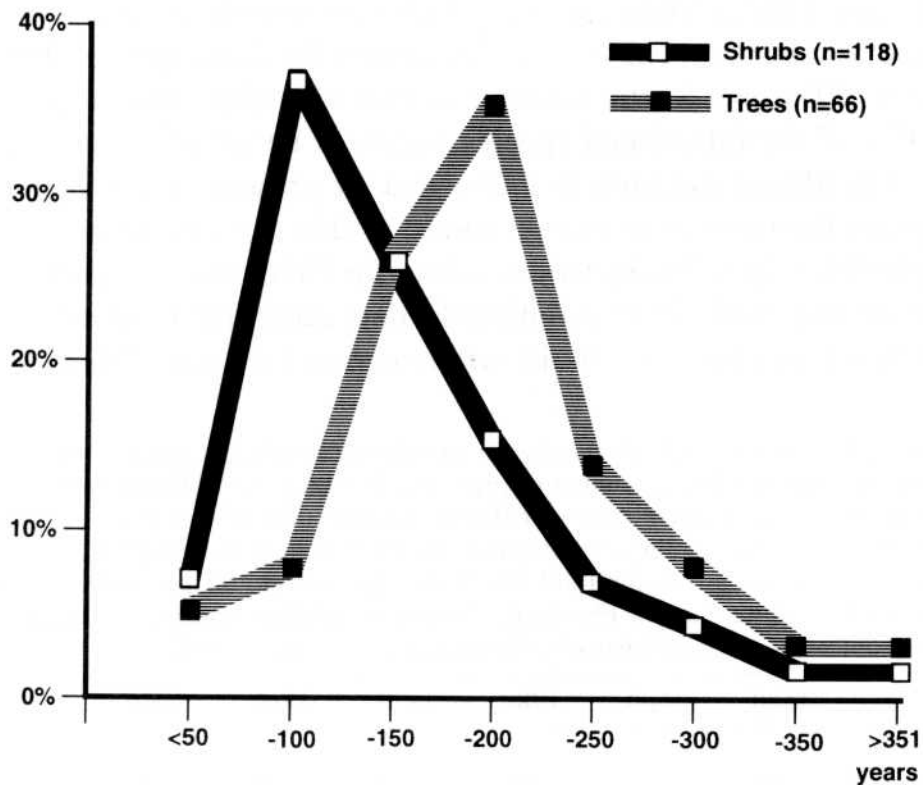


Fig. 5b.

Fig. 5. Time lags between the introduction and beginning of invasion of woody species in Brandenburg. (a) Calculation for 184 woody species grouped in 50-year-classes, (b) differentiation between trees ( $n = 66$ ) and shrubs (including woody climbers,  $n = 118$ ).

the European species began to spread, but only 10.9% of the American and 3.2% of the species from east Asia. In each of these three groups, the ratio between introductions and beginning invasions changes directionally through time, but with a delay in American and Asian species which were generally introduced later. (The slight decrease in the ratio of species from east Asia at the beginning of the 20th century is due to the extensive introductions at this time as shown in Fig. 2.) Considering the

variation in the length of time lags (Fig. 5a, b), it can be suggested that the trend in more recently introduced American and, especially, east Asian species will still be upwards. In consequence, the number of invasions breaking out will increase, even if no additional species were introduced.

### Success and failure

Most of the introduced woody species have remained unsuccessful in starting invasions: only 210 woody species spread outside their original range. For 182 of these species spreading in Berlin, the success or failure after the first escape from cultivation could be evaluated (Fig. 6). 29 or 16% of the species which began to invade failed (group I): 2 trees, 25 shrubs, and 2 woody climbers have become extinct. In the late 19th century, the performance of these species has been quite different: according to Bolle (1887) most of them had always been rare (e.g., *Myrica cerifera* and *Menispermum canadense*), sometimes however, performing "quite like an indigenous plant" (*Spiraea tomentosa*). Others, however, are known to have been abundant (*Rhus radicans*) or even apparently permanently established (e.g., *Robinia hispida*).

For 97 species (53%), success or failure has not yet been decided (group II): 41 trees, 55 shrubs, and 1 climber still occur as ephemerophytes in the wild without having become established. About a third of these initial invasions have led to a permanent establishment of 25 trees, 29 shrubs, and 2 climbers. Of these, 34 species (19%) have become naturalized as epikophytes in man-made vegetation (group III), and 22 species (12%) are considered to persist as agriophytes in natural vegetation even if human impact on these stands ceases (group IV).

Relating these data to the number of alien species currently cultivated in Germany (3150 species) or to the 2645 introductions to central Europe listed by Goeze (1916), shows that up till now only about 7% of these introduced species have begun to spread. About 2% have established successfully, and less than 1% have become permanent members of the natural vegetation.

Average time-lags were calculated for each of the groups I-IV, the largest being

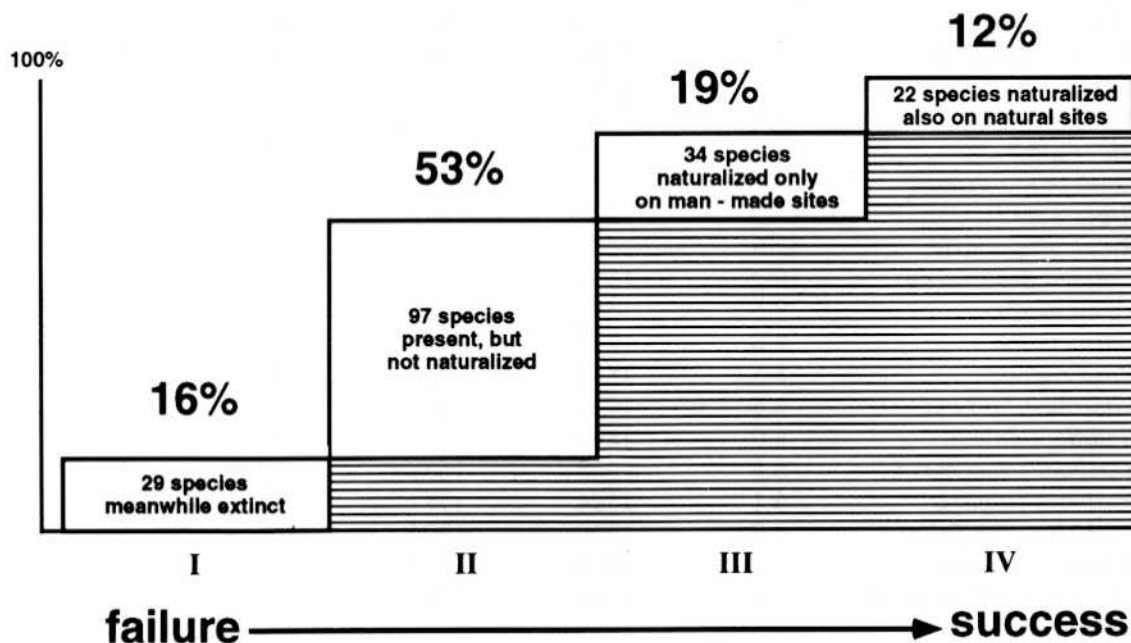


Fig. 6. Success and failure of 182 woody species which had been reported as starting invasion in Berlin in the period between 1787 and 1990 (grouped according to their degree of naturalization: I: extinct species, II: ephemerophytes, III: epikophytes, IV: agriophytes).

for the ephemerophytes (group II), which lagged 159 years on average. No distinct differences were found however, between the different groups. The results for groups I, III, and IV only range between 133 and 137 years, indicating that there is no relationship between the success in naturalization and the lag phase between introduction

Table 2. The most frequent trees, shrubs and woody climbers spreading in Brandenburg, Germany outside their original range. Data on introduction and beginning invasion refer to the area of Brandenburg. The species are ranked according to decreasing frequency in Berlin (see Kowarik 1992: Table 15, 17) The species are native to: 1: other parts of nemoral Europe, 2: meridional Europe, 3: western Asia, 4: central/northern Asia, 5: east Asia, 6: North America. x: Species of cultural origin.

	Relative frequency	First cultivation	First spread	Time-lag	Origin
<b>Trees</b>					
<i>Robinia pseudoacacia</i>	66.9	1672	1824	152	6
<i>Acer negundo</i>	61.0	1736	1919	183	6
<i>Prunus serotina</i>	58.5	1796	1825	29	6
<i>Aesculus hippocastanum</i>	42.6	1663	1787	124	2
<i>Quercus rubra</i>	37.2	1773	1887	114	6
<i>Ailanthus altissima</i>	34.9	1780	1902	122	5
<i>Populus x canadensis</i>	17.9	1787	1952	165	x
<i>Prunus domestica</i>	14.6	1594	1787	193	3
<i>Pyrus communis</i>	14.1	1594	1787	193	1-3
<i>Juglans regia</i>	14.1	<1594	1968	>374	2-3
<i>Prunus mahaleb</i>	13.8	1785	1839	54	1-3
<i>Laburnum anagyroides</i>	13.8	1663	1861	198	1
<i>Sorbus intermedia</i>	7.4	1796	1908	112	1
<i>Celtis occidentalis</i>	6.2	1785	1957	172	6
<i>Ulmus pumila</i>	5.1	1796	1985	189	4-5
<i>Hippophaë rhamnoides</i>	4.9	1663	1883	220	1-5
<i>Elaeagnus angustifolia</i>	4.1	1736	1883	147	3
<i>Quercus cerris</i>	2.8	1796	1957	161	2
<i>Larix decidua</i>	2.6	1594	1887	293	1
<b>Shrubs</b>					
<i>Mahonia aquifolium</i>	41.4	1822	1860	38	6
<i>Syringa vulgaris</i>	31.6	1663	1787	124	1
<i>Symphoricarpos albus</i>	30.7	1822	1887	65	6
<i>Ligustrum vulgare</i>	28.5	1594	1787	193	1-3
<i>Philadelphus coronarius</i>	21.9	1656	1839	183	2-3
<i>Lycium barbarum</i>	18.0	1769	1839	70	5
<i>Cornus stolonifera</i>	17.5	1785	1861	76	6
<i>Prunus persica</i>	16.1	<1594	1965	>371	5
<i>Ribes alpinum</i>	15.6	1736	1827	91	1-2
<i>Lonicera tatarica</i>	14.4	1770	1864	94	4
<i>Ribes aureum</i>	13.9	1822	1883	61	6
<i>Ribes grossularia</i>	12.9	1594	1787	193	1
<i>Colutea arborescens</i>	10.2	1594	1859	265	2
<i>Vinca minor</i>	9.5	1582	1787	205	1-2
<i>Cornus alba</i>	8.8	1773	1857	84	4
<i>Rosa rugosa</i>	8.5	1841	1960	119	5
<i>Viburnum lantana</i>	8.5	1736	1864	128	1-3
<i>Buddleja davidii</i>	8.0	1896	1952	56	5
<i>Sambucus racemosa</i>	6.8	1663	1857	194	1
<i>Berberis vulgaris</i>	6.1	1594	1787	193	1-3
<i>Sorbaria sorbifolia</i>	4.9	1796	1904	108	5
<i>Rubus laciniatus</i>	4.6	1808	1885	77	x
<i>Caragana arborescens</i>	3.9	1769	1964	195	4
<b>Woody climbers</b>					
<i>Clematis vitalba</i> *	-	1663	1883	220	1-2
<i>Parthenocissus inserta</i>	-	1663	1884	221	6

\*1787 as time of first spread (Kowarik 1992) has to be considered as doubtful.

and initiation of invasion.

The same is true for success in terms of frequency. The ranking of the most successful trees, shrubs, and climbers according to their frequency in Berlin (Table 2) does not correlate with increasing time lags. The three most frequent tree species, all native to North America, took the first step toward invasion between 29 years (*Prunus serotina*) and 183 years (*Acer negundo*) after their first cultivation in Brandenburg. High differences are also found in shrub species, and the frequent woody climbers were only reported as spreading about 220 years after their first cultivation in Brandenburg.

## Discussion

### *The risk of invasions: or testing the '10:10 rule'*

The risk of biological invasions has sometimes been estimated by relating the number of more or less successful invasions to the number of total introductions (Kowarik and Sukopp 1986; Williamson and Brown 1986; Weeda 1987; Di Castri 1989). Referring to the British flora, Williamson promulgated a '10:10 rule' as a rule of thumb, which means that 10% of the introduced species become established, and 10% of established species become pests (Williamson 1993). This approach is somewhat ambiguous because it combines two different dimensions of success. Ecologically, it refers to a species' capability of establishing self-sustaining populations. The denoting of species as 'pests' however, results from an anthropocentric evaluation of unwanted effects caused by an invasive species. But what is unwanted? Perrins *et al.* (1992) demonstrated the vagueness of categorizing species as weeds or pests by revealing large variation in the evaluations made by agriculturists or by conservation-

Table 3. Probability of initiated, succeeded, and failed invasions of alien woody species. The numbers of invading, established, and extinct woody species in Brandenburg/Berlin are related to the total introductions to Germany. Additionally, data on vascular plants which are considered as alien to central Europe are included for comparison.

	Brandenburg (woody species)		Berlin (woody species)		Central Europe (vascular plants)	
	No	%	No	%	No	%
Introduced	3150	100.0 <sup>1</sup>		?	12000	100.0 <sup>5</sup>
Producing feral individuals	2214	70.3 <sup>1</sup>		?		
Able to start invasions	210	>6.7 <sup>2</sup>	182	100.0 <sup>3</sup>		?
Extinct after invasion	>32	>1.0 <sup>4</sup>	29	15.9 <sup>3</sup>		?
Present, without established population	>114	>3.6 <sup>4</sup>	97	53.3 <sup>3</sup>		?
Self-sustaining population, established	>64	>2.0 <sup>4</sup>	56	30.8 <sup>3</sup>	417	3.5 <sup>6</sup>
Established in natural vegetation	>32	<1.0 <sup>4</sup>	22	12.1 <sup>3</sup>	228	1.9 <sup>7</sup>

<sup>1</sup>Kowarik (1992) calculating the data compiled by Bartels *et al.* (1991) for Germany

<sup>2</sup>referring to the area of Brandenburg

<sup>3</sup>referring to the area of Berlin

<sup>4</sup>estimated by considering the results from Berlin

<sup>5</sup>after Sukopp (1976) referring to central Europe

<sup>6</sup>after Jäger (1988) referring to the area covered by Rothmaler (1976)

<sup>7</sup>after Lohmeyer and Sukopp (1992) referring to central Europe

ists. Considering that some species such as *Colchicum autumnale*, which are currently listed in 'Red Data Books', were persecuted as pests only some decades ago (R. Kirsch-Stracke, personal communication, with reference to Northrhine-Westphalia, Germany), it could be advantageous to differentiate species' invasion success, at least for ecological considerations, exclusively in an ecological perspective. For this purpose, a species' ability to establish self-sustaining populations is considered in this paper. The results are summarized in Table 3.

The numbers in Table 3 are inconclusive, because the success of invading woody species is related to different geographical levels. But even if "roughly 10% means between 5 and 20%" (Williamson 1993: 220), there is little support from this study for the '10:10 rule'. About 7% of the woody species introduced to Germany started their invasion in Brandenburg during the last 200 years, but 16% of the invasions failed through extinction, and this rate is usually unknown or overlooked. Supposing that fewer species had been introduced to Brandenburg than to Germany, the invasion rate is probably higher than 7% and may fit the 10% category. However, most of the invading species are far from being established. Only about one third were able to establish self-sustaining populations, and among these 12% became permanent members of the natural vegetation. Relating these results to the total introductions, a '10:2:1 rule' could be suggested. (It also holds when only species which have become feral are considered as introduced, as done surprisingly by Williamson in 1993.) The '10:2:1 rule' means that roughly 10% (probably less) of the introduced woody species begin to spread, about 2% become established (*i.e.*, significantly less than 5%), and half of these species become members of the natural vegetation. It could be argued that there might exist a dimensional shift in the invasion success of woody species compared to other life forms. Data available for alien vascular plants in central Europe, however, confirm an approximate rate of establishment which is obviously lower than 5% of the total introductions (Table 3, third column), and this fits the dimensions of the '10:2:1' rule. In other areas the relationship between introduced, invading and established species may be different.

Rules derived from the ratio between introduced and spreading species might be suitable for quantifying the actual invasion success, but they would only be adequate to predict the future risk of invasions if the ratio between introductions and invasions was constant. The analyses of the invasion dynamics through time however, shows that the contrary is true (see Table 1). Considering, additionally, the large variation in time lags between the first introduction and the initiation of invasion, the following generalisation can be proposed: the longer an introduced species is present in an area, the higher the probability of its starting an invasion. In consequence, the number of invasions breaking out is expected to increase, even if no additional species were introduced.

These results may stimulate the debate on the question whether or not the number of new invasions breaking out will decrease in this century and in the future (see discussion in Trepl and Sukopp 1993). Although the number of deliberate introductions of new species is negligible in this century, compared to the 18th and 19th centuries (Jäger 1988), the number of new invasions has obviously increased during this century (Fig. 3). In consequence, the ratio between introduced and invading species will change in the future as it has done in the past.

As Table 2 shows, successful species are not necessarily quick in starting invasions. They may become very successful despite lagging longer than less successful

invaders. Thus, the performance of a species actually failing in spreading or in the establishment of self-sustaining populations could hide its future success.

### *Why is the lag phase so long?*

Even if through time the probability of invasions has increased, time itself cannot be considered a cause of such biological change (Johnstone 1986). Three kinds of factors which may influence the timing of invasion break outs are tackled: first, some intrinsic factors referring to species' life history traits, second, the role of climatic changes, and, third, the availability of safe sites. The causes to be discussed need not be mutually exclusive, and there are others usually analysed as attributes of successful invaders or of ecosystems susceptible to invasions (Orians 1986; Crawley 1987; Rejmánek 1989; Trepl 1990). In recent years, the 'rule of less ruleness' in explaining the invasion success of different species is accepted more often (Williamson and Brown 1986; Crawley 1989; Roy 1990). Consequently, no attempt is made to find new predictable factors, but attention is paid to the limits in predicting the success or failure of invasions, which is often done by referring to deterministic attributes of species or environments.

### *The role of intrinsic factors*

The minimal lag phase between the first release of a species and the start of an invasion is defined by the time needed to produce the first propagules. The more quickly a species can switch to the reproductive phase of its life cycle, the higher the probability of entering into invasion. Annuals and monocarpic perennials are not necessarily better invaders than perennials (Bazzaz 1986; Noble 1989; Roy 1990; Pyšek and Prach 1993), but they are supposed to be quicker in starting invasions. The lengthened lags of tree as compared to shrub species, which generally breed more quickly, confirm this hypothesis also for woody species (Fig. 5b). Rejmánek (1995) explains the varying invasion success of several *Pinus* species partly by differences in the maturation period. The initial and subsequent growth of a population is affected by other life history traits such as the quantity of seed production, specificity of germination requirements, and the mortality of seedlings. The failure or long lag phases of species which were only rarely planted can partly be explained by the concept of minimum viable populations (Richter-Dyn and Goel 1982). When seedlings occur only at a few sites and have become locally extinct, the chance is small that this first attempt at invasion will be observed.

It is doubtful that the large differences in time lags in those species which have been cultivated more frequently can be explained by this approach. Among the most frequent tree species listed in Table 1, are both pioneer and late successional species. The regeneration of *Prunus serotina*, for example, is enhanced by natural or man-made disturbance (Skeen 1976; Starfinger 1991), and this species is able to set seed after only 7 years (Starfinger 1990). In contrast, *Quercus rubra*, as a later successional species, only begins to fruit when 25 years old, and does not produce acorns abundantly until it is 50 years old (Fowells 1965). Thus, the invasion of *Prunus serotina*, which began almost four times earlier than that of *Quercus rubra* can be explained, at least partly, by the species' different life history traits. This explanation does not fit other frequent invaders, which behave like pioneer species in their areas

of original distribution as well as in Brandenburg: *Robinia pseudoacacia* (Boring and Swank 1984; Kowarik 1990a), *Acer negundo* (Sachse 1991, 1992), and *Ailanthus altissima* (Pan and Bassuk 1986; Kowarik and Böcker 1984). All of them are able to set seed within one to two decades, all are prolific seed producers, and all have been planted frequently since long before invasion started. However, *Ailanthus* lagged about 120 years, *Robinia* 150 years and *Acer negundo* 180 years (Table 2). Although the later invasion success of these species was promoted by an increasing availability of safe sites (see discussion below), a lack of these would probably not have excluded an earlier start of invasion. All three species spread in sites which were also available in former times (e.g., parks and gardens, road embankments).

Many but not all successful invaders may be characterized by a high level of genetic plasticity (e.g., Baker 1965; Barrett and Richardson 1986; Bazzaz 1986). Unfortunately, there is little information on the role of genetic adaptation in opening invasion windows for species which lag for long periods after their first introduction. In Australia, changes in flowering time have been found in divergent strains of *Trifolium subterraneum* (Cocks and Phillips 1979), and a switch to earlier flowering is also supposed to be a key factor in the dramatic invasion success of *Senecio inaequidens* during the recent decades in Europe (Werner *et al.* 1991). Another example is *Cynodon dactylon*, which is damaged by frost in the colder parts of Germany. In Berlin, one population with an increased winter hardiness was found and crossed successfully with an American population (Burton and Monson 1978).

As for the woody species considered in this study however, there is no information on genetic adaptation which may explain large time lags. In *Ailanthus altissima*, there is a high genetic variation in both American and Chinese populations (Feret and Bryant 1974). A comparison of significantly different growth and seed characteristics of several seed sources revealed a lack of correlation to climatic and edaphic features indicating that *Ailanthus* has not adapted to macro-environments in America (Feret 1985). In consequence, long lag phases which have been reconstructed for *Ailanthus* and other early successional species may not be sufficiently explained by genetic adaptation or other intrinsic factors.

### *The role of climatic changes*

Erkamo (1956) demonstrated that the rising temperatures in the first half of this century caused responses in the performance of single plant species as well as at the community level. In the last decade it has become evident in the international discussion that ecological theories on changes at the population or community level are insufficient when referring to climate as a constant. Climatic parameters change in a directional way through time, and these changes may affect plant communities, even if only over ecologically short periods such as decades or a few centuries are considered as the time scale (Davis 1986).

In consequence, Hengeveld (1987) stressed the necessity of non-equilibrium models leaving room for the history of populations expressed by the size of time lags. Davis (1986) illustrated big differences in both the magnitude and the timing of species' responses to the same climatic trend. She referred mainly to changes in abundance, demography, and geographical distribution of native species. Different response patterns to climatic changes however, may also be a key factor in determining the variation in lag phases preceding the start of biological invasions.

In this paper, the history of introduction and the initiation of invasion of alien woody species has been reconstructed with reference to the last 400 years. During this period several directional climatic changes have to be considered. The 'Little Ice Age' began around A.D. 1250, ending in the 17th and 18th century. After about 1850 however, the trend changed (Davis 1986). The aggregate change in temperature appears to be between  $0.5^{\circ}\text{C}$  and  $0.7^{\circ}\text{C}$  over the last century, but the rate of increase has been substantially higher in the last decade than at any previous time (Woodwell 1990). Davis (1986) stressed that community changes within forests occur less rapidly than the advances of the tree line, which are reported mainly from northern countries. Even if there is less evidence for changing frequencies in already existing populations of forest trees, the temperature increases since the 1850s may be decisive for those species whose regeneration by seed had previously been prevented by a less favourable climate. This suggestion is supported by Erkamo (1956) who analysed the capability of woody species to regenerate by seeds. He found that from the beginning to the middle of this century, a number of species extended their 'regeneration front' several latitudes northwards. This is true both for species such as *Quercus robur*, which is native to the south of Finland and for alien species such as the North American *Amelanchier spicata*.

For Berlin, as with other big cities, the effects of the climatic rewarming since the 1850s have been exacerbated by the rise in temperature of the urban climate. In the case of Berlin this involved a shift from a city with about 170,000 inhabitants in 1800 to a metropolitan area with 3.7 million inhabitants in 1910. Calculations of the increased warming effect of the urban climate are:  $0.2^{\circ}\text{C}$  for 1798-1804,  $0.7^{\circ}\text{C}$  for 1831-1837, and  $1.4^{\circ}\text{C}$  for 1886-1898 (Schlaak 1982, citing calculations by R. Scherhag). For the period 1961-1980, there was a difference in the annual mean air-temperature of more than  $2^{\circ}\text{C}$  between the centre and the surroundings of Berlin. This warming is correlated with a significant reduction of frost days (<64 days in the centre, >102 days in the surroundings, Von Stülpnagel 1987; Von Stülpnagel *et al.* 1990).

In consequence, the invasion of alien species with higher temperature requirements can be expected to be promoted, especially in big cities where the general trend to warmer temperatures is intensified by the effects of the urban climate. This hypothesis is supported by Fig. 3, showing an obvious increase in woody species starting to invade since the middle of the last century, coinciding with the changes in temperature: In 1756-1847, the winters were colder by  $-0.7^{\circ}\text{C}$  compared to 1848-1907, and there was a significantly higher frequency in extremely cold winters in the period before 1846 (Hellmann 1910, 1917).

Similar trends such as in Fig. 3, showing an exponential gain of new species in the second half of the 19th century, have been observed for annual and perennial herbs in Berlin (Scholz 1960) and for all established alien plant species in Germany (Jäger 1977). They had been explained mainly by a huge increase in incidental introductions and subsequent dispersal, promoted both by the new traffic systems and the increasing commercial exchange of goods, which coincided with a diversification of sites available in the urban environment (Sukopp 1976, Jäger 1977, Kowarik 1990b). Many of the alien invaders are native to warmer areas (Erkamo 1956, Scholz 1960), and they are considered to profit from a more favourable local climate, even on a small spatial scale, as Sarisaalo-Taubert (1963) found for small Finnish towns. Pyšek *et al.* (1995) described requirements for temperature increasing for successful invad-



ers of seminatural habitats through those invading man-made sites to unsuccessful aliens.

In contrast to weeds whose introduction and spread has been supported by a complex of diverse factors connected with urbanization and industrialization, the effects of climatic changes on the invasion of woody species which had been planted long before can be more clearly distinguished. Many woody species had already been cultivated during the 'Little Ice Age'. Thus, it is conceivable that for species with a long lag phase the changes in climate may have removed previous barriers to invasion. A cooler climate may prevent the invasion of a cultivated species in two ways: first, low temperatures may prevent seeds from germinating or seedlings from establishing as the performance of *Pinus longaeva* shows in California: for 200 years this species ceased to establish new seedlings, until the climatic conditions became more favourable (LaMarche 1973). This example illustrates how effectively a switch from a cooler to a warmer climate may affect the establishment of seedlings. The vegetation period may be either too short or too cool to allow the complete ripening of fruits.

In central Europe, the invasion success of *Robinia pseudoacacia* is higher in areas subjected to a subcontinental or submediterranean climate as compared with areas under oceanic influence (Kohler 1963; Kohler and Sukopp 1964). The same is true for *Ailanthus altissima*: in the Mediterranean or Pannonian regions, *Ailanthus* has spread abundantly through a broad range of sites (Kowarik 1983, Gutte *et al.* 1987). In central Europe however, it is virtually confined to warmer regions or to urban-industrial sites with a more favorable local climate (Kowarik and Böcker 1984). Considering that the continental climate is characterized by a longer growing period with an increased heat sum, it can be assumed that the spreading of *Robinia* has been promoted by the change to a more favorable climate in the 19th century. The invasion was noticed in 1824, but only in the second part of the last century did this species become frequent (Bolle 1887). The initial spread of *Ailanthus* was only noticed at the beginning of this century, although this species had been cultivated frequently since the end of the 18th century. Actually, it is more frequent in the warmed up zones of Berlin than on the urban fringe, and in Brandenburg it has been reported mainly in cities (Kowarik and Böcker 1984, Kowarik 1992, see also Table 3 in Kowarik 1995).

Apart from these species, *Prunus laurocerasus* and *Buddleja davidii* exemplify the possible limitations on invasions by low winter temperatures. *Buddleja* has been invasive since 1952, but it is actually less frequent in Berlin than in regions with milder winters (Kreh 1953; Burton 1983; Kunick 1990; Schmitz 1991). *Prunus laurocerasus* has been cultivated since 1663, but the first seedlings were not observed in Berlin until 1982. In regions with milder winter temperatures this species obviously succeeded better: it is common in London (Burton 1983), in cities in the northwest of Germany (personal observation), and has become a permanent member of natural forests in the Insubrian region (Gianoni *et al.* 1988). In Zurich, it has only begun to invade forests during recent years (Landolt 1991). Other species which are considered as thermophilous (indicator values for temperature >7 in Ellenberg *et al.* 1991; time lags in parenthesis) are *Laburnum anagyroides* (198 years), *Quercus cerris* (161 years) and the submediterranean *Colutea arborescens* (Kowarik 1985), which is native to the warmest sites in southwest Germany (Sebold *et al.* 1990). In

Brandenburg, 265 years elapsed before the spread of *Colutea* began in 1859. There is even larger time lag in *Vitis vinifera* and in *Juglans regia*, both of which have been cultivated in Brandenburg since 1200 A.D. (A. Brande, personal communication), but were first reported as invading in 1860 and 1968, respectively. The warmer climate may also have encouraged the spread of the frequently occurring *Prunus persica* and of the rarer *P. armeniaca*, both of which spread 300-400 years after their first cultivation (but see discussion below).

The example of *Syringa vulgaris* shows that the mode of spreading also has to be considered. This species was reported as an invasive early on (Willdenow 1787), but it usually spreads by clonal growth enlarging previous plantations. Even on rocky outcrops in the Rhine valley with a favourable local climate, fruits of *Syringa* do not ripen regularly (Lohmeyer and Sukopp 1992). In Brandenburg, *Syringa* spreads mainly by root suckers, but recently some established shrubs were discovered fruiting along abandoned railway areas in Berlin. It is assumed that the fruit ripening on these sites is promoted by the warmer urban climate. In this case, climatic changes would have enabled a species to enlarge its repertoire of spreading strategies.

#### *The role of safe sites*

There is a broad agreement that a biological invasion could not start without safe sites available for germination (Harper 1977; Johnstone 1986), and that invasion is facilitated by open communities subjected to natural or man-made disturbance (Trepl 1983; Fox and Fox 1986; Crawley 1987; Kowarik 1990b). There is some evidence that the lack of safe sites may have prevented some species from an earlier invasion. *Hippophaë rhamnoides* for example, occurs in central Europe originally on calcareous sites in dunes at the lake shore and on gravel banks of alpine rivers (Ellenberg 1988). Planted since 1663 in Brandenburg, its first spread was reported about 200 years later. It invades sand-pits where calcareous soils are exposed, and is spreading in urban areas (Kowarik 1992). From this spectrum of settled sites it can be concluded that the limited availability of open calcareous sites in the natural landscape of Brandenburg had prevented any earlier invasion by this species.

The demolition of larger parts of Berlin's centre during the Second World War resulted in a sudden shift in open space available for the colonization by plants. Responses to these changes on the community level have been studied in many cities which were bombed during the war. Many annual and perennial herbs conspicuously invaded the new sites (e.g., Salisbury 1943; Fitter 1946; Scholz 1956; Sukopp 1971). There is considerable evidence that the invasion rates of several woody species were amplified by the availability of new sites. The population growth of *Buddleja davidii* exploded in bombed cities (not in Berlin, but in cities with less cold winters such as Stuttgart and London (Kreh 1952; Burton 1983). In Berlin, there was an obvious increase in the population growth in *Ailanthus*, *Robinia*, *Acer negundo*, and also in *Clematis vitalba* (Scholz 1956; Kohler and Sukopp 1964). *Clematis* is not native to Brandenburg, but it is very frequent in other regions of Germany, growing on rich basic soils (Ellenberg 1988). It has been cultivated since 1663, but was first reported as spreading, but only rarely, after 1880. One of the first sites settled was a construction area near a railway station (Bünger 1884), and probably, a lack of suitable sites had prevented *Clematis* from beginning its invasion earlier.

The switch of *Ailanthus*, *Robinia*, *Acer negundo*, and *Clematis vitalba* to an exponential population growth since the 1950s could have resulted for several reasons: firstly, the effects of climatic changes, already discussed for *Ailanthus* and *Robinia*; secondly, the concept of the minimum viable population could explain why species whose invasion started some decades earlier needed some time to stabilize a founder population. In the case of these species, however, the sudden increase in the number of safe sites which became available after the war could be the key factor, despite the fact that the invasion by these species started before.

The case of *Platanus hybrida* illustrates the role of changing site qualities. In Berlin, *Platanus* has long been commonly planted, but was reported to spread only after the 1950s. Because moisture is required for germination (Brennenstuhl 1990), invasions of *Platanus* are virtually confined to the slopes of canals or channelized rivers which are moistened occasionally by waves (Kowarik 1984). Formerly, the urban canals had been used much more intensively for transport purposes, and it can be assumed that safe sites for *Platanus* only became available when, after the Second World War, the frequency of use decreased coincidentally with a decrease in maintenance.

Other sites may have become suitable for invasion due to the general trend toward eutrophication brought about by atmospheric deposition of nitrogen (e.g., Ellenberg 1985, Van Breemen and Van Dijk 1988). *Acer pseudoplatanus* and *A. platanoides*, both of which were formerly rare natives to Brandenburg, became more frequent even on sites formerly poor in nutrients (Sachse 1989). Correspondingly, *Sambucus racemosa* invaded oak-pine-forests on poor sandy soils in Berlin and elsewhere in Brandenburg, although this species had been confined to other parts of Germany as a common forest species on better soils (Ellenberg 1988).

Notwithstanding the existence of safe sites, invasion can only start if these sites became accessible (Heimans 1954). This statement is self-evident, though sometimes underestimated, despite being able to explain a high proportion of failing or succeeding invasions. Schroeder (1972) and Trepl (1984, 1990) have discussed in depth the role of stochastic events relative to invasion success: *Impatiens parviflora* would not have become the most successful invader in central European forests, had it not been dispersed incidentally by humans, and the non-arrival of most North American herbs to European forests may be explained by the absence of dispersal vectors. Conversely, the rapidly spreading *Prunus serotina* had been planted directly in forests (Starfinger 1990) and needed to bridge no gaps in reaching suitable sites for germination.

Finally, it is illustrated how the accessibility of safe sites may influence the length of lag phase. The reluctant spread of species such as *Vitis vinifera*, *Prunus persica*, *Prunus armeniaca*, and *Ficus carica* can be ascribed to climatic effects. Additionally, the popularization of these formally exotic fruits during the last decades has probably enlarged the dispersal of uneaten fragments of fruits to safe sites. *Prunus persica*, for example, has become common in a densely built-up area in Berlin (Böcker 1991), and fruit trees (*Prunus* spp.) conspicuously line some frequently used forest ways (W. Tigges, personal communication), as well as the railways of the urban transport system, when such space is not treated by herbicides. These sites had been available for more than 150 years, but they only became accessible through changes in dispersal conditions.

## Conclusions

The historical reconstruction of invasion dynamics of woody species alien to Brandenburg revealed that less than 10% of the introduced species began to spread within the last 200 years. The number of newly initiated invasions has increased, especially since the 1850s. Only about 2% of the introduced species were able to establish self-sustaining populations, and less than half of this group became members of the natural vegetation, whereas 1% became extinct after invasion. On average, species began to spread only 147 years after their first introduction to Brandenburg. Successful invaders (in terms of naturalization or frequency) are not necessarily more rapid in starting invasions than less successful species. From the discussion of these results, the conclusions can be summarized under two headings: firstly, emphasizing the role of chance and timing in invasions and, secondly, discussing some implications for the 'exotic species model'.

### *Chance and timing in biological invasions*

The first step to invasion may depend on deterministic factors such as the time needed for producing the first propagules. Considering that in many species, the length of lag phases is longer than the time expected to become feral, this stresses the role of other than intrinsic factors for the invasion success. The exponential population growth in *Ailanthus altissima*, *Acer negundo*, *Robinia pseudoacacia* or *Clematis vitalba* after the Second World War in Berlin cannot be explained sufficiently by the concept of minimum viable population. The key factor is considered to be the shift in open space available in bombed areas. Seen ecologically, this creation of safe sites resulted from stochastic events. The accessibility of safe sites may be also due to stochasticity, as shown by the example of exotic fruit trees compared to forest trees. There is some evidence however, that the opening of invasion windows does not necessarily result only from stochastic events (Johnstone 1986) but also from directional changes in environmental qualities. The invasion of several tree and shrub species has probably been enhanced by the trend to warmer temperatures since the 1850s, which moreover coincided in Berlin with an ameliorating urban climate. The invasion success of thermophilous species on bombed sites illustrates well the interaction of chance and timing in biological invasions. This has been emphasized recently by Crawley (1989). Supposing Berlin had been bombed 150 years before and the same pool of propagules was present, the colonization of the open space would differ conspicuously due to the less favourable climate. Who could have predicted in the last century the present-day success of species such as *Ailanthus*?

### *The risk of biological invasions and the 'exotic species' model*

The invasion of alien species into areas in which they have not evolved can be used as a model for the release of genetically engineered organisms to the environment (Sharples 1982; Regal 1986; Kowarik and Sukopp 1986; Kowarik 1990c, 1992). The advantages and limitations of this 'exotic species' model have recently been discussed by Regal (1993) and Sukopp and Sukopp (1993). There are two main implications for its appliance which can be derived from the results of this study:

a. Because of the lag phases preceding the invasion of species introduced several

decades or centuries previously, the ratio between introduced and spreading species is not constant (Table 1). Even if no new species were introduced, the number of invasive species will increase through time. Consequently, the risk of invasions breaking out is higher than anticipated by such rules as Williamson's (1993) '10:10 rule' or even if refined, as proposed, as a '10:2:1' rule. 10:2:1 means that less than 10% of the species introduced to an area begin to spread, roughly 2% become established, and 1% is established in the natural vegetation. Considering the high probability of future break outs of new invasions, such rules have to be ascertained from time to time.

- b. The analyses of invasion dynamics showed that the success of species may be delayed several decades and even centuries, considering both the beginning of invasion and a possible switch to a significantly higher rate of population growth. Being aware that the opening of invasion windows may result from deterministic as well as stochastic factors in concert with directional environmental changes, the failure of a new species under the current environmental conditions may hide its potential future success. Thus, risk assessments by short-termed experiments are completely insufficient in identifying the risk of future invasions. This is true for both currently successful and unsuccessful invaders. In this regard, there is no difference between introduced alien species and genetically engineered organisms.

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