NeoBiota 9: 49–70 (2011)
doi: 10.3897/neobiota.9.1469
www.pensoft.net/journals/neobiota

RESEARCH ARTICLE

A peer-reviewed open-access journal
NeoBiota
Launched to accelerate research on alien species and biological invasions

Secondary wind dispersal enhances long-distance dispersal of an invasive species in urban road corridors

Ingo Kowarik, Moritz von der Lippe

Department of Ecology, Technische Universität Berlin, Rothenburgstr. 12, D 12165 Berlin, Germany

Corresponding author: *Ingo Kowarik* (kowarik@tu-berlin.de)

Academic editor: *Ingolf Kühn* | Received 2 May 2011 | Accepted 28 June 2011 | Published 11 August 2011

Citation: Kowarik I, von der Lippe M(2011) Secondary wind dispersal enhances long-distance dispersal of an invasive species in urban road corridors. NeoBiota 9: 49–70. doi: 10.3897/neobiota.9.1469

Abstract

Roads contribute to habitat fragmentation and function as dispersal barriers for many organisms. At the same time many nonnative plant species are associated with road systems, a relationship that has been explained by the availability of disturbed habitats along roadsides and traffic-mediated dispersal of species. By studying secondary wind dispersal (SWD) over paved ground in an urban road corridor, we add the perspective of corridor-specific, but traffic-independent dispersal processes to the complex dispersal systems along roads. We analyzed (1) the seed shadow of an invasive tree *Ailanthus altissima* along a sidewalk subsequent to a strong wind and (2) the movements of painted samaras of this species released at ground level at the same site to identify the functioning of SWD. For the first experiment, we searched for samaras in the vicinity of an isolated tree three days after a strong wind. For the second experiment, we tracked the movement of the released samaras repeatedly over a period of 9–11 days, approximated probability-distance functions to the frequency distribution of samaras along the transect for different times after release, and related nearby measured wind data to changes in dispersal kernels. Single samaras from an isolated tree formed a seed shadow that extended for a distance of up to 456 m, and fragments of fruit clusters traveled up to 240 m. Forty-two percent of the sampled samaras were moved >100 m. The second experiment revealed that painted samaras released on the ground were moved up to 150 m over the pavement. Dispersal distances increased with time after seed release. A wider distribution of diaspores over the transect was significantly related to higher wind sums. Habitat shifts to safe sites for germination occurred during SWD, and different types of pavement influenced these processes. Smooth-surfaced pavement enhanced SWD, while cobbles with irregular surfaces slowed down or terminated SWD. During the observation period, 17% of released samaras accumulated in patches with a planted tree. Some were recaptured within the median strip and thus must have been lifted and moved over four lanes of heavy traffic. Our results suggest that impervious surfaces within road corridors can function as powerful avenues of wind-mediated long-distance dispersal and may counteract fragmentation of urban habitats. This also offers a functional explanation for the invasion success of *Ailanthus* at isolated urban sites.

Keywords

Alien species; anemochory; dispersal kernel; exotic species; habitat connectivity; seed tracking

Introduction

Roads contribute significantly to habitat fragmentation at local to regional scales and function as dispersal barriers for many species of plants and animals with consequences even at the evolutionary scale (Trombulak and Frissell 2000; Forman et al. 2002; Cheptou et al. 2008; Holderegger and di Giulio 2010). The level of fragmentation is especially high in urban settings (Robinson et al. 2005; Schleicher et al. 2011), but the ability to move in the urban matrix can counteract isolation effects as shown for many mobile animal species (Goddard et al. 2010). In plant species, human-mediated dispersal has been recognized as a powerful driver of long-distance dispersal leading to range expansion in many introduced species (Hodkinson and Thompson 1997; Kowarik and von der Lippe 2007). Despite this, human-mediated dispersal processes have barely been quantified in terms of dispersal distances (Carlton and Ruiz 2005), although a better understanding of mechanisms that drive long-distance dispersal (LDD) is crucial for assessing invasion processes and management options (Pyšek and Hulme 2005).

Since the pioneer work by Clifford (1959), several studies have illustrated the functioning of traffic-related dispersal by quantifying the number of species moved by vehicles. Propagules of plant species can travel either via mud-mediated adhesion to vehicles or in windshield wiper grooves and similar parts of vehicles (Schmidt 1989; Hodkinson and Thompson 1997; Zwaenepoel et al. 2006; von der Lippe and Kowarik 2007a). In addition, spillage from transports of harvest or seeds functions as an effective dispersal vector for crop species (von der Lippe and Kowarik 2007b; Kawata et al. 2009).

The efficiency of traffic-related dispersal in terms of seed rain and spatial reach has been recently quantified by sampling urban highway tunnels in Berlin. Vehicles moved 204 species, i.e., 12.5% of the total flora of Berlin. The share of transported native and nonnative species was the same, but long-distance dispersal was significantly more frequent in nonnative than in native species (von der Lippe and Kowarik 2007a). Vehicles moved propagules of more species, and more seeds of nonnative species, along outbound lanes than along inbound lanes (von der Lippe and Kowarik 2008). These results clearly illustrate a powerful role of traffic as dispersal pathway for introduced species. In addition to vehicles, people can also move species over long distances along road corridors directly via attachment of propagules to footwear or clothing (Mount and Pickering 2009; Wichmann et al. 2009).

Distribution patterns at regional scales illustrate that many nonnative plant species are associated with the road system (Gelbard and Belnap 2003; Dark 2004; Pauchard and Shea 2006). Correspondingly, range extension of invasive species has often been observed along roads (Ernst 1998; Lavoie et al. 2007; Jadoin et al. 2008; Essl et al. 2009; Pauchard et al. 2009), and increasing traffic or human mobility relates to the vector strength (Parendes and Jones 2000; Gelbard and Belnap 2003; Niggemann et al. 2009). Roadsides are also known to function as foci for the invasion of adjacent habitats (Tyser and Worley 1992; Gelbard and Belnap 2003). A better understanding of underlying mechanisms is thus an important challenge in invasion research.

Yet unfolding the mechanisms that drive plant invasions within road corridors requires disentangling the role of site- and vector-dependent mechanisms, as both may enhance plant migration along transportation systems. Plant dispersal and establishment along transport routes are mutually dependent processes. Habitats within road corridors are usually subject to high disturbance and provide safe sites for the establishment of numerous nonnative species (Hansen and Clevenger 2005; Rentch et al. 2005). Roadside habitats can thus favor the establishment of populations of species that are dispersed by vehicles and can, in turn, act as seed sources for subsequent adhesion to vehicles as shown by our previous study: the species composition of the sampled tunnel seeds was more similar to the regional roadside flora of Berlin than to the local flora around the tunnel entrances (von der Lippe and Kowarik 2007a).

In urban settings, roadside vegetation is mostly confined to habitats around planted street trees, joints and crevices in the pavement, and narrow strips with pervious surfaces either along the traffic lanes or adjacent to built structures (e.g., Langer 1994; Wittig and Becker 2010). Impervious surfaces of traffic lanes, sidewalks, or bicycle lanes clearly prevail in urban road corridors. Such sites are mostly perceived as hostile environments for plant dispersal and establishment and can even drive short-term evolutionary adaptation as shown for *Crepis sancta,* an herb that produces both dispersing and non-dispersing seeds. Patchy urban populations around trees showed a higher number of non-dispersing seeds compared to rural populations, which suggests a rapid evolution towards non-dispersing dispersal types in fragmented urban sites to prevent costs of dispersal losses over impervious urban surfaces (Cheptou et al. 2008).

Yet the escape of propagules in local populations that are embedded in a matrix of impervious urban surfaces could also lead to the establishment of new populations—assuming that propagules reach safe sites for germination within or adjacent to the road corridor. Here, the question arises whether or to what extent sealed urban surfaces hinder or enhance the secondary dispersal of propagules by wind after they have landed on the ground.

Secondary dispersal is generally acknowledged to be an important mechanism (Higgins et al. 2003), and studies on secondary wind dispersal over natural surfaces covered with snow (Matlack 1989) or in arid regions with sparse vegetation (Schurr et al. 2005) suggest a high potential for LDD in propagules after they have landed on the ground. We hypothesize that sidewalks and other linear structures with paved surfaces along roads may function—analogously to natural surfaces with missing or few barriers to seed transport—as avenues of secondary wind dispersal and may thus help to overcome spatial isolation of patchy urban habitats. We thus aim to add the perspective of corridor-specific, but traffic-independent dispersal processes to the complex dispersal systems functioning in road corridors.

To study secondary wind dispersal over impervious urban surfaces, we chose the tree *Ailanthus altissima* (henceforth *Ailanthus*) as model species. *Ailanthus* is native to China and northern Vietnam and invades urban and non-urban transport corridors in many regions worldwide with a temperate or Mediterranean climate (Kowarik and Säumel 2007). Colonized habitats include medians, cracks and crevices of sealed surfaces, patches with planted trees and, outside of cities, roadside habitats (Singh et al. 1992; Lenzin et al. 2001; Huebner 2003; Merriam 2003; Rentch et al. 2005). These patterns suggest the availability of safe sites for germination as well as an efficient dispersal in road corridors, but the functioning of different site- or dispersal-related mechanisms has not been disentangled thus far.

Samaras of *Ailanthus* are primarily dispersed by wind during a long and highly variable period of seed abscission that can extend until the next summer (Bory and Clair-Maczulajtys 1980). It remains an open question, however, whether wind plays a role as a secondary vector in moving samaras in addition to its function as a primary vector. Observation of wind-mediated seed transport in traffic corridors is anecdotal thus far.

To shed light on this mechanism, we first analyzed the seed shadow of an isolated tree in an urban road corridor and then performed a second experiment, releasing samaras at ground level, to quantify the role of secondary wind dispersal in road corridors. Diaspores are typically moved several times during secondary dispersal processes and may reach their final destination only after a considerable length of time. Following this process requires methods of direct seed tracking because seed traps would stop the dispersal process (Bullock et al. 2006). We therefore painted propagules of *Ailanthus* and released them in the same road corridor to track their movement over paved surfaces over a period of up to 11 days. We hypothesized that propagules of *Ailanthus* are repeatedly moved over paved urban ground and may overcome spatial isolation of patchy urban habitats by that dispersal pathway.

Methods

Seed shadow

Three days after a strong wind in March 2005 (maximum speed 7.7 m/s), we studied the seed shadow of an isolated *Ailanthus* tree along a section of the major urban road corridor “Unter den Eichen” in southwest Berlin, Germany, which runs in the direction of the prevailing winds (Fig. 1). Over a distance of 600 m, we sampled a strip 0.43–0.6 m wide that formed the border between the paved sidewalk area and the adjacent lots; the total sidewalk width between the traffic lanes and the adjacent private lots was 6–7 m. Over most parts of the sampled section, a wall with a fence on the top separated the paved public right-of-way from the private area, and corner blocks marked this boundary over the remaining parts. To increase the chance of identifying corridor-specific but traffic-independent dispersal processes we sampled that part of the sidewalk that was least exposed to traffic. The sampled strip was paved with small

Figure 1. A Urban road corridor "Unter den Eichen" in Berlin with an isolated tree of *Ailanthus altissima* as seed source. The red arrow indicates the sampled seed shadow in the prevailing wind direction; the lawn on the right side is part of the median **B** Habitats along the sidewalk. The site for the release experiment is marked by a circle with an X. Samaras were repeatedly tracked after release for their presence in different habitat types: H1, H3 – sidewalk pavement with small granite cobbles and large joints; H2 – sidewalk pavement with even surfaces and small joints; H4 – patches of open ground around planted trees, sparsely covered with ruderal vegetation; H5 – margin of the adjacent traffic lane close to the curb.

granite cobbles with a surface of about 5 x 7 cm, leaving joints about 0.5–1.5 cm wide in between (Fig. 1). The 8-m-tall *Ailanthus* tree grew in a garden close to this wall and parts of the crown stretched out in the road corridor. Hence, propagules were expected to reach the road corridor easily by primary wind dispersal.

We quantified the seed shadow of *Ailanthus* in segments of 20 meters and differentiated two types of propagules that are known to be dispersed by wind: single, one-seeded, spirally twisted samaras and fragments of panicles that can harbor up to 500 samaras prior to fragmentation during the abscission period (Bory and Clair-Maczulajtys 1980). Samaras from populations in Berlin average 4.7 cm in length and 0.9 cm in width (Kowarik and Säumel 2007). We did not measure the individual weights of the samaras because previous studies suggested that this parameter is not correlated with dispersal (Landenberger et al. 2007) or germination success (Delgado et al. 2009).

As we were only able to sample the seed shadow three days after the strong wind, the observed distribution of samaras along the sidewalk integrates the functioning of primary wind dispersal and subsequent wind-mediated lateral transport of samaras. To disentangle the contribution of the latter, i.e., the secondary dispersal pathway, we performed a release experiment at the same site.

Release experiment

At the same location, we placed three cohorts of samaras on consecutive days on the paved sidewalk and observed their lateral transport by wind for 9–11 days (Fig. 2). The first cohort had 70 samaras, each of the other cohorts had 100. We sprayed the samaras of the different cohorts with different colors to track their movement in time and space. As paint adds weight, the observed transport distances are likely underestimated. An experiment on a concrete surface in a wind tunnel allowed this effect to be quantified. Painting increases the mean lift-off velocity of 3.3 m/s in samaras of *Ailanthus* by 6–7% (Lemke et al. 2009).

Each day after release, we determined the transport distances along the sidewalk in the main wind direction and in the opposite direction. We determined the presence of samaras in different types of habitats as shown in Fig. 1b to assess their role in promoting or terminating secondary wind dispersal in road corridors. We also searched the adjacent habitats (traffic lanes, front gardens, median strip of the main road) for samaras that might have left the area of the sidewalk.

Measurement of wind

As we were not able to measure the wind speeds during the observation period at the release site, we used wind data collected on the roof of the nearby building of the Department of Ecology at a height of 23 m. The distance to the release site was only about 1 km, but wind conditions there may diverge from the measured data, mainly due to lateral and horizontal turbulence that frequently occurs in urban road corridors

Figure 2. A Fragmented fruit cluster as component of the seed shadow **B** Release site with the first cohort of painted samaras **C, D** Joints between granite cobbles and vegetation around planted trees as potential safe sites for germination.

(e.g., Zajic et al. 2011). The wall that bordered the sidewalk along most parts of the sampled section, for example, likely led to increased wind speeds. Yet as the measured data are supposed to represent differences in the local wind field we use them as proxies for relative differences in wind speed between different survey dates.

We therefore calculated wind sums, that is, the cumulative wind speed in the main wind direction over all measurement times, wind maxima, and wind sums for wind measurements that exceeded a speed of 3.7 m/s, which was measured in a wind tunnel as the minimum wind speed that could move painted samaras of *A. altissima* over the ground (Lemke et al. 2009).

Statistical analyses

Probability-distance functions were approximated to the frequency distribution of samaras along the sidewalk for different times after release. We pooled data of the first and second days, the third to fifth days and the sixth to eleventh days of all three cohorts to reveal differences in the shape of dispersal kernels in relation to time after release. Functions were fitted by non-linear regression using the log-normal function (Eqn. 1), which usually approximates wind dispersal data very well (Jongejans et al.

2008). In this equation *r* is the distance from the release site and *f*(*r*) the probability that a diaspore will be dispersed at that distance. The shape parameter *b* provides information about the skewness of the dispersal kernels, with lower values of *b* representing more right-skewed distributions. Increasing values of the scale parameter *a* represent a wider distribution of diaspores over the transect.

Eqn. 1:

$$f(r) = \frac{1}{b\ (2\pi)^{1/2}} \exp\left(\frac{-[\log r - a]^2}{2b^2} \right)$$

To relate wind data to the change in dispersal kernels, we fitted a lognormal function to the seed distribution of each single survey date, separately for each cohort of samaras. We then calculated changes between the location of the peak of the curves, the shape parameter *b* and the scale parameter *a* of the lognormal models for each two subsequent survey dates. As all parameters are probably affected by wind dispersal over the ground, these changes were related to wind sums and wind maxima that occurred between the two survey dates by linear regression. All analyses were performed with the statistical and programming language R 2.10 (R Development Core Team 2009). The package nls was used for nonlinear regression.

Results

Seed shadow

The seed shadow from the isolated *Ailanthus* tree, sampled after a strong wind, extended for 456 m along the sidewalk. Only 2% of all propagules were sampled in the direct vicinity (0–20 m) of the parent tree. The majority (58%) were moved up to 100 m, about one-third (34%) up to 200 m, 6% up to 300 m, and the remaining 2% up to 456 m from the parent tree (Fig. 3, Table 1).

Single samaras dominated the total of sampled propagules (85.2%). The remaining 14.8% were moved as fragmented parts of fruit clusters, up to a maximum distance of 240 m from the parent tree. The 16 cluster fragments had on average 9.4 samaras. The three largest clusters with 31–53 samaras were sampled at distances of 30–130 m from the seed source (Tables 1, 2). Single samaras were transported over longer distances than fruit clusters (Table 1).

Release experiment

Recapture rates and extent of secondary wind dispersal

The mean recapture rate of the released cohorts of samaras was 82.3% one day after release and decreased to 38.1% at the end of the experiment, 9–11 days later. Hence,

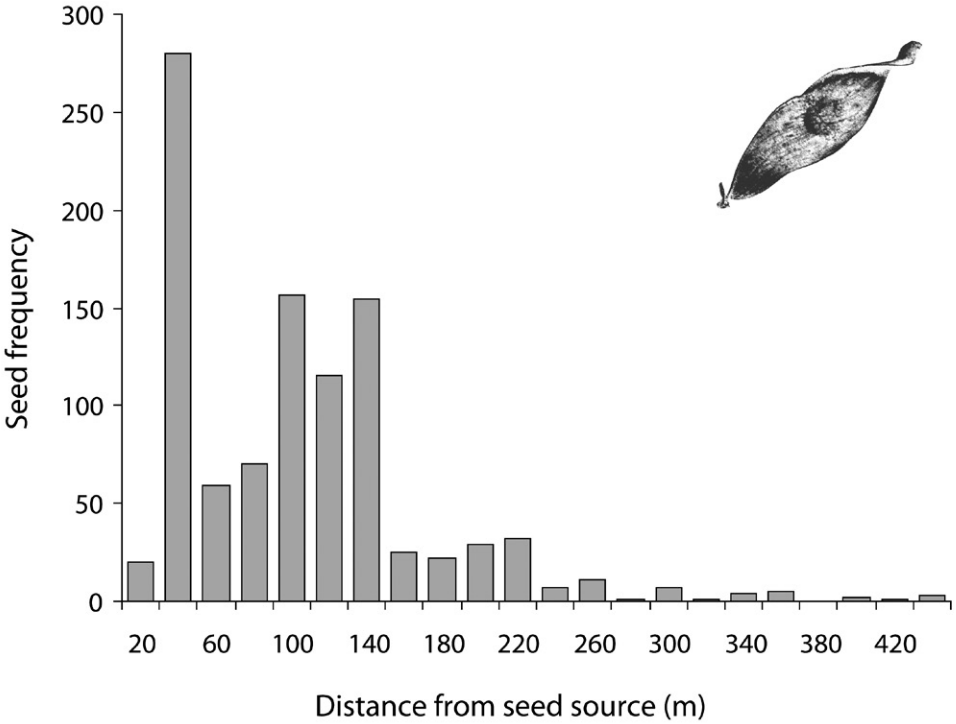

Figure 3. Seed shadow from an isolated *Ailanthus altissima* tree in an urban road corridor after a strong wind in March 2005. Propagules were recorded for 20-m sections of a sidewalk in the main wind direction. The peak in the 40-m section coincides with the presence of a bus shelter that clearly encouraged the accumulation of samaras.

62% of the exposed samaras vanished from the study area. Most of the samaras (72.4% of those recaptured one day after release) were found in the main wind direction along the sidewalk. Only a few samaras (9% one day after release) were transported in the opposite direction to an average distance of 30 m from the release site (one up to 50 m), and one percent were found on the median strip. Over the total observation period, wind moved the released samaras up to 150 m in the main wind direction along the sidewalk.

Shape of the dispersal kernel and transformation over time

The distribution of samaras along the transect followed a right-skewed humped curve with a peak at approximately 10 m between the first and second days of exposure and at approximately 20 m between the 6th and 11th days (Fig. 4a). The distance of the peak of the fitted dispersal kernel from the starting section, where the diaspores were laid out, increased significantly with time of exposure (Fig. 4b). Its location along the transect in the main wind direction shifted from a minimum of 3.2 m after one day to a maximum of 28.2 m after 11 days. Also the shape parameter *b* and the scale pa-

Table 1. Single samaras and samaras in fragmented fruit clusters as components of a seed shadow from an isolated *Ailanthus altissima* tree sampled after a strong wind in March 2005 in an urban road corridor.

Distance from seed source (m)	**All samaras**		**Single samaras**		**Samaras as part of fruit clusters**		
	n	%	n	% of all samaras moved this distance	Samaras (n)	Fruit clusters (n)	% of all samaras moved this distance
0–100	586	58.2	494	84.3	92	12	15.7
100–200	346	34.4	289	83.5	57	3	16.5
200–300	58	5.8	56	96.5	2	1	3.5
300–400	12	1.2	12	100			
400–456	4	0.4	4	100			
Total	1006	100	855		151	16	

Table 2. Number, size, and maximum transport distance of fruit clusters of *Ailanthus altissima* as components of a seed shadow along an urban sidewalk after a strong wind in March 2005.

Samaras per fruit cluster (n)	2	3	8	31	34	52
Clusters (n)	10	2	1	1	1	1
Observed maximum transport distance (m)	240	140	30	30	30	130

rameter *a* of the fitted lognormal models significantly increased with time of exposure (linear regression, $p = 0.005$ and $p = 0.002$ respectively).

While no significant relation between wind parameters and change in the location of the peak and the shape parameter of the fitted dispersal kernels was revealed, the change in the scale parameter *a* was significantly positively related to the sum of the measured wind speeds that were above the threshold of 3.7 m/s (Table 3). Hence, wind sums above the threshold to move a samara over paved surfaces showed a significant influence on distributing samaras over a wider section of the transect.

Habitat shifts

Within a period of 9–11 days, secondary wind dispersal resulted in conspicuous habitat shifts within the road corridor (Table 4). All exposed samaras vanished from the release site, and 7% of these remained in the paved strip with large joints between the granite cobbles, the habitat type in which the samaras were initially released (see Fig. 2). About 29% of all released samaras crossed the neighboring pavement with small joints, but no samara remained on this surface. Most of them (17%) were recaptured in adjacent patches with planted trees and another 3% in the pavement between these tree patches. This area had the same habitat structure as the pavement around the release site. About 10% of the released samaras were found at the edge of the traffic lane, close to the curb that serves as a border of the sidewalk area.

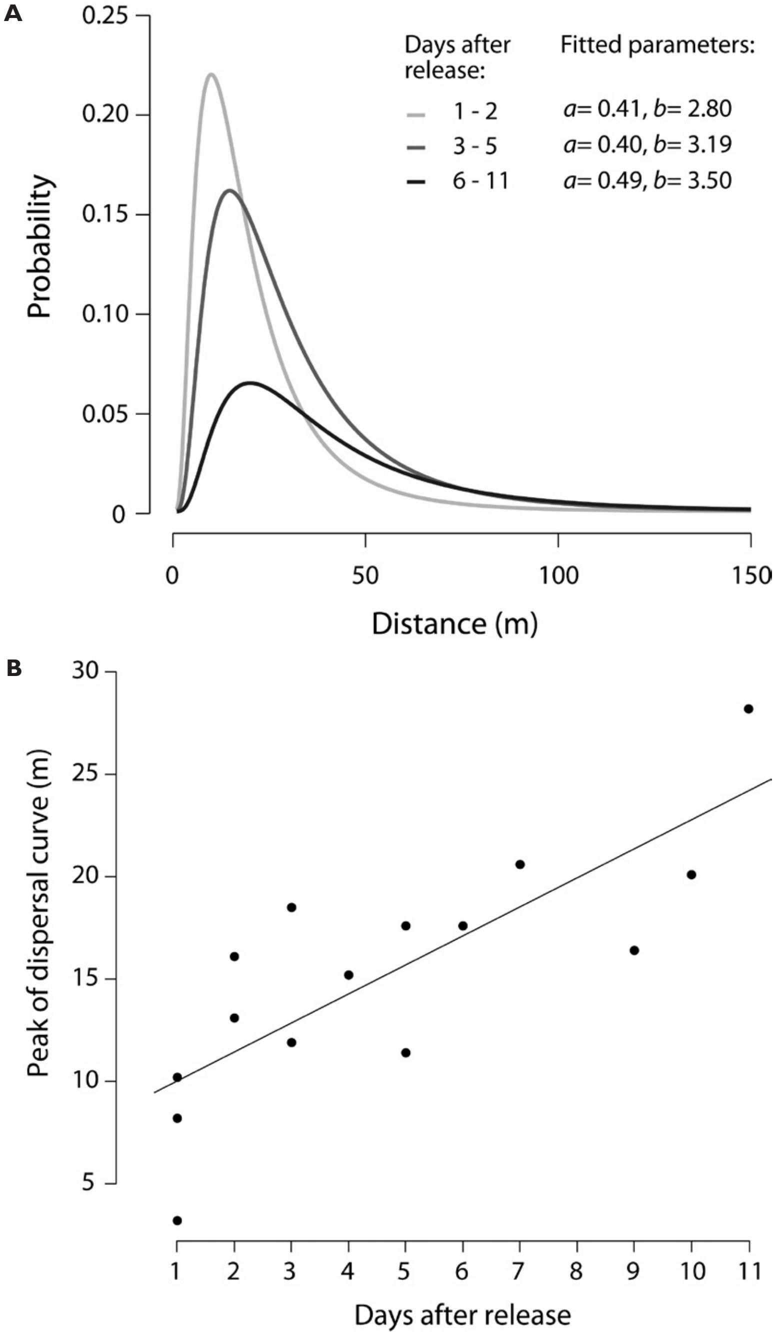

Figure 4.A Probability-distance distribution of samaras of *Ailanthus altissima* in the main wind direction after three different time spans of seed release in a paved road corridor (estimated by a lognormal function from three cohorts) **B** Effect of time after release on the location of the peak of the fitted dispersal kernel (lognormal function) along the road transect in the main wind direction. The least squares regression line is shown ($y = 1.42x+8.6$, Adj. $R^2 = 0.60$, $p < 0.001$).

Table 3. Linear regression models for the relation between wind parameters and the change in the location of the peak, and in shape and scale parameters for the fitted lognormal dispersal curves of subsequent sampling dates. The shape parameter *b* indicates the skewness of the dispersal curve, the scale parameter *a* indicates the dispersion of diaspores along the entire transect. Wind speeds and maxima were recorded at a nearby weather station over the period between each two sampling dates. The wind speed of 3.7 m/s was recorded as the average wind speed that caused any movement of samaras of *Ailanthus altissima* on a paved surface in a wind tunnel experiment (Lemke et al. 2009). Significant regression models are in bold.

	Coefficient	**P-value**	**Adj. R^2**
Dependency of Δpeak (change in location of the peak) on:			
Maximum wind speed	1.9727	0.338	<0.01
Wind sum	-0.0058	0.419	-0.03
Wind sum > 3.7 m/s	0.0153	0.089	0.19
Dependency of Δb (change in shape parameter) on:			
Maximum wind speed	0.0017	0.874	-0.09
Wind sum	>0.0001	0.994	-0.01
Wind sum > 3.7 m/s	>0.0001	0.671	-0.08
Dependency of Δa (change in scale parameter) on:			
Maximum wind speed	0.1787	0.112	0.16
Wind sum	-0.001	0.092	0.18
Wind sum > 3.7 m/s	**0.0025**	**0.008**	**0.47**

Table 4. Habitat shifts in three cohorts of samaras of *Ailanthus altissima* due to secondary wind dispersal in an urban road corridor 9–11 days after release at ground level on the pavement (habitat type H1). For the spatial arrangement of habitat types H1-5, see Fig. 1b.

	% Cohort 1 (n = 70)	**% Cohort 2 (n = 100)**	**% Cohort 3 (n = 100)**	**Mean**
Days after release	11	10	9	
Release site	0	0	0	0
Pavement with large joints (H1)	2.9	5	14	7.3
Pavement with small joints (H2)	0	0	0	0
Pavement with large joints (H3)	2.9	0	6	3.0
Tree patches (H4)	24.3	11	15	16.8
Margin of traffic lane (H5)	11.4	8	9	9.5
Median strip (lawn) beyond four traffic lanes	2.9	1	0	1.3
Total recaptured	44.4	26	44	38.1
Total vanished	55.6	74	56	61.9

Surprisingly, a total of nine samaras (3.3%) emerged on the median strip during the observation period, eight on a mowed lawn and one at the edge of the traffic lane, close to the curb. Two of these samaras still remained on the lawn of the median strip at the end of the observation period while the others continued their travels to unknown destinations.

Discussion

Long-distance dispersal is crucial for the spread of many invasive species but is usually difficult to observe due to the rarity of LDD events and the fact that propagules are often dispersed by more than one vector over longer periods of time (Higgins and Richardson 1999; Bullock and Clarke 2000; Ozinga et al. 2004). Our model species, *Ailanthus altissima,* is primarily dispersed by wind, but dispersal by water has recently been revealed as a further important dispersal process (Kaproth and McGraw 2008; Kowarik and Säumel 2008; Säumel and Kowarik 2010). Secondary wind dispersal in *Ailanthus* has been studied thus far only in natural settings, revealing negligible transport distances: within 27 days, no samara travelled > 0.25 m along the floor of a closed canopy forest with a 9% slope, and on a 48% slope only about 6% of all samaras were moved between 0.25 and 10 m (Kaproth and McGraw 2008). These results are not surprising because dense vegetation usually hampers secondary wind dispersal (Redbo-Torstensson and Telenius 1995). Our study demonstrates the importance of secondary wind dispersal in road corridors, i.e., in linear habitats with more or less smooth surfaces and usually sparse vegetation.

Primary versus secondary wind dispersal

Previous experiments and modeling studies suggest that primary wind dispersal rarely covers transport distances of more than 100 m, while secondary wind-mediated dispersal processes may move seeds over larger distances—a result that is usually attributed to stochastic processes (Matlack 1989; Higgens et al. 2003; Soons et al. 2004; Schleicher et al. 2011). The analysis of the seed shadow of an 8-m-tall isolated tree revealed a maximum distance for seed travel of 456 m (Table 1), which likely results from the combined functioning of primary dispersal by a strong wind and secondary wind-mediated dispersal of fallen samaras over a period of three days.

The maximum transport distance observed in the first experiment clearly extends the values reported for primary wind dispersal alone measured by using seed traps. A field study covering 6 months found that wind moved samaras at least 200 m over a hay field, with four 18-m-tall trees as seed sources (Kota 2005; Landenberger et al. 2007). As in many wind-dispersed species, there was a strong decline in seed density with increasing distance from seed sources. Landenberger et al. (2007) found a log-linear decrease in mean seed density per square meter with increasing distance from the seed source. Correspondingly in a Korean urban study, 75% of seedlings were found within 20 m of the parent tree, with single seedlings to a distance of about 65 m (Cho and Lee 2002).

Yet in our study, about 42% of the sampled seed shadow had been moved over distances of >100 m, a distance which is often used to define long-distance dispersal (Table 1). As the observed seed shadow integrates both primary and secondary wind dispersal over a period of three days, we tracked the movement of painted samaras to isolate the functioning of secondary wind dispersal over paved ground. Over the observation period, between 1 and 5.7% of the three released cohorts of samaras were moved at least 100 m over ground, with a maximum distance of 150 m from the release site. As painting reduces the lift-off velocity of samaras by 6–7% (Lemke et al. 2009), the true transport distances achieved by secondary wind dispersal are likely higher. Considering the modest wind speeds during the release experiment the measured transport distances are probably not rare events in road corridors but occur rather frequently in such habitats.

Hence, secondary wind dispersal alone can move *Ailanthus* samaras over long distances in urban road corridors, and a combined functioning of primary and secondary wind dispersal achieves transport distances far beyond those due to primary wind dispersal alone. Considering the negligible wind-mediated transport distances of samaras on a forest floor (less than 10 m; Kaproth and McGraw 2008), our study also adds evidence to the context specificity of secondary dispersal processes. Apparently, the specific habitat characteristics of urban road corridors, i.e. linear habitats with even surfaces and a high probability of increased wind turbulence, enhance secondary wind dispersal—a process which is often underestimated as it cannot by measured by traditional seed trap experiments. Yet this dispersal pathway is common in urban settings, and our study shows that it is well accessible to modelling approaches—as are other secondary dispersal processes (e.g., Schurr et al. 2005; Wichmann et al. 2009).

Figure 4 illustrates secondary wind dispersal of exposed samaras as a continuous process. With increasing time of exposure, the peak of the modeled dispersal curves shifts to higher distances. At the same time, a wider dispersion of diaspores along the sidewalk occurred, expressed by the increase in the scale parameter *a* of the fitted lognormal function. Also the shape of the dispersal curve changes with time from a strongly to moderately right-skewed distribution. This goes along with a loss of diaspores from the study area, which we couldn't control for in this experiment. The fate of these lost samaras remains unknown. It is likely however that at least a small proportion of these "losses" were transported beyond the borders of the study area to suitable germination sites.

The morphology of the samaras obviously facilitates wind-mediated lateral transport, likely because the twisted shape of the samaras increases the surface exposed to wind. Resulting movements can proceed with or without further rotations along the longitudinal axis. It is thus an open question whether our results can be generalized for other species with other seed morphologies.

In our release experiment, we found no significant relation between total wind sums and wind maxima and any change in parameters of the fitted dispersal kernels. This may be due to the mismatch between the wind data—measured nearby—and the local variation of the wind field in the studied road corridor. Yet the significant increase in the scale parameter *a* with higher wind sums above 3.7 m/s demonstrates the potential of wind to distribute diaspores over the pavement when the threshold for movement over the ground is exceeded. This is in accordance with the only existing mechanistic model for wind dispersal over the ground that accounts for a threshold in wind speed beyond which movement of diaspores is possible (Schurr et al. 2005).

As neither the change in the location of the peak nor the estimated shape parameter *b* showed significant dependencies on wind sums above 3.7 m/s, higher wind sums are not necessarily related to an increase in secondary dispersal distances in urban road corridors. This can be explained by the turbulent character of wind in road corridors. While wind speed is generally reduced in urban regions, turbulence often occurs in road corridors (Zajic et al. 2011), making the direction of wind dispersal over the ground more unpredictable than in open landscapes.

Vertical turbulence has been found to function as an important driver of LDD in propagules of herbaceous species with falling velocities < 0.5–1.0 m/s (Tackenberg et al. 2003). The value for *Ailanthus* is within this range (0.56 m/s; Matlack 1987). We did not directly observe vertical updraft of samaras, but our experiment provides indirect evidence of the functioning of this mechanism. A few samaras were moved from the sidewalk to the median strip of the road and must thus have been lifted over four lanes of heavy traffic and a curb that formed the border of the lawn on the median strip. During this travel, wind turbulence induced by vehicles may have enhanced the updraft of samaras, a phenomenon observed elsewhere (von der Lippe, pers. observ.).

Transport of single and clustered samaras

Within the sampled seed shadow, single samaras were generally transported over longer distances than fragments of fruit clusters with two and more samaras, but interestingly, clumps with more than one samara traveled up to 240 m from the seed source (Table 2). This is the first evidence of LDD of clustered samaras. The dispersal of such clumps can result in patches of closely related seedlings (Pan and Bassuk 1985), which can be advantageous for the occupation of safe sites and for establishing pioneer populations owing to an increased probability of germination of one or more seeds. As *Ailanthus* is a strictly dioecious tree (other reports appear to be wrong; Kowarik and Säumel 2007), the arrival of more than one seed at an isolated site could lead to the establishment of individuals of different sexes and thus enhance sexual regeneration.

Habitat shifts and potential safe sites

Studies on secondary wind dispersal in (near-)natural settings have shown that the density and structure of vegetation as well as morphological variation of the ground strongly affect the travel of propagules (e.g., Matlack 1987; Redbo-Torstensson and Telenius 1995; Schurr et al. 2005). Our study demonstrates that slight variations in the structure of paved surfaces also shape the dispersal processes in urban road corridors. During the observation period, conspicuous shifts occurred between habitats (Table 4). The crucial question for seedling establishment subsequent to dispersal is which of these can function as safe sites for germination.

The sidewalk was composed of two types of pavement that paralleled the traffic lanes (Fig. 1). About 10% of the exposed samaras remained in the strips with small granite cobbles, with most captured in the large joints between these cobbles. No samara remained on the adjacent pavement type with smooth-surfaced paving and very small joints in between. Yet the vast majority of the exposed samaras must have been moved over this surface because they were recaptured in habitats beyond or vanished from the study site. Clearly, this pavement enhances secondary wind dispersal, which is supported by the observation of samaras rolling over this type of surface, but ending their observed travel in adjacent habitats. In contrast, the morphological irregularities of the other pavement type slow down or even halt secondary dispersal processes.

During the observation period, 17% of exposed samaras accumulated in patches with sparse vegetation and a planted tree in the middle (Table 4). Almost all of them were recaptured there repeatedly, which indicates that their travels terminated there. Studies on the habitat association of *Ailanthus* in cities illustrate that patches with planted trees embedded in the pavement and usually extending along roads are suitable as safe sites for germination and seedling establishment (Lenzin et al. 2001). Due to the rapid juvenile stem elongation, young saplings can even compete with planted trees (I. Kowarik, personal observation). One-year-old seedlings can reach 1–2 m tall (Hu 1979), and 2-year-old seedlings on an urban site 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).

As germination occurs easily on bare soil (Kostel-Hughes et al. 2005), pavements with large joints, and analogously cracks and crevices in asphalt and concrete surfaces, are also suitable for germination and seedling establishment. Within a city block in Ithaca, New York, *Ailanthus* was relatively more frequent on sites with limited topsoil than in other habitats (Pan and Bassuk 1986), and 20% of mapped individuals in Basel, Switzerland, had colonized cracks and crevices (Lenzin et al. 2001). *Ailanthus* also tolerates drought, salt, and herbicide application, frequently occurring stressors along transport corridors (Kowarik and Säumel 2007). We thus conclude that secondary wind dispersal provides access to a range of safe sites in urban road corridors—and this certainly also holds for the road system outside of cities as shown by the colonization of an array of open or disturbed road sites by *Ailanthus* (e.g., Huebner 2003; Merriam 2003; Hulme 2004). Some studies have illustrated that such populations can function as foci for the invasion of adjacent habitats such as agricultural fields, meadows, vineyards, and old fields (Kowarik 1983; Facelli and Pickett 1991; Huebner 2003), but, to our knowledge, seed movement from road corridors to adjacent habitats has not been directly measured thus far.

Possible interaction with other dispersal vectors

The tail of a dispersal kernel is of significant ecological and evolutionary importance but is usually hard to capture (Williamson 2002; Soons and Ozinga 2005). As almost two-thirds of the exposed samaras vanished during the observation period, we were not able to track the tail of the dispersal kernel although we searched the road corridor and visibly accessible open spaces far beyond the study site as carefully as possible. It thus remains an open question whether the missing samaras were moved and crushed in the traffic or if some were lifted by vertical turbulence and then transported away from the road corridor, possibly by way of the local wind field.

The recapture of 10% of the exposed samaras at the edge of the traffic lane illustrates that some of the samaras can be moved from the sidewalk to the traffic lanes. Here, interactions between secondary wind dispersal and traffic-induced dispersal may occur and could increase the achieved transport distances. Vehicles have been shown to move samaras like that of *Ailanthus* over long distances (von der Lippe and Kowarik 2007a), and samaras can also be moved by the wind slip of passing vehicles (von der Lippe et al., unpubl.). As the traffic speed was low in our study area (< 50 km/h), and a lane with parked cars acted as a buffer between the moving traffic and the sidewalk area we assume a negligible influence of passing vehicles on the observed dispersal processes along the sidewalk. This idea is supported by results from another experiment on the movement of samaras in the wind slip of passing vehicles. In this case, samaras that were released on the shoulder of the road were scarcely moved, in contrast to those released in the lanes of traffic (von der Lippe et al., unpubl.).

Hence, our experiment illustrates the functioning of secondary wind dispersal as a traffic-independent driver of LDD in transportation corridors. Yet the unclear fate of the vanished diaspores in our experiment illustrates that this mechanism is one part of a multi-vector dispersal process along roads.

Conclusions

Our results suggest that impervious surfaces within road corridors can function as powerful avenues of secondary wind dispersal. Propagules of species with morphological adaptations to wind can be moved over long distances along roads even without interference of traffic. This vector thus offers a functional explanation for the invasion success of *Ailanthus* at isolated patchy urban sites. Our results suggest that the presence of such sites within the network of impervious surfaces such as asphalt, concrete or other types of pavement may enhance connectivity for species with adaptations to secondary wind dispersal such as *Ailanthus*. Yet it remains a challenge to test whether our results can be generalized for other species and how morphological variation of propagules of a larger species set as well as differences in urban surfaces relate to the vector strength.

Acknowledgements

We thank Dieter Scherer and Hartmut Küster for kindly providing wind data, two anonymous reviewers and Ingolf Kühn for stimulating comments and Kelaine Vargas for improving our English.

References

Bory G, Clair-Maczulajtys D (1980) Production, dissémination et polyphormisme des semences d'*Ailanthus altissima* (Mill.) Swingle, Simarubacées. Revue Générale de Botanique 88: 297–311.

Bullock JM, Clarke RT (2000) Long-distance seed dispersal by wind: Measuring and modelling the tail of the curve. Oecologia 124: 506–521. doi:10.1007/PL00008876

Bullock JM, Shea K, Skarpaas O (2006) Measuring plant dispersal: an introduction to field methods and experimental design. Plant Ecology 186: 217–234. doi:10.1007/s11258-006-9124-5

Carlton JT, Ruiz GM (2005) Vector science and integrated vector management in bioinvasion ecology: conceptual frameworks. In: Mooney HA, Mack RN, McNeely JA, Neville LE, Schei PJ, Waage JK (Eds) Invasive alien species. Island Press, Washington, 36–58.

Cheptou PO, Carrue O, Rouifed S, Cantarel A (2008) Rapid evolution of seed dispersal in an urban environment in the weed *Crepis sancta*. Proceedings of the National Academy of Sciences USA 105: 3796–3799. doi:10.1073/pnas.0708446105

Cho CW, Lee KJ (2002) Seed dispersion and seedling spatial distribution of the tree of heaven in urban environments. Korean Journal of Environment and Ecology 16: 87–93.

Clifford HT (1959) Seed dispersal by motor vehicles. Journal of Ecology 47: 311–315. doi:10.2307/2257368

Dark SJ (2004) The biogeography of invasive alien plants in California: an application of GIS and spatial regression analysis. Diversity and Distributions 10: 1–9. doi:10.1111/j.1472-4642.2004.00054.x

Delgado JA, Jimenez MD, Gomez A (2009) Samara size versus dispersal and seedling establishment in *Ailanthus altissima* (Miller) Swingle. Journal of Environmental Biology 30: 183–186.

Ernst, WHO (1998) Invasion, dispersal and ecology of the South African neophyte *Senecio inaequidens* in the Netherlands: From wool alien to railway and road alien. Acta Botanica Neerlandica 47: 131–151.

Essl F, Dullinger S, Kleinbauer I (2009) Changes in the spatio-temporal patterns and habitat preferences of *Ambrosia artemisiifolia* during its invasion of Austria. Preslia 81: 119–133.

Facelli JM, Pickett STA (1991) Indirect effects of litter on woody seedlings subject to herb competition. Oikos 62: 129–138. doi:10.2307/3545257

Forman RTT, Sperling D, Bissonette JA, Clevenger AP, Cutshall CD, Dale VH, Fahrig L, France R, Goldman CR, Heanue K, Jones JA, Swanson FJ, Turrentine T, Winter TC (2002) Road ecology: science and solutions. Island Press, Washington, 481 pp.

Gelbard JL, Belnap J (2003) Roads as conduits for exotic plant invasions in a semiarid landscape. Conservation Biology 17: 420–432. doi:10.1046/j.1523-1739.2003.01408.x

Goddard MA, Dougill AJH, Benton TG (2010) Scaling up from gardens: biodiversity conservation in urban environments. Trends in Ecology and Evolution 25: 90–98. doi:10.1016/j.tree.2009.07.016

Hansen MJ, Clevenger AP (2005) The influence of disturbance and habitat on the presence of non-native plant species along transport corridors. Biological Conservation 125: 249–259, doi:10.1016/j.biocon.2005.03.024

Higgins SI, Richardson DM (1999) Predicting plant migration rates in a changing world: the role of long-distance dispersal. The American Naturalist 153: 464–475. doi:10.1086/303193

Higgins SI, Nathan R, Cain ML (2003) Are long-distance dispersal events in plants usually caused by nonstandard means of dispersal? Ecology 84: 1945–1956. doi:10.1890/01-0616

Hodkinson DJ, Thompson K (1997) Plant dispersal: The role of man. Journal of Applied Ecology 34: 1484–1496. doi:10.2307/2405264

Holderegger R, di Giulio M (2010) The genetic effects of roads: A review of empirical evidence. Basic and Applied Ecology 11: 522–531. doi:10.1016/j.baae.2010.06.006

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.

Hulme PE (2004) Islands, invasions and impacts: A Mediterranean perspective. In: Fernández-Palacios JM, Morici C (Eds) Island Ecology. Asociación Española de Ecología Terrestre (AEET). Cabildo Insular de La Palma, La Palma, 359–383.

Jodoin Y, Lavoie C, Villeneuve P, Theriault M, Beaulieu J, Belzile F (2008) Highways as corridors and habitats for the invasive common reed *Phragmites australis* in Quebec, Canada. Journal of Applied Ecology 45: 459–466. doi:10.1111/j.1365-2664.2007.01362.x

Jongejans E, Skarpaas O, Shea K (2008) Dispersal, demography and spatial population models for conservation and control management. Perspectives in Plant Ecology, Evolution and Systematics 9: 153–170. doi:10.1016/j.ppees.2007.09.005

Kaproth MA, McGraw JB (2008) Seed viability and dispersal of the wind-dispersed invasive *Ailanthus altissima* in aqueous environments. Forest Science 54: 490–496.

Kawata M, Murakami K, Ishikawa T (2009) Dispersal and persistence of genetically modified oilseed rape around Japanese harbors. Environmental Science and Pollution Research 16: 120–126. doi:10.1007/s11356-008-0074-4

Kostel-Hughes F, Young TP, McDonnell MJ (1998) The soil seed bank and its relationship to the aboveground vegetation in deciduous forests in New York City. Urban Ecosystems 2: 43–59. doi:10.1023/A:1009541213518

Kota NL (2005) Comparative seed dispersal, seedling establishment and growth of exotic, invasive *Ailanthus altissima* and native *Liriodendron tulipifera*. MS Thesis, West Virginia University.

Kowarik I (1983) Naturalization and phytogeographical behaviour of the tree of heaven (*Ailanthus altissima* (Mill.) Swingle) in the French Mediterranean (Bas-Languedoc). Phytocoenologia 11: 389–405.

Kowarik I, Säumel I (2007) Biological flora of Central Europe: *Ailanthus altissima* (Mill.) Swingle. Perspectives in Plant Ecology, Evolution and Systematics 8: 207–237. doi:10.1016/j.ppees.2007.03.002

Kowarik I, Säumel I (2008) Water dispersal as an additional pathway to invasions by the primarily wind-dispersed tree *Ailanthus altissima*. Plant Ecology 198: 241–252. doi:10.1007/s11258-008-9398-x

Kowarik I, von der Lippe M (2007) Pathways in plant invasions. In: Nentwig W (Ed) Biological Invasions. Ecological Studies 193: 29–47.

Landenberger RE, Kota NL, McGraw JB (2007) Seed dispersal of the non-native invasive tree *Ailanthus altissima* into contrasting environments. Plant Ecology 192: 55–70. doi:10.1007/s11258-006-9226-0

Langer A (1994) Flora und Vegetation städtischer Straßen am Beispiel Berlin. Landschaftsentwicklung und Umweltforschung Sonderh 10: 1–199.

Lavoie C, Jodoin Y & de Merlis AG (2007) How did common ragweed (*Ambrosia artemisiifolia* L.) spread in Quebec? A historical analysis using herbarium records. Journal of Biogeography 34: 1751–1761. doi:10.1111/j.1365-2699.2007.01730.x

Lemke A, von der Lippe M, Kowarik I (2009) New opportunities for an old method: using fluorescent colours to measure seed dispersal. Journal of Applied Ecology 46: 1122–1128. doi:10.1111/j.1365-2664.2009.01691.x

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

Matlack GR (1989) Secondary dispersal of seed across snow in *Betula lenta*, a gap-colonizing tree species. Journal of Ecology 77: 853–869. doi:10.2307/2260990

Matlack GR (1987) Diaspore size, shape, and fall behavior in wind-dispersed plant species. American Journal of Botany 74: 1150–1160. doi:10.2307/2444151

Merriam RW (2003) The abundance, distribution and edge associations of six non-indigenous, harmful plants across North Carolina. Journal of the Torrey Botanical Society 130: 283–291. doi:10.2307/3557546

Mount A, Pickering CM (2009) Testing the capacity of clothing to act as a vector for non-native seed in protected areas. Journal of Environmental Management 91: 168–179. doi:10.1016/j.jenvman.2009.08.002

Niggemann M, Jetzkowitz J, Brunzel S, Wichmann MC, Bialozyt R (2009) Distribution patterns of plants explained by human movement behaviour. Ecological Modelling 220: 1339–1346. doi:10.1016/j.ecolmodel.2009.02.018

Ozinga WA, Bekker RM, Schaminee JHJ, Van Groenendael JM (2004) Dispersal potential in plant communities depends on environmental conditions. Journal of Ecology 92: 767–777. doi:10.1111/j.0022-0477.2004.00916.x

Pan E, Bassuk N (1985) Effects of soil type and compaction on the growth of *Ailanthus altissima* seedlings. Journal of Environmental Horticulture 3: 158–162.

Parendes L A, Jones JA (2000) Role of light availability and dispersal in exotic plant invasion along roads and streams in the H. J. Andrews Experimental Forest, Oregon. Conservation Biology 14: 64–75. doi:10.1046/j.1523-1739.2000.99089.x

Pauchard A, Shea K (2006) Integrating the study of non-native plant invasions across spatial scales. Biological Invasions 8: 399–413. doi:10.1007/s10530-005-6419-8

Pauchard A, Küffer C, Dietz H, Daehler CC, Alexander J, Edwards PJ, Arevalo JR, Cavieres LA, Guisan A, et al. (2009) Ain't no mountain high enough: Plant invasions reaching new elevations. Frontiers in Ecology and the Environment 7: 479–486. doi:10.1890/080072

Pyšek P, Hulme PE (2005) Spatio-temporal dynamics of plant invasions: Linking pattern to process. Ecoscience 12: 302–315. doi:10.2980/i1195-6860-12-3-302.1

R Development Core Team (2009) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Redbo-Torstensson P, Telenius A (1995) Primary and secondary seed dispersal by wind and water in *Spergularia salina*. Ecography 18: 230–237. doi:10.1111/j.1600-0587.1995.tb00126.x

Rentch JS, Fortney RH, Stephenson SL, Adams HS, Grafton WN, Anderson JT (2005) Vegetation-site relationships of roadside plant communities in West Virginia, USA. Journal of Applied Ecology 42: 129–138. doi:10.1111/j.1365-2664.2004.00993.x

Robinson L, Newell JP, Marzluff JA (2005) Twenty-five years of sprawl in the Seattle region: growth management responses and implications for conservation. Landscape and Urban Planning 71: 51–72. doi:10.1016/j.landurbplan.2004.02.005

Säumel I, Kowarik I (2010) Urban rivers as dispersal corridors for primarily wind-dispersed invasive tree species. Landscape and Urban Planning 94: 244–249. doi:10.1016/j.landurbplan.2009.10.009

Schleicher A, Kleyer M, Biedermann R (2011) Dispersal traits determine plant response to habitat connectivity in an urban landscape. Landscape Ecology 26: 529–540. doi:10.1007/s10980-011-9579-1

Schurr FM, Bond WJ, Midgley GF, Higgins SI (2005) A mechanistic model for secondary seed dispersal by wind and its experimental validation. Journal of Ecology 93: 1017–1028. doi:10.1111/j.1365-2745.2005.01018.x

Singh RP, Gupta MK, Chand P (1992) Autecology of *Ailanthus glandulosa* Desf. in Western Himalayas. Indian Forester 118: 917–921.

Soons MB, Nathan R, Katul GG (2004) Human effects on long-distance wind dispersal and colonization by grassland plants. Ecology 85: 3069–3079. doi:10.1890/03-0398

Soons MB, Ozinga WA (2005) How important is long-distance seed dispersal for the regional survival of plant species? Diversity and Distributions 11: 165–172. doi:10.1111/j.1366-9516.2005.00148.x

Tackenberg O, Poschlod P, Kahmen S (2003) Dandelion seed dispersal: The horizontal wind speed does not matter for long-distance dispersal - it is updraft! Plant Biology 5: 451–454. doi:10.1055/s-2003-44789

Trombulak SC, Frissell CA (2000) Review of ecological effects of roads on terrestrial and aquatic communities. Conservation Biology 14: 18–30. doi:10.1046/j.1523-1739.2000.99084.x

Tyser RW, Worley CA (1992) Alien flora in grasslands adjacent to road and trail corridors in Glacier National Park, Montana (USA). Conservation Biology 6: 253–262. doi:10.1046/j.1523-1739.1992.620253.x von der Lippe M, Kowarik I (2007a) Long-distance dispersal of plants by vehicles as a driver of plant invasions. Conservation Biology 21: 986–996. doi:10.1111/j.1523-1739.2007.00722.x

von der Lippe M, Kowarik I (2007b) Crop seed spillage along roads: a factor of uncertainty in the containment of GMO. Ecography 30: 483–490.

von der Lippe M, Kowarik I (2008) Do cities export biodiversity? Traffic as dispersal vector across urban-rural gradients. Diversity and Distributions 14: 18–25. doi:10.1111/j.1472-4642.2007.00401.x

Wichmann MC, Alexander MJ, Soons MB, Galsworthy S, Dunne L, Gould R, Fairfax C, Niggemann M, Hails RS, Bullock JM (2009) Human-mediated dispersal of seeds over long distances. Proceedings of the Royal Society B-Biological Sciences 276: 523–532. doi:10.1098/rspb.2008.1131

Williamson M (2002) Overview and synthesis: the tale of the tail. In: Levey DJ, Silva WR, Galetti M (Eds) Seed dispersal and frugivory: ecology, evolution and conservation. CAB International Press, Oxfordshire, 431–442.

Wittig R, Becker U (2010) The spontaneous flora around street trees in cities. A striking example for the worldwide homogenization of the flora of urban habitats. Flora 205: 704–709.

Zajic D, Fernando HJS, Calhoun R, Princevac M, Brown MJ, Pardyjak ER (2011) Flow and turbulence in an urban canyon. Journal of Applied Meteorology and Climatology 50: 203–223. doi:10.1175/2010JAMC2525.1

Zwaenepoel A, Roovers P, Hermy M (2006) Motor vehicles as vectors of plant species from road verges in a suburban environment. Basic and Applied Ecology 7: 83–95. doi:10.1016/j.baae.2005.04.003