
Long-Distance Dispersal of Plants by Vehicles as a Driver of Plant Invasions

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Abstract: *Roadsides are preferential migration corridors for invasive plant species and can act as starting points for plant invasions into adjacent habitats. Rapid spread and interrupted distribution patterns of introduced plant species indicate long-distance dispersal along roads. The extent to which this process is due to species' migration along linear habitats or, alternatively, to seed transport by vehicles has not yet been tested systematically. We tested this by sampling seeds inside long motorway tunnels to exclude nontraffic dispersal. Vehicles transported large amounts of seeds. The annual seed rain caused by vehicles on the roadsides of five different tunnel lanes within three tunnels along a single urban motorway in Berlin, Germany, ranged from 635 to 1579 seeds/m²/year. Seeds of non-native species accounted for 50.0% of the 204 species and 54.4% of the total 11,818 seeds trapped inside the tunnels. Among the samples were 39 (19.1%) highly invasive species that exhibit detrimental effects on native biodiversity in some parts of the world. By comparing the flora in the tunnel with that adjacent to the tunnel entrances we confirmed long-distance dispersal events (>250 m) for 32.3% of the sampled species. Seed sources in a radius of 100 m around the entrances of the tunnels had no significant effect on species richness and species composition of seed samples from inside the tunnels, indicating a strong effect of long-distance dispersal by vehicles. Consistently, the species composition of the tunnel seeds was more similar to the regional roadside flora of Berlin than to the local flora around the tunnel entrances. Long-distance dispersal occurred significantly more frequently in seeds of non-native (mean share 38.5%) than native species (mean share 4.1%). Our results showed that long-distance dispersal by vehicles was a routine rather than an occasional mechanism. Dispersal of plants by vehicles will thus accelerate plant invasions and induce rapid changes in biodiversity patterns.*

Keywords: long-distance plant dispersal, plant invasions, roadside flora, seed rain, vehicle plant dispersal

La Dispersión de Plantas a Larga Distancia por Vehículos como un Agente de Invasiones de Plantas

Resumen: *Las orillas de caminos son los corredores migratorios preferenciales de plantas invasoras y pueden actuar como puntos de inicio para la invasión de hábitats adyacentes. La rápida expansión y los patrones de distribución interrumpidos de las especies de plantas introducidas son indicadores de dispersión a larga distancia a lo largo de los caminos. A la fecha, no se ha probado sistemáticamente la extensión en la que este proceso se debe a la migración de especies a lo largo de hábitats lineales o, alternativamente, al transporte de semillas por vehículos. Probamos esto muestreando semillas dentro túneles largos para excluir la dispersión no causada por el tráfico. La lluvia de semillas anual debida a vehículos en los bordes de cinco carriles diferentes dentro de tres túneles a lo largo de una vía urbana en Berlín, Alemania, varió entre 635 y 1579 semillas/m²/año. Las semillas de especies exóticas comprendieron 50.0% de las 204 especies y 54.4% de las 11,818 semillas recolectadas en los túneles. Entre las muestras había 39 (19.1%) especies altamente invasoras que tienen efectos perjudiciales sobre la biodiversidad nativa en algunas partes del mundo. Al comparar la flora del túnel con la adyacente a las entradas de los túneles confirmamos los eventos de dispersión de larga distancia (>250 m) para 32.3% de las especies muestreadas. Las fuentes de semillas en un radio de 100 m alrededor de las entradas de túneles no tuvieron efecto significativo sobre la riqueza de especies y la*

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composición de especies de las muestras de semillas del interior de los túneles, lo que indica un fuerte efecto de la dispersión a larga distancia por vehículos. Consistentemente, la composición de especies de las semillas de túneles fue más similar a la de flora regional de bordes de camino que a la flora local cercana a las entradas de túneles. La dispersión a larga distancia ocurrió significativamente más frecuentemente en semillas de especies no nativas (proporción media: 38.5%) que en especies nativas (proporción media: 4.1%). Nuestros resultados mostraron que la dispersión a larga distancia por vehículos fue una rutina y no un mecanismo ocasional. Por lo tanto, la dispersión de plantas por vehículos acelerará las invasiones de plantas e inducirá cambios rápidos en los patrones de biodiversidad.

Palabras Clave: dispersión de plantas a larga distancia, dispersión de plantas por vehículos, flora ruderal, invasión de plantas, lluvia de semillas

Introduction

Human agency facilitates plant invasions by a broad array of pathways leading to species' introduction to new regions and to subsequent invasion processes (Hodkinson & Thompson 1997; Kowarik 2003). Understanding the mechanisms of range expansion is a crucial prerequisite for both prevention and management of invasions (Pyšek & Hulme 2005). In colonization processes long-distance dispersal (LDD) may lead to rapid range expansion, which has been highlighted by modeling approaches (Higgins & Richardson 1999) and by reconstructing former colonization sequences (Cain et al. 1998; Soons & Ozinga 2005). Despite methodological advances, however, evidence for LDD in general is still based upon limited data (Nathan et al. 2003).

In plant invasions LDD is crucial for the exponential range expansion of many invasive species after a slow initial spread subsequent to their introduction (Kowarik 1995; Pyšek & Hulme 2005). Human agency also provides nonstandard means of dispersal and may thus move species with morphologies that are not adapted specifically to LDD (Higgins et al. 2003; Pyšek & Hulme 2005). Nathan et al. (2003) state that "human activities substantially increase the variety of long-distance transport avenues," and they conclude that this challenges future estimations of LDD events. We attempted to quantify LDD events along roadsides, which are known as migration corridors for many invasive plant species and which may foster the rapid colonization of large new areas.

It is a well-documented pattern that roadside verges generally tend to have a higher richness of non-native species than adjacent habitats (e.g., Parendes & Jones 2000; Gelbard & Belnap 2003). Increased cover and richness of non-native plants with negative impacts on native species richness are observed even more than 100 m from roadside verges (Gelbard & Belnap 2003). Thus, dispersal of invasive species from roadsides to interior habitats may affect biodiversity on a landscape scale. Consistently, road density is positively correlated with increased non-native species richness in large bioregions (Dark 2004).

The effectiveness of roadside corridors for the migration of invasive plant species has often been linked to altered site conditions along roads due to increased disturbance, soil compaction, or salinity (Scott & Davison 1985; Greenberg et al. 1997; Gelbard & Belnap 2003). This most likely promotes the establishment of non-native species by reducing the competitive strength of the native roadside flora. The invasion histories of some roadside plant species, however, indicate that, in addition to site-related changes, traffic also promotes LDD, resulting in rapid dispersal and disconnected founder populations of roadside species. Roadside populations of numerous coastal species in the British Isles showed segregated initial distributions that were unconnected with coastal populations (Scott & Davison 1985). Since the 1980s, the exponential range expansion of the South African *Senecio inaequidens* DC in many European countries was primarily due to spread along roadsides and railways, exceeding by far the species' natural dispersal ability (Ernst 1998; Heger & Böhmer 2005). In the United States *Asclepias syriaca* L. and *Lytbrum salicaria* L. have migrated long distances along roadsides (Wilcox 1989; Wyatt 1996).

Analyzing roadside invasion patterns does not, however, allow the effect of diaspore transport by vehicles to be separated from that of enhanced establishment through altered site conditions. Previous studies revealed that vehicles may move seeds of a high number of species from different plant functional groups. In those studies seeds were collected directly from the surface of vehicles (Clifford 1959; Schmidt 1989; Hodkinson & Thompson 1997; Zwaenepoel et al. 2006) or were derived from the mud of a car wash (Wace 1977). These methodological approaches do not allow estimations of the real magnitude of seeds released by vehicles at roadsides or of the distances that seeds were moved by vehicles. In addition to long-lasting attachment to vehicles, other mechanisms, such as repeated short-distance transport by several vehicles or enhanced dispersal by airflow, may also contribute to seed deposition at roadsides. Thus, the spatial effectiveness of vehicles as dispersal vectors and the magnitude to which they contribute to seed deposition at roadsides has not been investigated.

We attempted to better describe the spatial and quantitative effectiveness of traffic as a dispersal vector by addressing the role of vehicles in long-distance dispersal and by quantifying seed deposition at roadsides. We collected seeds in long motorway tunnels so as to exclude the influx of seeds from dispersal vectors other than vehicles. By comparing traffic-derived seed samples from inside the tunnels with the flora in the vicinity of the tunnels and the regional roadside flora, we addressed the following questions: (1) What is the magnitude of propagules released by vehicles on roadsides, and how substantial is the contribution of non-native species to this deposition? (2) To what extent do seed samples transported by vehicles reflect the flora in the vicinity of the sampling sites or the regional roadside flora? (3) How common is LDD in vehicle-derived dispersal? (4) Is LDD by vehicles enhanced for non-native species compared with native species?

Methods

Study Sites

We used long motorway tunnels (length between 700 and 1050 m) as sampling sites to isolate seed samples from dispersal vectors other than traffic and to differentiate the influence of local seed sources in the vicinity of the tunnels from that of more distant seed sources. Sampling took place in three tunnels of an urban motorway in the northwestern outskirts of Berlin, Germany. The motorway is one of the most frequented arterial roads of Berlin, providing composite samples from up to 50,000 vehicles/lane/day (Senatsverwaltung für Stadtentwicklung Berlin 2001). The first tunnel (urban tunnel) was in a dense residential housing area, the second (suburban tunnel) in a low-density housing area with a high proportion of urban wasteland and railroad areas in the surroundings, and the third (forest tunnel) in a forest in the urban fringe with low-density, single-family housing in the vicinity. The distance between the tunnels was approximately 2 km. There was no access for pedestrians to the tunnels.

Seed Traps and Sampling Design

Special seed traps were constructed to provide a large sampling surface close to the ground (Fig. 1). Each trap consisted of a flat 1.9-m-long container ($1.9 \times 0.08 \times 0.05$ m) made of sheet metal with a removable funnel of aluminum for protection from airflow. The sampling surface provided by the funnel was 1.9×0.115 m, giving a sampling surface of 0.22 m², approximately 10 cm above the ground. Drainage was not important because even on the days of heavy rainfall there was no serious spread of water from the roadsides into the traps. The capacity



Figure 1. Photo of a seed trap installed in motorway tunnels. On top is a removable, aluminium funnel that covers a flat container of $5 \times 8 \times 190$ cm. The total sampling surface area is 0.22 m².

of the traps was sufficient because on all sampling dates none of the containers were filled to the limit.

We controlled for possible impact of wind dispersal with two additional funnel seed traps installed 1.5 m above the ground traps and deployed during two sampling periods in the suburban tunnel. These traps consisted of a round PVC funnel 15 cm in diameter (0.07 -m² sampling surface) and a cotton bag fixed at the base of the funnel for seed collection.

The tunnels were divided along their entire length by solid walls and thus provided independent samples for both directions of the motorway. In the urban and suburban tunnels both lanes were sampled, whereas in the forest tunnels access was only provided for the inbound lane. To protect samples from wind dispersal, traps were sited 150 m from the tunnel entrances. In all sampled lanes five traps were placed parallel to the road with a distance of 2 m between each two traps. These traps provided five replicates at each sampling date to estimate the within-tunnel variation of seed deposition.

In a 1-year sampling period between 30 October 2002 and 29 October 2003, we took six seed samples each

from a total of 25 seed traps. Because access to the tunnels was limited to the regular dates of street cleaning, the exposure periods varied. The first two sampling intervals covered the winter and spring seasons (133 and 98 days of exposure). Afterward the traps were emptied three times at nearly monthly intervals (33–43 days of exposure). For the final sample, the traps were deployed for 23 days. The routine cleaning of the tunnels preceding each sampling period ensured that the major share of the seeds in the samples was transported into the tunnels by vehicles within each sampling period.

As a pretest, we took a sample in the urban tunnel in October 2002 after 100 days of exposure of a total of 18 traps. This sample increased the sample size for the compilation of the vehicle-borne flora but was not incorporated in any comparisons between the different tunnels.

Glasshouse Germination of Seed Samples

For the determination of species the seed samples were germinated in a glasshouse according to Ter Heerd et al. (1996). Besides the seeds, the samples contained a lot of mud and sandy soil. Depending on the weather conditions, samples were slightly damp to moist. To standardize germination conditions, the damp samples were kept for 6 weeks in an unlighted climate chamber at 3–5° C for cold stratification and afterward air dried for 2 days in an unlighted room at 18–22° C. Samples were weighed after drying and then concentrated by wet sieving (sieve of 0.2-mm mesh size) and spread out thinly (<0.5 cm) in germination trays (32 × 50 cm) over sterilized potting soil.

Every sample was kept in a temperature-controlled (minimum 15° C; maximum 30° C) glasshouse for 12 months after sowing. We watered trays as necessary to keep the soil surface moist. After identification seedlings were removed from the germination trays. Seedlings that could not be identified were potted and grown until identification was possible. If not differentiated explicitly, non-native species are referred to as the sum of archaeophytes (pre-1492 aliens) and neophytes (post-1492 aliens) (Richardson et al. 2000). Nomenclature followed Wisskirchen and Haeupler (1998); native and non-native species (archaeophytes, neophytes) were differentiated according to Wisskirchen and Haeupler (1998) and Prasse et al. (2001).

The tables with the germination trays were enclosed by a tent of garden fleece to avoid seed influx by wind. On every sowing date we set up three to five trays (approximately 10% of the trays used) with only sterilized potting substrate to control for possible impacts of wind-dispersed seeds and account for viable seeds in the potting mixture. Five species germinated sparsely in the control trays toward the end of the germination periods and were omitted from the data set. One species (*Betula pen-*

dula Roth) germinated rarely in the control trays, but occurred at two orders of magnitude more frequently in trays with seeds collected from tunnels. Although the measured abundances of this species might be slightly biased, it was kept in the data set because removing it would have biased the estimates of seed deposition by vehicles even more.

No seeds were found in the aboveground traps inside the tunnel, confirming no relevant impact of wind dispersal into the ground traps.

Inventories of the Adjacent Flora and the Roadside Flora of Berlin

To test for the impact of adjacent versus distant seed sources on species composition and abundance in the seed samples, we made an in-depth survey of the flora within 50 and 100 m of the tunnel entrances. In both areas we recorded spontaneous and planted species during two survey periods: between 5 May and 15 May 2003 and between 20 July and 2 August 2003. Species abundance was estimated on three levels: rare, <5 individuals; few, 5–50 individuals; and common, >50 individuals.

To compare the species composition of the tunnel samples with that of the regional roadside flora, we used data from Langer (1994), who analyzed the roadside flora of 61 road sections within seven representative neighborhoods in Berlin. Altogether 27 km of roadside vegetation were surveyed in the study, providing a reliable estimation of the regional roadside flora. For comparisons with the tunnel samples, we used species frequencies in the roadside flora represented as the percentage of their occurrences in the seven independent neighborhoods.

Statistical Analyses

We used linear regression to determine whether the seed content of tunnel samples was dependent on the weight of mud in the samples (i.e., to determine whether seed deposition is primarily controlled by the transported substrate). We therefore plotted the number of seeds in each sample against the weight of the samples subtracted by the weight of the seeds. To estimate the weight of the seeds, we summed the mean seed weights of the species in the samples (data from Otto 2002) and multiplied that value by the species' abundance. The relationship between species frequencies in the seed samples of all 25 traps and their frequency in the regional roadside flora was analyzed with Spearman rank correlation.

For the analysis of factors affecting the abundance of species in the seed samples and for comparisons of the share of LDD between native and non-native species, we conducted generalized linear mixed-effect models (GLMMs) to take into account both the non-normal distribution of the response variables and the subsampling (nesting) within each tunnel lane (Pinheiro & Bates 2000). We used a penalized quasi-likelihood method to

apply GLMMs (glmmPQL; Venables & Ripley 2002). Sampling sites (tunnel lanes) were included as a random effect nested in the fixed effect for all models.

To test how species abundance in the samples was affected by the distance to the next known seed source and the abundance of the species in the adjacent flora around the tunnels, species seed counts in the samples were used as response variable in a GLMM with Poisson errors. Species occurrence in one of the two 50-m distance zones around the corresponding entrances was treated as fixed effect. We performed the same analysis with species affiliation to one abundance class in the surrounding flora as a fixed effect.

We compared the tunnel samples with the flora around the corresponding entrances against traffic flow (i.e., with the potential local seed sources) to calculate the proportion of LDD events out of the total seeds deposited. We used a distance-based definition of LDD for which dispersal events > 250 m were regarded as LDD (see Nathan et al. 2003 on the need for a context-specific definition of LDD). Accordingly all recorded seeds of species absent in the 100-m radius around the entrance had been transported long distances because the buffer zone between the entrances of the tunnels and the seed traps already covered 150 m.

To test whether proportions of LDD differed between native and non-native species, we used GLMMs with binomial errors. Proportions of species transported long distances were taken as the response variable, coded as a dichotomous vector with richness of species not present in the vicinity of the tunnel as "success" and richness of species present in the vicinity as "failure." The same analysis was carried out with proportions of seeds transported long distances as the response variable. The response vectors were calculated separately for native and non-native species, and native status was specified as fixed effect in both analyses.

To compare the impacts of local and distant seed sources on species composition of the seed samples, we used Simpson's similarity index because it is not very sensitive to differences in species richness between the compared samples (Kühn & Klotz 2006). We calculated a similarity matrix in which the total seed sample from each of the five tunnel lanes was compared with each of the five surrounding floras of the sampled tunnel lanes and the regional roadside flora. The resulting matrix was analyzed by a resampling approach to test for significant differences of similarity between the three possible comparisons: (1) tunnel samples versus seed sources around the entrance of the same tunnel lane ($n = 5$), (2) tunnel samples versus seed sources around entrances of the four other tunnel lanes ($n = 20$), and (3) tunnel samples versus the regional roadside flora ($n = 5$). We therefore resampled the mean of five randomly chosen similarity indexes out of the 20 comparisons between the tunnel samples and the seed sources around entrances of the

four other tunnel lanes 10,000 times. We then calculated significant differences between the mean of these resampled values and the means of the two other comparisons from the confidence interval of the z standard deviate. All statistical analysis was carried out in the statistical and programming package R (version 2.2.0, the R Foundation for Statistical Computing, Vienna).

Results

Magnitude of Seed Deposition by Vehicles

Overall 11,818 seeds of 204 species germinated from the total samples, including the pretest samples. During the 1-year sampling period, 6252 viable seeds were trapped, representing an average seed rain between 635 and 1579 seeds/m²/year in the different tunnel lanes (Fig. 2a). The majority of the seedlings (86.1%) belonged to the 20 most frequent species (Table 1), whereas 48 (26%) species were represented by only a single seedling. Non-native species as the sum of archaeophytes (pre-1492 aliens) and neophytes (post-1492 aliens) accounted for 54.5% of the total seeds, with an average seed rain between 296 and 881 seeds/m²/year (Fig. 2a). Seed deposition was lowest in both lanes of the tunnel closest to the city and was on average two times higher in the suburban tunnel and the forest tunnel (Fig. 2a).

The estimated total seed weights in the samples reached only between 0.002% and 0.66% of the respective sample weights. This means that mud and other substrates deposited by vehicles constituted more than 99% of the samples' mass. Seed numbers in the samples were positively correlated with the weight of the air-dried samples subtracted by the estimated seed weights ($r^2 = 0.391$, $p < 0.001$, Fig. 3).

Contribution of Non-Native Species to the Tunnel Flora

Exactly half of the species in the seed samples were not native to the area of Berlin. Neophytes made up 33.8% of the samples and 16.2% were archaeophytes (Table 2). In the seed samples of different tunnel lanes, the average proportion of total non-native species varied from 39.4% to 60.8%. Compared with their proportion in the flora of the direct surroundings of the tunnels, non-native species were slightly overrepresented in the overall seed samples (44.3% vs. 50%; Table 2).

The tunnel samples included 39 species (19.1%) listed as problematic invasive alien species in a worldwide overview (Weber 2003). Some of these are frequently planted along roadsides (e.g., *Acer platanoides* L., *A. negundo* L., *Robinia pseudoacacia* L.). Among the non-native species, there were five highly invasive species classified as problematic in Germany (*Acer negundo* L., *Buddleja davidii* Franch., *Lupinus polyphyllus* Lindl., *Robinia*

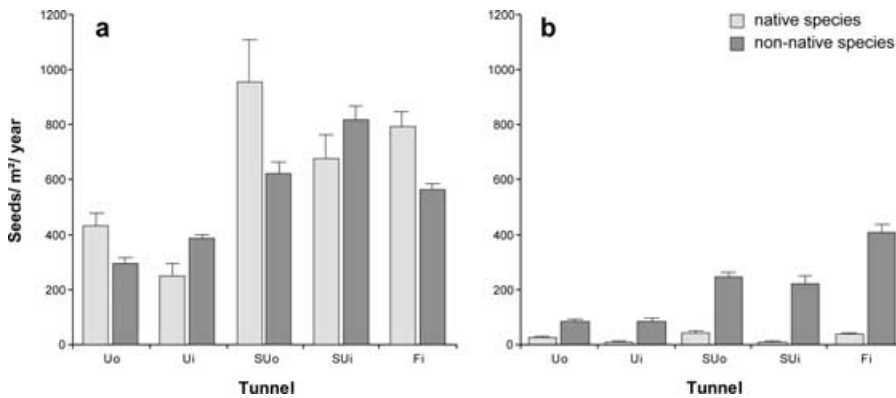


Figure 2. Mean annual seed rain per square meter on the roadside of five separate tunnel lanes of an urban motorway (n = 5 per lane): (a) seed rain of native species (archaeophytes and neophytes) and (b) long-distance dispersal seed rain of species not present in the flora in a 100-m radius around the tunnel entrances for native species and non-native species. Error bars show 1 SE. Tunnel abbreviations: Uo, urban tunnel, outbound lane; Ui, urban tunnel, inbound lane; SUo, suburban tunnel, outbound lane; SUI, suburban tunnel, inbound lane; Fi, forest tunnel, inbound lane.

pseudoacacia L., *Solidago canadensis* L.; Kowarik 2003). We found seven species with no record in the present flora of Berlin (Prasse et al. 2001). Five of these were escaped ornamentals (*Aurinia saxatilis* [L.] Desv., *Campanula poscharskiana* Degen, *Cyperus eragrostis* Lam., *Impatiens walleriana* Hook. f., *Solanum pseudocapsicum* L.), one was an exotic fruit species (*Physalis peruviana* L.), and one was a coastal species (*Cochlearia danica* L.) that is spreading rapidly along motorway verges in Germany (Lienenbecker 2000).

Relationship between Tunnel Flora and Potential Local and Regional Seed Sources

Of 204 species sampled in the three tunnels, 143 (70.1%) were part of the regional roadside flora of Berlin, which includes 340 species (Langer 1994). The tunnel species thus represented 42.0% of the regional roadside flora (Table 2). One hundred forty-one (69.1%) of the tunnel species were found in the flora within a 100-m radius of the tunnel entrances. Seeds of species that were part of the regional roadside flora provided the majority (98.5%) of all seeds in the samples, whereas seeds of species occurring in the vicinity of the tunnels contributed a smaller share (92.9%).

Species' frequencies in the regional roadside flora were positively correlated with their frequencies in the 25 seed traps of the tunnel lanes. This finding holds for both the species that occurred in the seed samples and in the roadside flora ($r_s = 0.444, p < 0.0001$) and the total species' set of the regional roadside flora, including zero values for those species missing in the tunnel samples ($r_s = 0.547, p < 0.0001$).

Comparisons of the floristic composition of the seed samples with potential local and distant seed sources revealed no significant effect of the flora in the direct vicin-

ity of the tunnel entrances on the species composition of the tunnel samples. The resampling procedure revealed that similarity indexes for comparisons of tunnel samples with the flora in the vicinity of the related entrance against traffic flow were not significantly different from those for comparisons of the seed samples with the surrounding floras of the four other tunnel lanes ($z = 0.345, p = 0.730$). There was a significantly higher similarity

Table 1. The 20 most frequent species in the total seed rain on the roadside of five separate tunnel lanes of an urban motorway in Berlin, Germany.^a

Taxon	No. of seeds in all tunnel samples
<i>Triticum aestivum</i> L. em. Fiori et Paol. ^b	1969
<i>Conyza canadensis</i> (L.) Cronquist ^b	1936
<i>Betula pendula</i> Roth	1492
<i>Sagina procumbens</i> L.	1089
<i>Poa annua</i> L.	741
<i>Lepidium ruderales</i> L. ^b	578
<i>Plantago major</i> subsp. <i>major</i> L.	498
<i>Secale cereale</i> L. ^b	446
<i>Chenopodium album</i> L. ^b	256
<i>Brassica napus</i> L. ^b	201
<i>Polygonum aviculare</i> agg. L.	160
<i>Solidago canadensis</i> L. ^b	137
<i>Herniaria glabra</i> L. ^b	117
<i>Urtica dioica</i> L.	112
<i>Sonchus oleraceus</i> L.	100
<i>Taraxacum</i> sect. <i>Ruderalia</i> Kirschner	80
<i>Capsella bursa-pastoris</i> (L.) Med.	65
<i>Lolium perenne</i> L.	65
<i>Acer negundo</i> L. ^b	64
<i>Veronica chamaedrys</i> L.	64

^aSeed numbers are the sum of a total of seven samples from 33 seed traps collected between July 2002 and October 2003.

^bNon-native species (archaeophytes and neophytes).

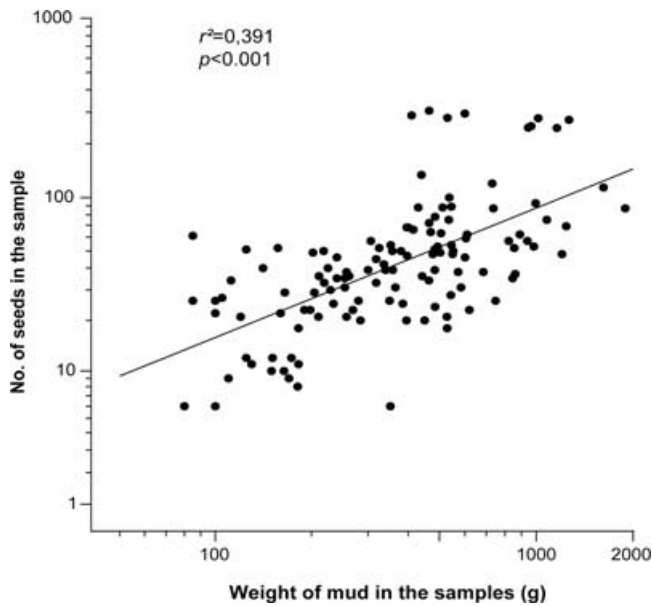


Figure 3. Relationship between weight and seed content of 123 air-dried samples of mud collected in seed traps along five separate tunnel lanes of an urban motorway. The least-squares regression line is shown. Both axes have log scales.

for comparisons of the seed samples with the regional roadside flora than for comparisons with the surrounding floras of the tunnels ($z = 5.571, p < 0.0001$).

Neither the distance of surrounding seed sources nor the abundance of species in the surroundings of the tunnel entrances significantly affected the number of seeds per species in the tunnel traps as indicated by GLMMs. Species that occurred in the 50-m radius around the tunnels were not significantly more abundant in the seed samples than species occurring in the 100-m radius ($df = 4, t = 0.4233, p = 0.6938$). In addition, species with a higher abundance (>50 specimens) in the vicinity of the tunnels were not significantly more abundant in the corresponding seed samples than species less abundant (<50 specimens) in the vicinity ($df = 4, t = -1.907, p = 0.1292$).

Long-Distance Dispersal by Vehicles

Nearly one-third (32.3%) of the total species found in the tunnel traps were not present in any of the areas surrounding the tunnel entrances, indicating a large share of LDD. Comparisons between seed samples from single lanes and their corresponding surroundings revealed even higher proportions of LDD. Between 38% and 52% of the species trapped in single lanes were not present in the corresponding 50-m radius around the tunnel entrance. Together with the 150-m buffer zone this resulted in a minimal dispersal distance (MDD) of 200 m over which these species were transported. For the 100-m radius (MDD = 250 m) the proportions ranged from 29% to 42%.

The mean deposition of seeds due to LDD ranged between 91 and 445 seeds/m²/year with a clear dominance of non-native species (Fig. 2b). The quantitative extent of seed deposition on account of LDD thus reached a proportion between 15.0% and 36.5% off all trapped seeds in the different tunnel lanes.

The proportion of species missing from the vicinity of the tunnels was about two times higher for non-native species than for natives (Fig. 4a). The share of seeds of non-native species that were moved over long distances by traffic varied greatly among the five tunnel lanes, but was consistently higher than that of native species (Fig. 4b). Hence, non-native species were more often subject to LDD by traffic than natives both absolutely and relative to their overall proportion. In the GLMMs, native versus non-native status had a significant effect on the proportion of LDD from all species ($df = 4, t = 7.3170, p = 0.0019$) and on the proportion of all seeds ($df = 4, t = 6.9058, p = 0.0023$).

Discussion

Our sampling approach allowed us to estimate the actual magnitude of seed deposition by vehicles on the studied roadsides. The observed deposition between 635 and

Table 2. Species composition and contribution of non-native species in the seed samples from five separate tunnel lanes of an urban motorway in Berlin, the flora in the vicinity of the tunnels (100 m around the entrances), and the regional roadside flora of Berlin (Langer 1994).

	Tunnel samples		Vicinity of the tunnels		Regional roadside flora	
	species	%	species	%	species	%
Total species	204		386		340	
Native species	102	50.0	215	55.7	164	48.2
Pre-1492 non-native species (archaeophytes)	33	16.2	47	12.2	53	15.6
Post-1492 non-native species (neophytes)	69	33.8	124	32.1	123	36.2
Total non-native species	102	50.0	171	44.3	176	51.8
Species invasive in natural vegetation (Germany)	5	2.4	12	3.1	10	2.9
Species invasive in natural vegetation (other parts of the world)	39	19.1	71	18.4	63	18.5

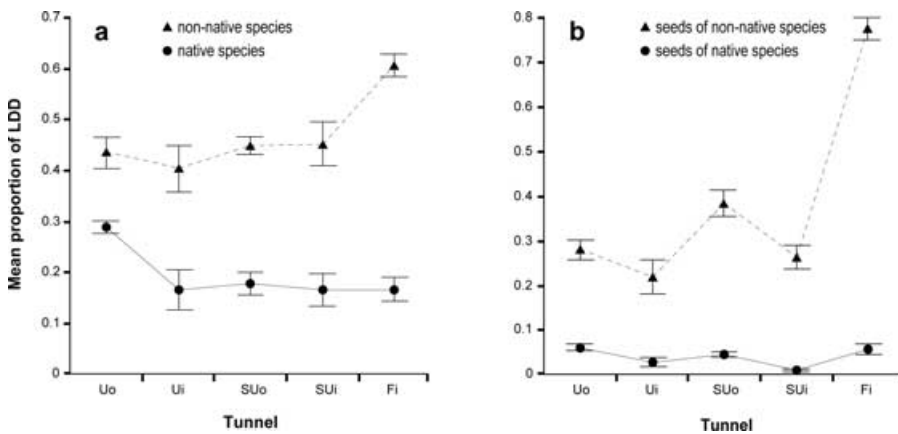


Figure 4. Mean proportion of long-distance dispersal events (LDD, dispersal events of >250 m) from (a) total species and (b) total seed numbers of native and non-native species in all roadside seed samples from five tunnel lanes of an urban motorway. Differences between native and non-native species are highly significant as indicated by generalized linear mixed effect models: (a) $df = 4$, $t = 7.3170$, $p = 0.0019$ and (b) $df = 4$, $t = 6.9058$, $p = 0.0023$. Error bars show 1 SE. See Fig. 2 for explanation of tunnel abbreviations.

1579 seed/m²/year was in a range comparable to sites with sparse vegetation such as alpine sites (1096–3557 seed/m²/year; Urbanska & Fattorini 2000), early successional stages on glacier forelands (381–685 seed/m²/year; Erschbamer et al. 2001) or abandoned mining areas (487–1584 seed/m²/year; Kirmer & Mahn 2001). It was also comparable to seed rain in acidic grasslands (992 seeds/m²/year; Pakeman & Small 2005), but approximately an order of magnitude lower than the seed rain in species-rich and productive grassland habitats (8079 seed/m²/year; Chabrierie & Alard 2005).

Although there are no analogous measures of the magnitude of seed rain at roadsides, our results show that dispersal by vehicles adds a substantial share to it. Even if the seed shadow of roadside vegetation were comparable to that of species-rich grassland, the contribution of the vehicle-borne seed rain would still be on the order of 10%. Because roadside vegetation is usually rather sparse, it is likely that the seed deposition by vehicles along roadsides is of a similar magnitude to that deposited by the roadside flora.

In our study the magnitude of seed deposition was analyzed for an urban motorway with a high volume of traffic of up to 50,000 vehicles per lane and per day. The observed seed rain thus provides an example of a high-use road in an urban area. We assumed deposition rates for smaller roads and rural areas would be lower. This is in accordance with findings of increasing impacts of roads on adjacent vegetation with a higher level of road improvement (Parentes & Jones 2000; Gelbard & Belnap 2003), as such differences may partly be attributed to a higher seed deposition due to higher volumes of traffic.

The positive correlation between seed content and weight of the samples (Fig. 3) suggests that propagule transport by vehicles depends at least partly on mud and other substrates that promote seed attachment to vehicles. The variation in seed deposition among the differ-

ent tunnel lanes (Fig. 2a) suggests that factors we could not control for in the experiment, such as width of lanes, varying speed of vehicles in different tunnels, or differential travel patterns of vehicles in the vicinity of different tunnels (e.g., rates of travel on dirt surfaces where vehicles may pick up seeds), may also influence the rates of seed deposition.

The vehicle-borne flora sampled in the three tunnels represented 12.5% of the present flora of Berlin (197 of 1606 species excluding extinct species; Prasse et al. 2001). Seven additional species had not been recorded before in Berlin. In accordance with previous studies (Clifford 1959; Wace 1977; Zwaenepoel et al. 2006), only a few frequent species contributed the major share of the seeds that were dispersed by traffic. Because rare transport events can lead to the establishment of new founder populations of a species (Moody & Mack 1988; Williamson 1996), the high species richness of the samples demonstrates a high potential for traffic to promote chance dispersal.

Non-native species contributed 54.5% to the seed rain caused by vehicles and 50% to the vehicle-borne flora of the tunnels (Table 2), revealing a high importance of traffic-derived dispersal for plant invasions. The overall proportion of non-native species in the seed samples exceeded that in the surrounding flora by more than 5%. Thus, dispersal by vehicles not only reflected the already high proportion of exotics in urban areas but promoted their further spread. This might be due to the general high frequency of non-native plant species along roadsides (e.g., Greenberg et al. 1997) that can act as seed sources for the attachment to vehicles. Additionally, successful non-native colonists may simply produce more seeds (i.e., are generally more ruderal) than the average native species.

The detection of seven new species in the seed samples for the flora of Berlin illustrates the capacity of traffic to

serve as a vector for the introduction of new species. Cape gooseberry (*Physalis peruviana* L.), for example, had no record in the flora of Berlin but emerged from samples out of two different tunnels. It is highly invasive in Australia (Weber 2003).

The potential threat of vehicle-derived dispersal for global plant biodiversity was highlighted by the high number of species in the samples that are highly invasive in other regions of the world (Weber 2003). In particular some of the species in the samples that are not invasive in Germany are of major concern for other regions of the world. This is illustrated by the presence in the samples of some of the fastest-spreading invaders along U.S. roadsides and adjacent habitats such as *Bromus tectorum* L. (Gelbard & Belnap 2003) and *Lythrum salicaria* L. (Wilcox 1989).

In contrast to the results of previous studies (Wace 1977; Schmidt 1989; Zwaenepoel et al. 2006), we found a significant relationship between traffic-dispersed species and the regional roadside flora. This is possibly due to the fact that our approach allowed for the measurement of the actual seed rain deposited by vehicles along roadsides rather than seeds attached to vehicles. The high congruency of traffic-dispersed species and the regional roadside flora as well as the positive correlation between species' frequencies in the roadside flora and their frequencies in the seed samples suggest a relevant impact of traffic-derived dispersal on roadside biodiversity and, in turn, an effect of roadside vegetation as a seed source for dispersal by vehicles.

Despite the relatively high correspondence between the vehicle-borne flora of the motorway tunnels and the regional roadside flora of Berlin, comparing species composition of the tunnel and the surrounding floras showed no significant effect of the local flora on the species composition of seeds transported by vehicles. Moreover, species abundance in the vicinity of the tunnels and species occurrence in either the 50-m or the 100-m radius around the tunnel entrances did not significantly affect species' seed counts in the samples.

These results seem contradictory at first glance but can be interpreted in terms of a large-scale homogenization of the roadside flora. If dispersal by vehicles affects roadside vegetation far beyond the local scale and over a long period, a good match between the vehicle-borne flora and the regional roadside flora is to be anticipated if the sampling site has been exposed over a long period to a high volume of traffic. Because our methodological approach provided an efficient isolation of the seed samples from other local dispersal vectors than traffic, the results revealed a reduced importance of local versus regional seed sources along roadsides. In this regard the weak similarity between local seed sources and the vehicle-borne seed rain in the tunnels indirectly highlights the role of traffic for LDD.

Accordingly, rates of LDD among the species in the seed samples were consistently high in all five assessed tunnel lanes. The observed proportions of the tunnel species that were absent in the adjacent vegetation around the tunnel entrances (38–52% in the 50-m radius, 29–42% in the 100-m radius) were exceptionally high compared with results of other studies that measured the seed rain in above-ground vegetation. The majority of seeds in seed-trap experiments are released from the adjacent aboveground vegetation within a range of only several meters (Jefferson & Usher 1989; Erschbamer et al. 2001).

Our results demonstrate that LDD by traffic is a routine mechanism rather than an exception. The absolute seed deposition of species absent in the adjacent vegetation ranged from 91 to 445 seeds/m²/year in the tunnels and represented far more than rare or exceptional dispersal events. For a few species we were able to reconstruct dispersal distances of several kilometers. The most reliable example is that of *Chenopodium pumilio* R. Br., which occurred at several sampling dates in samples of lanes leading out of the city. This Australian species has only a few known populations within Berlin (B. Seitz, floristic mapping of Berlin, unpublished data). The next known locality is more than 5 km away from the tunnel in which it was found.

At our study sites non-native species especially profited from traffic as a dispersal vector because their seeds were transported over long distances at a significantly higher proportion than those of native species (Fig. 4). This holds for all sampled lanes and both at the species and seed level. Thus, traffic as a dispersal pathway selectively increased the dispersal distances of non-native species. Because non-native species are equally overrepresented along roads in the nearer and farther surroundings of the tunnels, their general overrepresentation in the roadside flora cannot explain the overrepresentation of non-natives among the seeds that were transported long distances. This effect suggests that, on average, the time of adhesion to vehicles lasts longer in non-native compared with native species.

Possible explanations can be attributed to seed traits such as size or weight of seeds, which have been shown to promote attachment to vehicles (Hodkinson & Thompson 1997; Zwaenepoel et al. 2006) and might also influence the time span and distance over which propagules are moved by vehicles. A positive correlation between seed traits and invasion success was found for some, but not for all, species groups (Rejmánek & Richardson 1996). Further investigations should elucidate to what extent seed traits can explain LDD in the total species sample and in the groups of native and non-native species moved by vehicles.

The findings of enhanced dispersal distances for non-native species could account for some of the characteristics of roadside invasions. Routine long-distance

dispersal by vehicles may cause rapid spread rates of invasive species along roads and can explain the frequent occurrence of isolated founder populations and discontinuous distributional patterns during roadside invasions.

Our results clearly demonstrate that, besides altered site conditions, traffic-born dispersal is an important cause for the high non-native species richness of roadside verges. Although disturbance and other traffic-related effects on site conditions mainly provide suitable linear habitats for the establishment of non-native species, our results highlight that dispersal by vehicles was a major driver of the speed of invasion processes along roadsides. Moreover, this vector can link formerly isolated habitats. As a result it may also set off invasions by species that would never have reached a certain landscape without it. Thus, for management purposes, it is important to avoid impacts on roadsides and to take into account the connectivity that evolves from roadsides, especially in the process of constructing new roads. An important implication also arises for all kinds of roadside plantings. Because we found many propagules from typical non-native roadside trees, it is obvious that roadside plantings can act as a seed source for subsequent roadside invasions. Given the high potential of vehicles as vectors of LDD, planted populations of invasive species could easily overcome spatial isolation. This stresses the importance of using native species and plants of local provenance along roadsides (Harper-Lore & Wilson 2000).

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