



## Tree seed dispersal among forest fragments: II. Dispersal abilities and biogeographical controls

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### Abstract

**Aim** To investigate the medium to long-distance dispersal abilities of temperate hardwood tree species and the ecological controls on dispersal, including distance to and connectivity with seed sources, seed source strength, and species dispersal mechanism and seed size.

**Location** A fragmented forest system in the Long Point region, Southern Ontario.

**Methods** Pine plantations were the 'seed traps' in which seedlings of hardwood species were enumerated to indicate past dispersal events. The influence of distance to seed sources, dispersal mechanism and seed mass on the probability of dispersal to plantations were evaluated using logistic analysis. Regression analysis was used to determine the effect of seed source strength (mature tree abundance within 150 m of plantations) on seedling density in plantations. Connectivity was assessed by comparing the strength of correlations between seedling abundance in plantations and the abundance of mature trees around plantations in connected vs. unconnected source areas.

**Results** Seedling presence in plantations decreased significantly with distance from the nearest potential seed source for species grouped according to dispersal mechanism. Probabilities of seedling presence were  $\geq 0.8$  at 25 m distances, decreasing to under 0.3 at 175 m distances. While twenty-seven of twenty-nine species were present in at least one plantation with a seed source within 25 m, only thirteen of twenty-seven species occurred in plantations with a seed source  $\geq 100$  m away, and only nine of twenty-four species in plantations  $\geq 150$  m from seed sources, indicating limited potentials for interfragment migration. Seed source strength was significantly related to seedling density in plantations for twelve of fifteen species tested, indicating the importance of species commonness to interfragment migration. Connectivity was not related to dispersal frequency in the system, but this finding applies to a relatively well-connected system of forests and plantations and is expected to differ for systems with greater patch isolation. In addition to these general controls, dispersal was related to species dispersal mechanism. Seed size was negatively related to dispersal frequency, but only within the rodent dispersal spectra. Bird-dispersed species appeared to have superior interfragment dispersal abilities, closely followed by lighter seeded rodent- and wind-dispersed species. Large-seeded rodent-dispersed species (*Juglans* spp., *Quercus macrocarpa*) and species lacking well-developed adaptations for dispersers were infrequent in plantations generally, and with the exception of *Q. macrocarpa*, were absent from plantations more than 50 m from seed sources. Species dispersal abilities were ranked according to dispersal mechanism and seed size such that: bird > lighter-seeded rodent = wind > larger-seeded rodent = unspecialized.

**Main conclusions** Distance to seed sources appears to be a key determinant of patch colonization. Infrequent dispersal over distances of > 100–150 m for most species in this system raises concerns about the abilities of tree species to be sustained in fragmented

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forests. For some species, distances of as little as 50 m appear to be isolating, and these, in particular, risk regional extinctions over time scales depending on their local population persistence. Artificial introductions may be needed to maintain fragmented tree populations, particularly for rare species and those with poor dispersal indicated in this study.

### Keywords

Biodiversity conservation, eastern deciduous forests, forest fragmentation, medium to long-distance dispersal, metapopulations, tree migration.

## INTRODUCTION

European settlement of eastern North America marks an episode of extensive deforestation and forest fragmentation, similar to those that occurred earlier in Eurasia and continue throughout the tropics (Curtis, 1956; Burgess & Sharpe, 1981; Laurance & Bierregaard, 1997). While parts of the northeast have been allowed to reforest (Foster, 1992), large areas remain, in which forest covers less than 15% of the landscape. Forest fragmentation represents a huge change in the biogeographical 'context' of tree communities to which species populations are only now adjusting. In theory, plant diversity may be expected to decline in fragmented systems unless interpatch migration can compensate for local extinctions (MacArthur & Wilson, 1967; DeAngelis *et al.*, 1979; Goodman, 1987; Burkey, 1989). However, quantitative information on processes of long-distance plant dispersal with which to test this prediction is lacking.

The available literature indicates a number of factors that may influence interfragment dispersal, relating to the properties of the fragmented system and to the species themselves. They include: (1) the distance separating fragments from seed sources, (2) the size of fragments and plant populations in them supplying seed (i.e. the source strength), (3) the presence of vegetative connections between fragments, (4) species dispersal mechanisms, and (5) seed sizes.

The influence of distance on dispersal is easily appreciated by examining dispersal kernels. Seed fall is highly concentrated about the source, with a rapid, often exponential, decline with increasing distance therefrom (Harper, 1977; McClanahan, 1986; Portnoy & Willson, 1993; Willson, 1993). There appears to be a continued decline in dispersal frequency at intermediate to long distances (100–200 m) from seed sources (Holthuijzen & Sharik, 1985; Johnson, 1988; Greene & Johnson, 1995), suggesting that isolation reduces the amount of seed rain arriving in a fragment. Plant species richness of second growth woodlots is often inversely related to their distance from species-rich forest, supporting this suggestion (Matlack, 1994; Peterken & Game, 1984; Dzwonko & Loster, 1992). Seed source strength, defined as the abundance of trees supplying seeds in the landscape, influences seed rain to a patch, presumably by increasing the number of dispersal 'trials' (Cremer, 1965). However, computer studies indicate that the size of a source area becomes unimportant above a certain threshold (2 ha) (McClanahan,

1986). Given the implications for rare species conservation, the relationship between source strength and dispersal needs to be clarified.

A growing body of literature suggests that vegetative connections between fragments such as hedgerows, tree rows and riparian forests promote animal migration. The evidence comes from computer simulation models (Fahrig & Merriam, 1985), empirical (Wegner & Merriam, 1979; Johnson & Adkisson, 1985; Bennett, 1990; Lorenz & Barrett, 1990; Wauters *et al.*, 1994) and experimental studies (Gonzalez *et al.*, 1998). It follows that plants with animal vectors will benefit from the presence of connecting structures. However, studies document only the animal movements rather than movement of seeds they may be carrying, so the role of corridors in plant migration remains unclear (but see Johnson & Adkisson, 1985).

Species dispersal mechanism may influence the local pattern of seed deposition and probably does so at larger spatial scales (van der Pijl, 1982; Willson, 1993). Plant species with volant dispersers (wind and bird) may travel distances of several hundred metres (van der Pijl, 1982; Johnson & Adkisson, 1985; Dzwonko & Loster, 1992), while non-volant dispersers such as rodents typically achieve dispersal distances of just a few tens of metres (Sork, 1984; Abbott & Quink, 1970). Certain conditions may increase rodent dispersal distances, for example, the need to avoid seed cache piracy during years of food scarcity (Stapanian & Smith, 1986). In fragmented landscapes, rodents may travel several hundred metres in order to reach other fragments (Wauters *et al.*, 1994; Diffendorfer *et al.*, 1995). Nevertheless, these distances do not compare to the maximum dispersal distances of several kilometres recorded for birds and wind.

Seed mass seems to be inversely related to dispersal ability. Within wind-dispersed taxa (*Pinus*, *Acer*, and *Leguminosae*), heavy-seeded species had the greatest descent velocities, and increases in the size of the dispersal structure appeared not to compensate for aerodynamic constraints on large seeds (Greene & Johnson, 1993). Animal-dispersed tree species with large, heavy seeds experience limited long-distance transport relative to smaller-seeded species (Ranney & Johnson, 1977; Darley-Hill & Johnson, 1981).

This literature sheds light on the medium to long-distance plant dispersal process. However, ecological theory remains

limited by insufficient empirical support. Specific information on the dispersal characteristics of the majority of temperate tree species remains obscure. For example, the enigmatic *Carya* species (e.g. *C. cordiformis*, *C. ovata*) are believed to lack effective long-distance dispersal mechanisms, and yet palaeoecological evidence suggests they achieved rapid post-glacial migration rates (Hanson *et al.*, 1990; Clark & Fastie, 1998). In an accompanying study (Hewitt & Kellman, 2002), we have shown that pine plantations can act as 'traps' for seed dispersed in fragmented forests in Southern Ontario. Here, data on seed dispersed to those plantations are used to evaluate the dispersal abilities of hardwood tree species in the system.

## RESEARCH DESIGN

If young hardwoods in plantations are assumed to represent dispersal events, the seed sources would be the reproductively mature individuals of hardwood species existing in the surrounding landscape. While exact parentage cannot be determined, the distribution and abundance of fruiting trees in the landscape should be correlated with seedling abundances in plantations. Therefore, hardwood species seedlings in plantations and the mature, fruiting individuals of each species growing in the surrounding landscape within zones of increasing distance from, and degrees of connectivity with plantations were enumerated. Using these two data sets, the following hypotheses were tested:

1. The frequency of dispersal to plantations is negatively related to the distance to the nearest seed source.
2. The frequency of dispersal to plantations is positively related to the abundance of fruiting trees (source strength) in the surrounding landscape.
3. Dispersal mechanism influences the frequency of dispersal to plantations such that species with volant means of dispersal have superior long-distance dispersal abilities relative to species lacking volant means.
4. Species with large seed mass have lower frequencies of dispersal than species with small seed mass within particular dispersal spectra.
5. Vegetative connections between plantations and seed sources promote dispersal.

While most hardwood species in the region demonstrate a capacity to disperse to and establish in plantations, they differ in their establishment rates (Hewitt & Kellman, 2002). To minimize the potential complications caused by differences in establishment, two procedures were adopted: (1) species' dispersal abilities were evaluated based on the presence/absence of their seedlings in plantations rather than their abundances, and (2) interspecific comparisons were performed on species grouped according to dispersal mechanism and seed size and results were interpreted in relation to their relative establishment rates indicated in the accompanying article (Hewitt & Kellman, 2002).

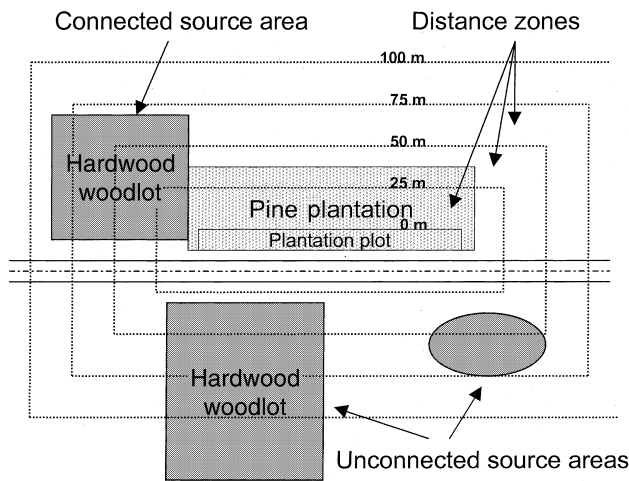
## Limitations to the study

The principal means of assessing distance effects was to determine the frequency with which seedlings had colonized plantations in relation to the distance to the nearest conspecific(s). Comparisons were then made between plantations with increasing distance and the nearest seed source. The difficulty is that some seeds will inevitably have arrived from more distant zones than those containing the nearest conspecific(s), and it is impossible to determine their contribution. Therefore, the analysis is not intended to indicate the frequency of colonization from seed sources at particular distances. Rather, it indicates how colonization frequency changes as more proximate sources are removed. A second procedure was used to quantify seed rain – source tree abundance relationships where only plantations with species seed sources in one or two adjacent distance zones are counted. However, this method yields a much smaller sample size because of the limited availability of plantations with species seed sources in isolated distance zones. It should be emphasized that these conditions are not unique to this research design, but are common constraints on field studies of extra-local, interpatch dispersal. Nevertheless, empirical information of the sort provided here should be at least as valid as the more widely available information from simulation models, and is in fact essential to corroborate those theoretical and mathematical findings.

## MATERIALS AND METHODS

The study area is a fragmented system of eastern deciduous forest located on the north shore of Lake Erie, southern Ontario (42°40' N, 80°29' W). Forest fragments range in size from under 1 to 49 ha and are separated by mean distances of 215 m to the four nearest neighbours, 144 m to the nearest three, 79 m to the nearest two. Known animal dispersers in the region include Bluejays (*Cyanocitta cristata*), squirrels (*Scuirus nigra*, *S. caroliniensis*), and perhaps chipmunks (*Tamiascivrus* spp.) for nut tree seeds (e.g. *Fagus grandifolia*, *Quercus* spp., *Carya* spp.), and a variety of avian frugivores as well as rodents and possibly raccoons (*Procyon lotor*) for species with fruit-encased seeds. Further information about the study area, pine plantations and sampling of hardwood seedling populations in these are provided in Hewitt & Kellman (2002).

Seedling counts, as stems emerged to 1.5 cm basal diameter, in pine plantations were used as measures of dispersal of the twenty-nine species present in plantations (Hewitt & Kellman, 2002). The seedling class encompassed a 4–11 year dispersal period, depending on the species. Mature trees, the potential seed sources, were enumerated within 25 m wide concentric zones of increasing distance from the edges of the enumerated area within plantations to a distance of 150 m, for a total of six distance zones (Fig. 1). Surveys were conducted along compass lines parallel to the limits of each distance zone at 12.5-m intervals. This interval allowed all trees to be viewed from compass lines while



**Figure 1** Source areas around, and surveyed areas within, pine plantations. Distance zones in which source trees were enumerated, and connected and unconnected source areas are indicated.

preventing repeat counts. As tree canopies were often out of visual range, and because of the large number of trees being enumerated, it was not possible to use direct evidence of fruiting to identify seed trees. Reproductive maturity was indicated by stem diameter at breast height (d.b.h.) based on information in the literature [10 cm d.b.h. for canopy species such as *Fagus grandifolia* Ehrh., *Liriodendron tulipifera* L.; 5 cm d.b.h. for subcanopy species, *Cornus florida* L., *Amelanchier arborea* (Michx. F) Fern, *Carpinus caroliniana* Walt., and *Ostrya virginiana* (Mill.) K. Koch] (Burns & Honkala, 1990). Smaller individuals were checked for signs of flowering or fruiting during surveys in June–August 1997. Mature individuals were occasionally present in plantations, particularly in the older ones. As these were potential seed sources, they were added to tree counts in the 0–25 m distance zone. Individuals in each distance zone were classified as being either connected or unconnected to the plantation, using treeless ground >15 m as a criterion for lack of connection.

Because of the elongated shape of the area enumerated within plantations, the distances delimiting distance zones are conservative estimates of the actual distances seeds would have travelled. For example, a seedling located at the opposite end of the 100 m long plantation plot from the source tree in the adjacent, 0–25 m distance zone could have dispersed up to 125 m (Fig. 1). Therefore, the upper limit of the distance zones was used to indicate the distance between conspecifics in a zone and seedlings in plantations that potentially originated there: hence, trees in the 0–25 m distance zone were classified as being 25 m away from plantations, and so on.

Species were classified by dispersal mechanism as wind-, bird-, or rodent-dispersed according to the literature (Darley-Hill & Johnson, 1981; Johnson & Adkisson, 1985; Burns & Honkala, 1990). Species that were both bird- and rodent-dispersed (*F. grandifolia* and some *Quercus* species)

were classified as bird-dispersed, as birds were expected to achieve longer distance transport than mammals, an issue of central concern here. Three species lacking well-developed adaptations for either wind or animal dispersal (*O. virginiana*, *Tilia americana* L., *C. caroliniana*) were classified as species of 'unspecialized' dispersal.

## DATA ANALYSIS

In order to indicate the distances that species had dispersed, for each species, the following were determined: (1) the distance zone containing the closest fruiting tree to each plantation and (2) the presence or absence of young individuals (newly emerged—1.5 cm basal diameter) of that species in the plantation. A logistic model (Proc LOGISTIC, SAS Institute, 1990) was then used to assess the influence of distance and dispersal mechanism on the probability of seedling presence in plantations. The dependent variable was the logit proportion of plantations in which seedlings of a species were present [ $= \log(\text{proportion of plantations in which seedlings present/proportion in which absent})$ ] and the independent variables were distance to the nearest fruiting tree, dispersal mechanism and the distance  $\times$  dispersal mechanism interaction. Distance was modelled as a continuous variable, after determining that the response of the logit to distance was linear (Hosmer & Lemeshow, 1989), and dispersal mechanisms were coded as design (categorical) variables. Logistic models involving continuous and categorical independent variables are similar to analysis of covariance, but are designed to handle binary dependent variables such as the species presence/absence data in this study.

To determine the significance of both distance and dispersal mechanism in the model, each was sequentially removed from the full, multivariate model and its contribution assessed using a log-likelihood ratio test between models containing and not containing the variable (Hosmer & Lemeshow, 1989). Wald chi-square tests and z-tests were used to indicate significant differences among dispersal mechanisms in the model. Because of the low establishment probabilities indicated for species of unspecialized dispersal and the small number of species in this group, unspecialized species were excluded from the analyses. The results of these tests were interpreted in relation to the intergroup differences in seedling establishment indicated in the accompanying article (Hewitt & Kellman, 2002).

To investigate relationships between seed size and dispersal ability, seed size was added as a third independent variable in the logistic model containing dispersal mechanism and distance, and a log-likelihood ratio test used to indicate significance. Species were grouped into seed size classes (<0.01 g, 0.01–0.99 g, 1–5 g and >5 g) which were coded as design variables. Because the effect of seed size might depend on the species dispersal mechanism, separate tests for each dispersal mechanism were also run. As before, results were interpreted in light of intergroup differences in seedling establishment.

To get an approximation of seed rain density per source tree at medium to long distances, species in each plantation for which the nearest seed source was more than 75 m away were identified. Then the total number of the species seedlings in the 1500 m<sup>2</sup> plantation plot was divided by the number of fruiting trees contained in the source zone(s) around it. This procedure was performed only in cases where conspecific trees occurred in a single or two adjacent zones, so that the probable seed sources could be traced to a particular distance zone(s). Because of the small number of observations meeting these criteria, results were not assessed statistically.

Regression analysis was employed to determine whether there was a positive relationship between source strength and frequency of dispersal. The independent variable was the number of mature trees enumerated around plantations to a distance of 150 m and the dependent variable was the density of seedlings in plantations ( $n = 16$  per species). Only species that were common around plantations were considered to minimize the number of zero observations in the independent and dependent variables. Variables were logarithmically transformed to improve normality and homoscedasticity.

The influence of vegetative connectivity was assessed by comparing correlations between seedling abundance in plantations and (1) tree abundance in source areas *connected* to plantations to correlations with (2) tree abundance in *unconnected* source areas. It was hypothesized that if connectivity promoted seed dispersal to plantations, seedling abundance in plantations would be more strongly correlated with tree abundance in connected than unconnected source zones. The procedure involved running, for each species, a series of Spearman rank correlations between seedling density in plantations (dependent variable) and mature tree abundance (independent variable) in distance zones that were (1) connected to plantations via other woody vegetation and (2) separated from plantations by open ground ( $n = 16$  per species). Correlations were run by sequentially adding in the fruiting individuals in ever more distant zones to the independent variable assuming that the source zones were cumulatively contributing seeds to plantations. Individuals in the 0–25 m distance zone were excluded from source areas in the correlation analysis as they would not represent distance equally between the connected and unconnected classes: fruiting individuals in the latter had to be separated from plantations by at least 15 m of open ground. Thus, for example, to assess relationships with connected source areas, correlations were first run with mature tree abundance within 25–50 m as the independent variable, then mature trees within 25–50 m, 25–75 m, etc. Then, to test the prediction that connected source zones supplied more seed than unconnected, the highest correlation coefficient obtained for a species for the correlations with each of the connected and unconnected source areas was chosen and compared by means of a one-tailed sign test. Only the highest coefficient was used because the correlations were non-independent.

## RESULTS

### Effects of distance and dispersal mechanism on frequency of dispersal

Species tended to be more frequent in plantations with seed sources within 75 m than those with more distant sources (Table 1). Twenty-seven of the twenty-nine species (93.1%) were present in at least one plantation with a source within 25 m, seventeen of twenty-two species (77.3%) were present when a source was within 50 m, but only nine of twenty-four species (37.5%) occurred in plantations with a source > 150 m away. The number of dispersal events in a 1500 m<sup>2</sup> area of plantation per fruiting tree  $\geq 75$  m away was extremely low (Table 2). Over half (twenty-six of forty-five) of the observations provided no evidence of dispersal. In the other instances, five or fewer (mean 2.3,  $n = 17$ ) seedlings/fruiting tree had established over the 4–11-year period recorded, except in the case of *Acer rubrum*, which had much higher numbers (10.7, 15.4 seedlings per fruiting tree). Dispersal frequencies appeared to be lower when seed sources were > 125 m away, although this cannot be tested statistically.

Logistic regression indicated a highly significant, negative relationship between distance to seed sources and seedling presence in plantations ( $-2$  log-likelihood ratio 200.52, 1 d.f.,  $P < 0.0001$ ). The probability of seedling presence decreased by a mean of 25% from one 25 m wide distance zone to the next (odds ratio = 0.521) (Fig. 2). Dispersal mechanism (wind, bird, rodent) was also significantly related to seedling presence in plantations ( $-2$  log-likelihood ratio = 15.29, d.f. = 2,  $P < 0.001$ ). There was no interaction between dispersal mechanism and distance ( $-2$  log-likelihood ratio statistic = 3.79, 2 d.f.,  $P > 0.1$ ) indicating that the probability of dispersal to plantations declined with distance at a similar rate for all dispersal mechanisms. Rodent-dispersed species were more frequent in plantations than wind-dispersed species at equal distances from the seed sources (odds ratio = 1.72), but the difference was not significant (Wald chi-square = 2.62,  $P = 0.1055$ ). Bird-dispersed species were significantly more frequent than wind-dispersed species (odds ratio = 3.817, Wald chi-square = 14.199,  $P < 0.0002$ ) and were more frequent than rodent-dispersed species, but not significantly (odds ratio = 2.219;  $z = 2.116$ ,  $P > 0.05$ ). Unspecialized species were not included in the analyses, but raw values show none of them occurring in plantations more than 50 m from a seed source.

### Effect of seed mass on dispersal ability

There was a significant effect of seed mass ( $-2$  log likelihood ratio statistic = 33.721, d.f. = 3,  $P < 0.0001$ ) on the logit of species presence in plantations, and no interaction between seed mass and distance ( $-2$ -log likelihood ratio statistic = 1.903, 3 d.f.,  $P > 0.01$ ). The interaction among seed mass and dispersal mechanism could not be tested due to the fact that each dispersal mechanism contained only two of the four seed mass categories. Seed size groupings differed in

**Table 1** Presence of hardwood species seedlings (0–1.5 cm basal diameter) in plantations relative to seed source proximity. Values present the ratio of the number of plantations at a given distance from the nearest seed source (indicated in the column) in which seedlings of the species were present (numerator) vs. the total number of plantations sampled at that distance from the nearest seed source (denominator)

Disp.mech.	Seed size	Species	Zone containing nearest fruiting individual (m from plantation edge)						
			0–25	25–50	50–75	75–100	100–125	125–150	> 150
W	2	<i>Acer negundo</i>	1/2		1/1				4/13
W	2	<i>A. nigrum</i>	2/2						1/14
W	2	<i>A. rubrum</i>	14/14					1/1	1/1
W	2	<i>A. saccharinum</i>	3/3	1/3	0/1	1/1			0/1
W	2	<i>A. saccharum</i>	9/9	2/2	1/1	1/1			0/1
W	1	<i>Betula alleghaniensis</i>	5/6	0/1	0/1		1/1		0/1
W	2	<i>Fraxinus</i> spp.*	11/12	3/3	1/1				0/6
W	2	<i>Liriodendron tulipifera</i>	3/4	1/2				0/1	0/9
W	1	<i>Populus deltoides</i>	2/6	0/4		1/1		0/1	0/4
W	1	<i>P. grandidentata</i>	4/7					0/1	0/2
W	1	<i>P. tremuloides</i>	0/3	0/1	0/2				0/2
W	2	<i>Ulmus</i> spp.**	5/8	1/1	1/1			0/1	0/5
B	2	<i>Amelanchier arborea</i>	5/5	2/2	2/2	2/4			2/3
B	2	<i>Cornus florida</i>	8/9	3/3	2/2	1/1			1/1
B	2	<i>Fagus grandifolia</i>	5/5	2/2	3/3	0/1			2/5
B	2	<i>Nyssa sylvatica</i>	1/1	1/1			1/2	0/1	0/11
B	2	<i>Prunus serotina</i>	14/14	2/2					
B	3	<i>Quercus velutina</i>	11/11	1/2	2/2			0/1	
B	2	<i>Sassafras albidum</i>	6/6		0/2	0/1	1/2		3/5
R	3	<i>Carya cordiformis</i>	3/3	3/3	4/4				0/6
R	3	<i>C. ovata</i>	4/4	1/1	5/5	1/2			0/4
R	4	<i>Juglans cinerea</i>	1/1	1/1			0/1	0/1	0/12
R	4	<i>J. nigra</i>	2/5		0/1				0/10
R	3	<i>Q. alba</i>	7/8	3/3	0/1	0/1	1/2	1/1	
R	4	<i>Q. macrocarpa</i>	1/1				0/1		2/14
R	3	<i>Q. rubra</i>	8/8	2/2	3/3	0/1			2/2
U	2	<i>Carpinus caroliniana</i>	1/2	1/2	0/5	0/1		0/1	0/5
U	2	<i>Ostrya virginiana</i>	0/5	0/1	0/3	0/2		0/1	0/4
U	2	<i>Tilia americana</i>	1/3	0/5	0/1	0/1			0/6

\**Fraxinus americana/pennsylvanica*; \*\**Ulmus americana/rubra*.

Dispersal mechanisms are: W = wind; B = bird; R = rodent; U = unspecialized; seed size classes are: 1 = seeds < 0.01 g; 2 = 0.01–0.99 g; 3 = 1–5 g; 4 = > 5 g. Nomenclature follows Burns & Honkala (1990).

their probability of occurring in plantations such that both the heaviest (class 4) and lightest seeded species (class 1) were significantly ( $P < 0.05$ ) less likely to be present in plantations compared with intermediate seed size classes (odds ratios, heavy to intermediate, classes 2 and 3: 13.81 and 9.32, respectively, light to intermediate classes 2 and 3: 7.83 and 5.28). Heavy and light seeded species did not differ significantly (odds ratio light: heavy = 1.76). In order to control for dispersal mechanism when comparing seed mass, separate logistic regressions were run on seed mass within each dispersal mechanism. This confirmed that only the lightest and heaviest seed size classes had significantly lower probabilities of seedling presence in plantations, and these occurred only within the wind and rodent dispersal mechanisms, respectively (Table 3).

Given the pattern of influence of seed mass on frequency of dispersal to pine plantations, and the relationship between seed size and dispersal mechanism, a new logistic model was created that incorporated the

effects of both seed mass and dispersal mechanism. Species were grouped into categories reflecting the influence of both dispersal mechanism and seed mass on the logit probability of seedling presence in plantations. Seed mass categories that did not differ significantly in their effect on the logit were combined so that groups 2 and 3 were treated as an 'intermediate' category, group 1 was treated as 'light', and group 4 as 'heavy'. This is consistent with a parsimonious method of model-building (Crawley, 1993). Thus, five dispersal mechanism-seed mass categories were created: (1) Wind-dispersed-light-seeded, or simply, Wind-Light, (2) Wind-Intermediate, (3) Bird-Intermediate, (4) Rodent-Intermediate, and (5) Rodent-Heavy. Figure 3 shows the predicted probability of seedling presence in plantations vs. distance to seed sources for each of these categories. Bird-Intermediate had the highest probabilities, followed by Rodent-Intermediate, Wind-Intermediate, Rodent-Heavy, and Wind-Light. Only the difference between the first three groups (Bird-Intermediate,

**Table 2** Seedling colonization densities (stems/1500 m<sup>2</sup>) per source tree for hardwood species in plantations in relation to the distance to seed sources. The numerator is seedling density in a plantation and the denominator is the number of mature trees present at the distance indicated in the column. The solution is the number of colonization events expected per fruiting tree at a given distance from plantations over the 4–11 years establishment and survival period that seedlings record

Species	Distance (m) to the nearest fruiting tree(s)					
	75	75–100	100	125	125–150	150
<i>Acer rubrum</i>				30.7/2 = 15.4		10.7/1 = 10.7
<i>A. saccharinum</i>						0/1 = 0
<i>A. saccharum</i>						0/1 = 0
<i>Amelanchier arborea</i>	20/4 = 5		5/1 = 5 8/2 = 4			
<i>Betula alleghaniensis</i>	0/5 = 0				1/4 = 0.25	0/2 = 0
<i>Carpinus caroliniana</i>						0/2 = 0
<i>Carya cordiformis</i>	1.1/1 = 1.1 4.7/1 = 4.7					
<i>C. ovata</i>		3/3 = 1 1.1/3 = 0.4				
<i>Cornus florida</i>	19/8 = 2.4					
<i>Fagus grandifolia</i>	9/2 = 4.5					
<i>Fraxinus</i> spp.	6.7/1 = 3					
<i>Juglans nigra</i>	0/3 = 0					
<i>Liriodendron tulipifera</i>				0/1 = 0		
<i>Nyssa sylvatica</i>				1/2 = 0.5		0/10 = 0
<i>Ostrya virginiana</i>		0/2 = 0				0/1 = 0
<i>Populus deltoides</i>			2/1 = 2		0/10 = 0	
<i>P. grandidentata</i>				0/1 = 0		0/1 = 0
<i>P. tremuloides</i>						0/3 = 0 0/1 = 0
<i>Quercus alba</i>	0/1 = 0		0/1 = 0		0/4 = 0 3.3/5 = 0.7	1/3 = 0.33
<i>Q. macrocarpa</i>				0/1 = 0		
<i>Q. rubra</i>		6.7/2 = 3.4	0/1 = 0			
<i>Q. velutina</i>				0/2 = 0		
<i>Sassafras albidum</i>	0/1 = 0 0/1 = 0		0/1 = 0		0/8 = 0 3.3/10 = 0.33	
<i>Ulmus</i> spp.					0/6 = 0	

Rodent–Intermediate, Wind–Intermediate) and the last two (Rodent–Heavy, Wind–Light) was significant.

### Seed source strength

There was a significant positive relationship between seedling density in plantations and tree abundance to 150 m distance for twelve of the fifteen species tested (Table 4). The  $R^2$  statistics were  $> 0.50$  for many of the species, indicating that source strength explained a large proportion of the variability in seedling abundance.

### Role of connectivity

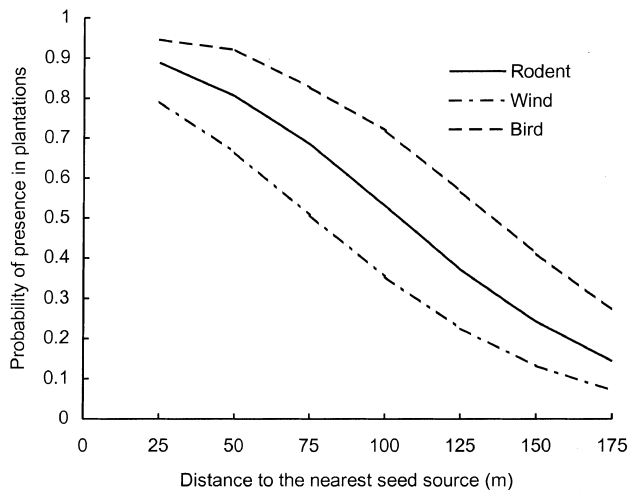
Table 5 lists the highest rank correlation coefficients obtained for relationships between species seedling abundances in plantations and fruiting tree abundance in connected and unconnected source areas. Seedling abundance was not better correlated with tree abundance in connected source areas than unconnected areas ( $n = 24$ ,  $R = 11$ ,  $P > 0.25$ ). Neither was there a tendency for

positive contrasts to be most frequent among animal-dispersed species that had been expected to respond to connecting structures (wind: six of nine; bird: two of six; rodent: three of six; unspecialized: one of two).

## DISCUSSION

### Relationship between distance and dispersal frequency

The most general and perhaps obvious dispersal pattern found in the study was one of marked decline in dispersal frequency as seed sources became increasingly distant. The pattern occurred over a range of about 0–150 m, suggesting that there is a continued decline in tree seed dispersal over intermediate to long distances. Greene & Johnson's (1995) computer simulation study indicated no appreciable change in the probability of conifer and hardwood species seed deposition between 300 and 1600 m from a seed source, implying that dispersal over longer distances than measured here may not respond to incremental changes in distances or that the probability of dispersal becomes so low that a



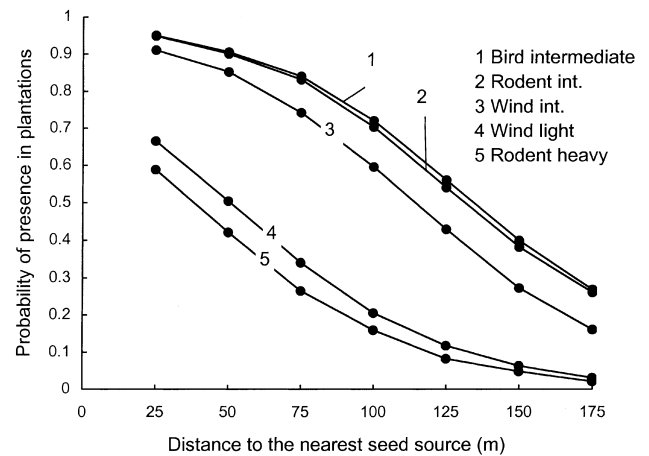
**Figure 2** Probabilities of seedling presence in plantations in relation to the distance to the nearest seed source predicted by the logistic regression model. Species are grouped according to dispersal mechanism. The analysis indicated no significant interaction between dispersal mechanism and distance so the model reflects this.

further percentage decrease is insignificant. If accurate, fragmentation above a certain threshold level may not further isolate populations within fragments. However, this does not take into account the negative effects of source strength on dispersal frequency, which would presumably decline with increasing fragmentation.

While the findings highlighted the general importance of proximity to seed sources, they also indicated some important details about the dispersal process relating to the probabilities of dispersal at different distances, interspecies variation in dispersal and the influence of source strength on dispersal frequency. The probabilities of dispersal to and establishment in plantations declined by approximately 78% between plantations 25 m to those 175 m from seed sources. When grouped according to dispersal mechanism, species had a 2.6–26.8% chance of dispersing 175 m distances over the 4–11-year period encompassed by seedling counts. However, on an individual basis, fewer than half of the species in the system had dispersed those long distances. Those that had, were present in only about 58% of plantations at that distance, and at very low frequencies.

#### Influence of species attributes: dispersal mechanism and seed size

Interspecies variation in seedling presence in plantations was related to dispersal mechanism and seed size according to the



**Figure 3** Predicted probabilities of seedling presence in plantations in relation to distance to the nearest seed source for species grouped according to both dispersal mechanism and seed size. Intermediate (Int.) is seed size class 0.1–5 g, Light is seeds < 0.1 g, and Heavy is seeds > 5 g.

logistic model shown in Fig. 3. There was a marked distinction between three groups of more frequently occurring species in plantations (bird-dispersed species, wind-dispersed species and the lighter seeded of the rodent-dispersed species) and two groups of infrequently occurring species (heavy-seeded rodent-dispersed species and light-seeded wind-dispersed species). However, the significance of these findings to dispersal must be assessed in relation to the establishment abilities of the groups. The greater, but not significantly, seedling frequencies for the Bird–Intermediate category relative to the Rodent- and Wind-Intermediate groups suggest better dispersal, given their relatively lower probabilities of seedling establishment. The low probability of seedling presence for Rodent-Heavy species probably reflects dispersal limitations, given that both rodent-dispersed and large-seeded species had greater establishment probabilities than other dispersal mechanism and seed size groupings. However, the low ranking for Wind-Light species is assumed to reflect establishment constraints, rather than poor dispersal, or perhaps that their seed is more widely dispersed and was not accounted for by the measured seed sources within 150 m of plantations.

The finding that bird-dispersed species are superior interfragment dispersers is repeated in the literature (Carlquist, 1967; Hubbell, 1979; Darley-Hill & Johnson, 1981; van der Pijl, 1982; Johnson & Adkisson, 1985). It is probably a function of the birds ability to travel long-distances as well as their tendency to direct seed to vegetated

Dispersal mechanism	d.f.	Wald chi-square	Odds ratio	P-value
Wind	1	16.129	0.139 (class 1 vs. 2)	<0.0001
Bird	1	0.284	1.638 (class 2 vs. 3)	0.5941
Rodent	1	11.325	9.534 (class 3 vs. 4)	0.0008

**Table 3** Logistic regressions of the effect of seed size category on the logit of seedling presence in plantations for wind, bird and rodent-dispersed species



**Table 4** Relationship between abundance of mature trees around plantations (to 150 m distance) and seedlings in plantations

Species	$r^2$
<i>Acer rubrum</i>	0.51**
<i>A. saccharum</i>	0.27***
<i>Amelanchier arborea</i>	0.22 <sup>NS</sup>
<i>Betula alleghaniensis</i>	0.37*
<i>Carya cordiformis</i>	0.80***
<i>C. ovata</i>	0.49**
<i>Cornus florida</i>	0.04 <sup>NS</sup>
<i>Fagus grandifolia</i>	0.50**
<i>Fraxinus</i> spp.	0.82***
<i>Prunus serotina</i>	0.16 <sup>NS</sup>
<i>Quercus alba</i>	0.68***
<i>Q. rubra</i>	0.84***
<i>Q. velutina</i>	0.48**
<i>Sassafras albidum</i>	0.64***
<i>Ulmus</i> spp.	0.31*

NS  $P > 0.05$ , \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ .

patches in the landscape to which they are attracted (McDonnell & Stiles, 1983; McClanahan & Wolfe, 1987). While wind also has a high potential for long distance seed transport, it scatters seeds randomly downwind of seed sources resulting in seed loss to the non-forested matrix in a fragmented landscape. Bird-dispersed trees may therefore become more important in fragmented systems relative to non-bird-dispersed species, as has happened to *Prunus serotina* compared with wind-dispersed *A. saccharum* in Wisconsin (Auclair & Cottam, 1971).

A surprising result was that small-seeded rodent-dispersed species had only marginally lower probabilities of long-range dispersal than bird-dispersed species, and were comparable with wind-dispersed species. Had it been possible to measure dispersal over longer distances, perhaps there would have been a decline in rodent dispersal relative to other mechanisms. The 150–175 m distances measured may encompass the range of dispersal distances for rodents, but perhaps not birds (Darley-Hill & Johnson, 1981; van der Pijl, 1982; Johnson & Adkisson, 1985). However, it is possible that rodents travelled farther than usual in this fragmented system in order to move between forest patches (Wauters *et al.*, 1994; Diffendorfer *et al.*, 1995). Another conceivable explanation for this finding is that birds augment the dispersal distances of typically non-bird-dispersed species, including rodent and wind. Birds are reported to occasionally transport *Carya* species (Hanson *et al.*, 1990). Wilkinson (1997) argued that the rapid post-glacial migration rates achieved by wind-dispersed species in Europe were because of their occasional dispersal by birds. Occasional bird transport of rodent-dispersed species would account for the only marginally lower frequencies of wind-dispersed species in the pine plantations relative to bird-dispersed species in this study.

Species unspecialized for a particular dispersal mechanism were generally infrequent in plantations. While this may partly reflect low probabilities of seedling establishment (see Hewitt & Kellman, 2002, Table 6), their complete absence from plantations > 50 m from seed sources implicates dispersal. These species may be dispersed by both wind and animals. However, poor adaptations for either mechanism in

**Table 5** Spearman rank correlation coefficients obtained for correlations between seedling densities in plantations and tree densities in connected and unconnected source areas. The last column shows the sign of the contrasts between coefficients for connected and unconnected source areas. Only species with fruiting trees in at least three distance zones per connectivity class were included in the analysis

Disperser	Species	Connected	Unconnected	Contrast
Wind	<i>Acer rubrum</i>	0.7095	0.7504	–
W	<i>A. saccharinum</i>	0.6271	0.7063	–
W	<i>A. saccharum</i>	0.8076	0.6981	+
W	<i>Betula alleghaniensis</i>	0.68	0.555	+
W	<i>Fraxinus</i> spp.	0.9225	0.6391	+
W	<i>Liriodendron tulipifera</i>	0.7259	0.7176	+
W	<i>Populus deltoides</i>	0.4142	–0.2275	+
W	<i>P. grandidentata</i>	0.5478	0.7844	–
W	<i>Ulmus</i> spp.	0.6219	0.5012	+
Bird	<i>Amelanchier arborea</i>	0.5765	0.0293	+
B	<i>Cornus florida</i>	0.2848	0.7753	–
B	<i>Fagus grandifolia</i>	0.6731	0.8026	–
B	<i>Prunus serotina</i>	0.2508	0.5461	–
B	<i>Quercus velutina</i>	0.5621	0.5461	+
B	<i>Sassafras albidum</i>	0.6086	0.6979	–
B	<i>Nyssa sylvatica</i>	0.9975	0.9975	=
Rodent	<i>Carya cordiformis</i>	0.8491	0.7665	+
R	<i>C. ovata</i>	0.5283	0.5045	+
R	<i>Juglans cinerea</i>	0.7303	0.392	+
R	<i>J. nigra</i>	0.534	0.6104	–
R	<i>Q. alba</i>	0.8414	0.8695	–
R	<i>Q. rubra</i>	0.7485	0.8933	–
Unspec.	<i>Carpinus caroliniana</i>	0.9979	0.3263	+
U	<i>Tilia americana</i>	–0.1234	0.1173	–

terms of an efficient structure for wind entrainment or nutritious seed to attract animals means that wind moves their seeds only a few metres from parent plants (Johnson, 1988; Burns & Honkala, 1990) and animals probably disperse them in very small numbers. Unspecialized species achieve limited dispersal and colonization in other patchy systems (Dzwonko & Loster, 1992; Kadmon, 1995).

Seed size was negatively related to dispersal frequency, but only within the rodent dispersal spectra suggesting an interaction between seed size and rodent dispersal behaviour. As the large-seeded *Q. macrocarpa* and *Juglans* species are the preferred diet for the major rodent dispersers in eastern deciduous forests, *Sciurus niger* and *S. carolinensis*, the interaction is not likely to relate to food preference (Smith & Follmer, 1972; Stapanian & Smith, 1986; personal observation) and is more likely to be because of the high energetic costs and awkwardness of moving large, heavy seeds. Ranney & Johnson (1977) attributed the absence of *J. nigra* colonization of tree plantations in South Dakota to squirrels caching heavy seeds close to the source for retrieval later.

Thus, large-seeded rodent-dispersed and unspecialized species may face particularly high extinction risks in patchy systems. In continuous communities, diffusion across the landscape via local dispersal could maintain regional populations of such species. However, in patchy systems, where suitable habitat is sparsely distributed and widely separated, ineffective dispersal may result in extinction over time scales that depend on the persistence of local populations. In fact, limited dispersal may explain the local extinction of *J. nigra* in fragmented systems in Wisconsin, in addition to xeric conditions in small fragments suggested previously (Curtis, 1956; DeAngelis *et al.*, 1979). For these species, artificial introductions may be necessary to maintain them in fragmented forests.

These findings suggest that the dispersal abilities of North American hardwood species may be ranked according to dispersal mechanism and seed size such that: bird > light-seeded rodent  $\geq$  wind > heavy-seeded rodent  $\geq$  unspecialized. These rankings may be compared with those of other community-wide dispersal comparisons, such as for herbs and shrubs in eastern North America (Matlack, 1994) and trees in Poland (Dzwonko & Loster, 1992). The studies are similar in their relatively high ranking of wind and bird, and low ranking of large-seeded rodent or unspecialized species. The relatively high efficiency of light-seeded rodent-dispersed species in the present study is a little unusual, and is discussed above.

While quantitative analyses were not conducted on individual species, certain qualitative patterns are revealed by these data. Several species were absent from plantations more than 100 m from seed sources, suggesting limited dispersal. These species included six of the twelve wind-dispersed species (*A. saccharinum* L., *L. tulipifera*, *Ulmus* spp., *Populus deltoides* Bart. ex Marsh, *P. grandidentata* Michx. and *P. tremuloides* Michx.), one of seventeen bird-dispersed species (*Quercus velutina* Lam.), four of six rodent-dispersed species [*Carya cordiformis* (Wang.) K. Koch, *C. ovata* (Mill.) K. Koch, *Juglans cinerea* L., *J. nigra*] and all

three unspecialized dispersers. Dispersal constraints, however, are not necessarily responsible for these patterns. Limited seedling establishment may explain *Populus* species absence, as other studies suggest that their seed are widely dispersed (Burns & Honkala, 1990). Low seed viability (often under 5%) may explain *L. tulipifera*'s absence, and the absence of *Q. velutina* may be because of small sample size of plantations with a seed source > 100 m away ( $n = 1$ ).

For the other species, dispersal constraints seem likely. Dispersal limitations among wind-dispersed species probably relate to the aerodynamic characteristics of the seeds. For example, *A. saccharinum* is the largest seeded *Acer* species in this system, perhaps reducing its dispersal ability. No general effect of seed size on dispersal of wind-dispersed species was found. However, Greene & Johnson (1993) determined that seed size potentially limits dispersal capacity within wind-dispersed taxa such as *Acer*. Heavy-seeded wind-dispersed species colonized forest fragments in Poland less often than lighter-seeded species (Dzwonko & Loster, 1992). In the case of the rodent-dispersed *C. cordiformis*, bitter tasting seeds reportedly make it less attractive to rodent dispersers than other nuts (Burns & Honkala, 1990), although, this does not explain the similarly limited dispersal of *C. ovata*. The role of large seed size in the poor dispersal of *Juglans* species has already been discussed.

#### Influence of source strength

Another important influence on dispersal frequency was seed source strength. The relationship was present and the correlation strong ( $R^2 > 0.50$ ) for the majority of species examined, in spite of the presence of the confounding variable, distance to seed sources. Common species (e.g. *Fraxinus* spp., *A. rubrum*) shared the relationship, suggesting that the influence of seed source strength continues across the range of source tree abundances, contrary to the findings of a computer simulation study (McClanahan, 1986). It is interesting that all three species not having this relationship were bird-dispersed. In light of the superior dispersal abilities of birds, it is possible that the source area considered did not encompass the area supplying seeds for these species and that, if it had, a relationship would have existed. This finding is consistent with Greene's (2000) significant correlation between source strength (tree basal area) and seedling density in strip cuts, with 50% of the variance explained. The finding has implications for land management and species conservation. First, it suggests that heavily fragmented systems with little forest cover may experience low seed rain densities because of both great interfragment distances and small source strength. Secondly, it indicates that rare species may be more extinction prone than common species in fragmented systems, regardless of their dispersal abilities.

#### Influence of vegetative connectivity

Connectivity had no influence on dispersal to plantations, perhaps because breaks in cover tended to be short (15–30 m

of open field or roadway) and were insufficient to deter animal passage. In systems with greater patch isolation, connectivity may become important. Other studies have shown that short breaks in cover such as roads bar small animal traffic (Oxley *et al.*, 1974; Mader, 1984; Gonzalez *et al.*, 1998). Nevertheless, connectivity seems to have little effect on dispersal in the present system where open expanses are brief. Distance to seed sources seems to be the critical biogeographical parameter influencing migration.

## CONCLUSIONS

This study provides information on the medium to long-range dispersal abilities of twenty-seven tree species and their associated dispersal syndromes. While estimates of dispersal distances are imprecise because of uncertainty of the exact whereabouts of particular source individuals, the study provides some of the only comprehensive, community-wide dispersal information for an eastern forest and is important in that it presents the first dispersal curves for animal-dispersal seed that we are aware of.

The species in the present study system generally exhibited low frequencies of dispersal over intermediate to long distances and some had no record of dispersal over more than a few tens of metres. Assuming that dispersal frequencies continue to decline beyond the 175 m measured in this study, fragments in highly dissected systems may have little propagule input, even by relatively efficient dispersers, and rarity will compound particular species extinction risks. The present study system is representative of fragmented eastern forests in the region (19% forest cover excluding Backus Woods, 39.8% including). Other eastern forests may be relatively more (e.g. New England forests; see Foster, 1992) or less heavily forested (e.g. parts of the Midwest; Curtis, 1956). Forest patches in the latter can be expected to experience much lower dispersal frequencies than those measured here because of the effect of source strength on the probability of dispersal. The dispersal frequencies measured here may thus be conservative for heavily deforested landscapes. Therefore, spontaneous processes of dispersal may be insufficient to sustain the tree diversity in heavily fragmented forests. This statement is based on the evidence that species require patch colonizations to be sustained over the long-term because of the prevalence of local extinctions (Goodman, 1987; Burkey, 1989).

These conclusions are somewhat at odds with the palaeorecord of rapid northward tree migration during the recent post-glacial period (Davis, 1987; Clark, 1998). However, it is reasonable to suppose that even rare long-range dispersal occurring at levels observed here would permit colonization and rapid spread in an undeveloped landscape largely open to tree establishment, but might be insufficient in modern landscapes with vastly reduced source and sink areas. Disruption of animal populations by human activity is another condition that may prevent historical tree migration patterns from being repeated.

Thus, management intervention may be necessary to promote tree colonization and maintain tree species populations

in fragmented forests. Small-scale reforestation and the planting of tree-rows are recommended to increase the strength and proximity of seed sources to fragments. However, for rare species and species with strong dispersal and establishment constraints, a strategy of artificial seed or seedling introductions may be required.

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