

Estimating dispersibility of *Acer*, *Fraxinus* and *Tilia* in fragmented landscapes from patterns of seedling establishment

W. Carter Johnson

Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061

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Abstract

Relative dispersibility of *Tilia americana* L., *Acer saccharum* Marsh. and *Fraxinus pennsylvanica* Marsh. was inferred from the ratio among species-specific regression coefficients (β) computed from seedling density-distance plots. Density counts were made in spatially-uniform old fields adjacent to single seed sources or monotypic fencerows. Resultant seedling shadow curves approximate the negative exponential form expected for many seeds ($\log y = a - OX$). This basic curve shape fit species of differing dispersibility, dispersal under a range of wind directions and one-year-old or all-aged cohorts. The ratios of β were 1:2.6:3.2 for *Tilia*, *Acer* and *Fraxinus*, respectively, in order of increasing dispersibility. Vegetation patches isolated from seed sources by several hundred meters or more should have extremely low input of seeds, especially *Tilia* and *Acer*.

The finding that *Fraxinus* disperses farther than *Acer* was unexpected, since the samaras of the former have faster terminal velocities. The relationship can be explained by better performance of *Fraxinus* samaras in the stronger winds experienced by trees in open landscapes, poorer formation of the samara abscission layer, and release of samaras following leaf abscission and during the winter when winds are the strongest. Both the samara plan and dispersal phenology need to be considered in estimating relative dispersibility among species.

Introduction

Emergence of the fields of island biogeography and landscape ecology has intensified the traditional interest of ecologists in seed dispersal (MacArthur and Wilson 1967; Burgess and Sharpe 1981; Forman and Godron 1986). Both emphasize that plant vagility (dispersibility) can affect the species richness and dynamics of habitat patches isolated by an inhospitable intervening matrix of water, strongly dissimilar vegetation or human land uses. Estimates of seed dispersal are needed to assess the future consequences of anthropogenic fragmentation (Curtis

1956; Risser *et al.* 1984) and to evaluate how well island biogeographic theory may apply to landscapes (*e.g.*, Middleton and Merriam 1983).

As a means of estimating seed dispersal by wind, a common analytical practice has been to graphically represent measured seed density along an axis of distance from a known point or area seed source. A variety of curve shapes results. Under experimental conditions when seeds are released *en masse* from a uniform height under stable winds the curve shape is typically right-skewed (Isaac 1930; Augspurger and Franson 1987). In numerous other studies, density-distance curves have been constructed to

evaluate the re-seeding potential of clear-cuts and strip-cuts (Ronco and Noble 1971; Franklin and Smith 1974; Randall 1974; Noble and Ronco 1978). Seed density curves in strip-cuts often approach an inverse j-shape; density initially decreases exponentially away from the leeward edge but then increases toward the inward side. A common curve for diverse groups of plants under natural conditions is the negative exponential form, *i.e.*, seed density decreases as a constant percent over equal units of distance (Werner 1975; Stergios 1976; Harper 1977; Dirzo and Dominguez 1986; McClanahan 1986).

For a given population of plants, both the height and slope of the dispersal curve may exhibit considerable annual variation. Curve height increases with increasing seed production and may or may not be accompanied by a significant change in slope. Noble and Ronco (1978) showed increasing slope with increasing seed crop for *Picea engelmannii* in clear-cuts, but Stergios (1976) showed little significant change in slope for *Hieracium* in different seed years. Annual differences in the frequencies of wind speeds have perhaps the greatest single effect on the slope parameter; slope percent generally increases with decreasing wind speed. Over a number of years, a population would exhibit a family of annual dispersal curves with regression coefficients exhibiting some measure of central tendency characteristic for the species. Thus, the slope parameter can be used to define the relative dispersibility of species and their colonization potential (Levins and Culver 1971; Levin 1977).

The obvious difficulty in obtaining good estimates of seed dispersal in nature for many species under varied environmental conditions has prompted use of experimental and modeling approaches. Seed fall velocity in calm air is easily measured and has been used as an index of relative dispersibility among species (Isaac 1930; Siggins 1933; McCutchen 1977). It is assumed that seeds with slow fall velocities would be carried by winds farther than those with fast fall rates, all other factors being equal. Additional parameters such as the stability of seeds in strong winds have also been considered (Green 1980, 1983). Fall velocity was integrated with climate in a detailed mathematical simulation model of seed dispersal by Sharpe and Fields

(1982). Dispersal curves and slope parameters can be estimated from such an environmentally-based model.

An alternative to extensive, long-term seed trapping experiments and to more experimental and modeling approaches in obtaining estimates of the slope parameter is to sample established seedlings and construct seedling density-distance curves analogous to those for seeds. The slope parameter of density-distance curves based on samples of seedling populations integrates dispersal since the year of initial seedling establishment. The relationship between seed dispersal and establishment is complex and variable, but the slope parameter of seed and seedling density-curves should be similar if the micro-environmental conditions for germination and survival and the spatial distribution of seed predators are both reasonably uniform along the distance axis. This requires careful selection of field sites.

This research had two major objectives: (1) to examine the correspondence between dispersal curves based on seedling-sapling numbers and the negative exponential model expected for the seeds of many plants, and (2) to use the above sampling approach to estimate relative dispersibility of heavy-seeded, wind-dispersed species (*Acer*, *Fraxinus*, *Tilia*) in the highly-fragmented forests of southeastern Wisconsin. Dispersibility coefficients could be ultimately utilized as one basis for predicting regional co-existence and altered successional trajectories potentially caused by anthropogenic patterning. Knowledge of dispersibility of species, along with competitive ability and local extinction probability (Christiansen and Fenchel 1977) is fundamental to predicting regional co-existence.

Methods

Abandoned agricultural fields with adjacent isolated seed trees or a single, monotypic fencerow of trees provided the best field conditions from which to construct recruitment curves. The two field sites selected were generally level with spatially-uniform land use. The *Acer* field site was a 2 ha pasture abandoned in 1971 and located near the North

Kettle Moraine State Forest in Ozaukee County, Wisconsin. The seed source was an isolated *Acer saccharum* Marsh. tree (7 dm dbh) located on a north-south fence line which formed the western border of the abandoned field. No mowing or grazing had occurred since abandonment. Field sampling occurred in October 1978.

Five transects were laid out along NE, ENE, E, ESE and SE compass directions emanating from near the canopy drip-line. Transects were all extended to the end of the field, but because of the radial pattern and shape of the field, transects were of variable length (45–120 m). Within each 10 m stratum on NE, E and SE transects, a 5 m long sample plot was randomly located. On ENE and ESE transects, 20 m strata were used. Sample plot width was 3 m in most cases, but when fewer than about 1 seedling/m² occurred, the width was increased to 5 m. Thus, sample plots were 15 m² and 25 m² in area. A total of 37 quadrats was sampled. All *Acer saccharum* reproduction within sample quadrats was counted and aged from terminal bud scars.

The *Fraxinus* field site was on the grounds of the University of Wisconsin-Milwaukee Field Station near Saukville. *Fraxinus pennsylvanica* Marsh. trees formed an east-west fencerow on the north border of a 6 ha corn field abandoned in 1964. Because the trees constituted a line seed source rather than a point source as was the case for *Acer*, parallel transects were arranged perpendicular to the fencerow in a S compass direction. Six transects each 130 m long were laid out at 20 m intervals. Quadrats 1 m x 5 m were randomly placed within each 10 m stratum. Sampling was conducted in October 1978.

Tilia americana L. dispersal was measured from a single large tree occurring in the mostly *Fraxinus* fencerow at the Field Station. Transects were laid out in S and SE compass directions. Seedlings were sampled in contiguous 2 m x 2 m quadrats until density declined to near 1 seedling/m²; the width of subsequent quadrats was enlarged to 4 m. Sampling occurred in late September 1979.

No reproductive individuals were observed in any of the above fields. All individuals were < 3 cm dbh. Tree height was similar for *Fraxinus* and *Tilia* [13.7 m (average of six trees) vs. 15.2 m, resp.],

while the *Acer* tree was somewhat taller (18.3 m).

Standard linear regression programs (Statistical Analysis System) were used on the IBM 3032 Computer at Virginia Polytechnic Institute and State University. Contour maps of seedling density were produced using SYMAP (Harvard University).

Results

Acer site

The site was well colonized by *Acer saccharum* reproduction, however, density near the seed source was unlikely so great as to cause disproportionately greater seedling mortality from intraspecific competition. A total of 1139 seedlings occurred in the 37 sample plots. Quadrat density ranged from 0–19 seedlings/m² with an average of 2/m². Densities were highest near the seed source and generally decreased monotonically towards the distal ends of the transects. Densities were roughly equivalent for corresponding strata on NE, E, ESE and SE transects; density was relatively high in stratum I on the E transect and low in the ENE transect.

The mapped patterns of seedling density were similar for both one-year-old (Fig. 1a) and all-aged (Fig. 1b) seedlings. This correspondence is in part due to the large proportion of one-year-old seedlings in the total population; one-year-old seedlings comprised about half of the total density. Classes of density around the seed source are generally concentric except where interrupted by the lower densities on the ENE transect. This low density trough does not appear to be due to relatively low wind speeds blowing towards the ENE; mean (1965–1974) wind speed of SW winds during October–November at Milwaukee was only slightly less than NW winds (4.7 vs. 4.9 m/sec, respectively – NOAA 1978). Moreover, the NW and SW winds exhibited highly similar frequencies in the standard wind speed classes. Depressed seedling densities were more likely due to the spatially non-uniform competitive influence of *Poa pratensis* sod which appeared especially dense and unbroken along the ENE transect. Data from this transect were excluded from further analysis.

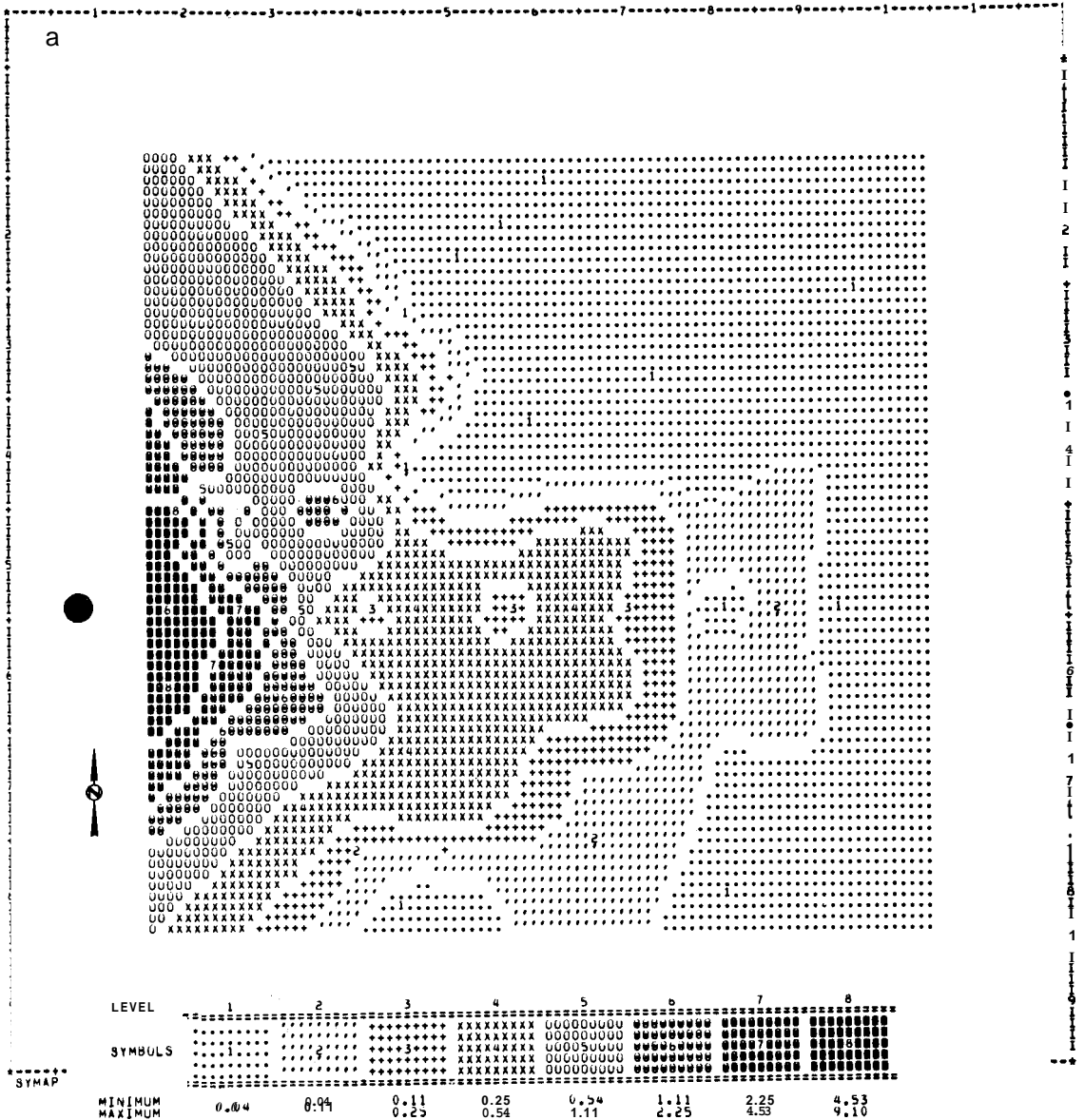


Fig. 1. One-year-old (a) and all-aged (b) seedling distribution pattern around an isolated seed source (large black dot) of *Acer saccharum*. Seedling density is number/m². Field length is 115 m.

Both one-year-old and all-aged seedling density curves approximated the negative exponential form, *i.e.*, by inspection the untransformed data clearly approximated a straight line when graphed in logarithmic series (Figs. 2–3). Moreover, the linear regression models exhibited high correlation coefficients (0.79–0.99) indicating a highly intense relationship between the log of *y* (seedling density)

and *x* (distance from the seed source). Six of the eight regressions exhibited values of *r* greater than 0.90. The fit was almost perfect in two transects (*r* = 0.99). Poorest fit was for the E transect due to greater variability in seedling density near the mid-range of distances. Curves for seedlings ≥ 2 years old (*i.e.*, excluding one-year-old data) had a similar form but correspondingly lower correlation coeffi-

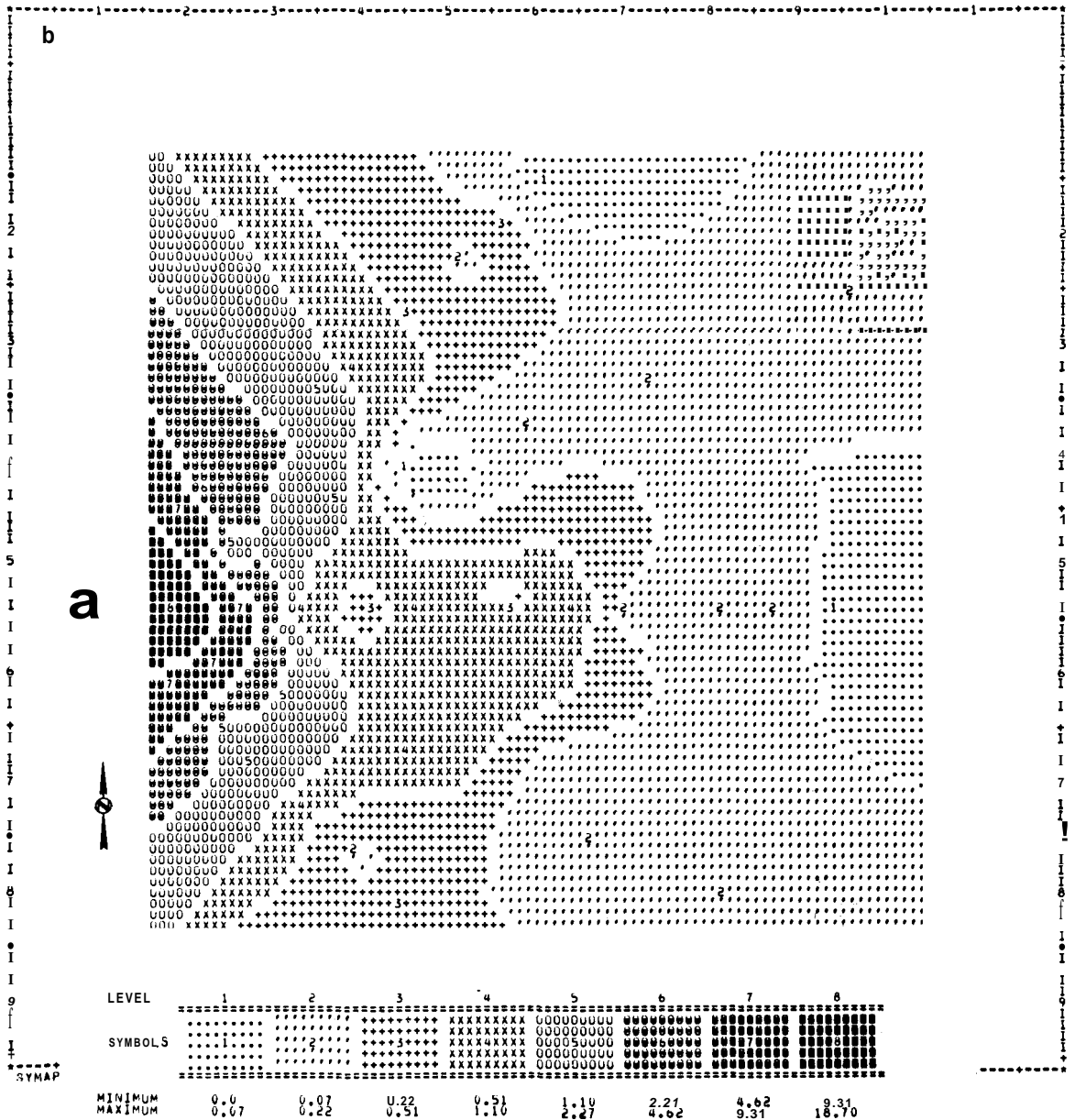


Fig. 1b

cients (0.91, 0.85, 0.65, 0.76, resp. NE to SE) except for transect E where the correlation coefficient was slightly higher than in the one-year-old data. Overall, there was a highly consistent curve form and correlation level ranging across compass direction and seedling age class.

Regression coefficients (β) ranged from -0.0175 to -0.0477 for one-year-old seedlings and from -0.0199 to -0.0329 for all-aged seedlings. Average

β for the one-year-old regressions (-0.0314) was smaller than for the all-aged regressions (-0.0253); however, β pooled values ($\Sigma Sxy/\Sigma Sxx$) were highly similar (-0.0256 and -0.0233 , resp.). The largest difference in average β occurred between one-year-old and \geq two-year-old regressions (-0.0314 and -0.0178). Larger β values (more gentle slope) would be expected for curves based on multiple dispersal seasons (e.g., all-aged data) compared to a

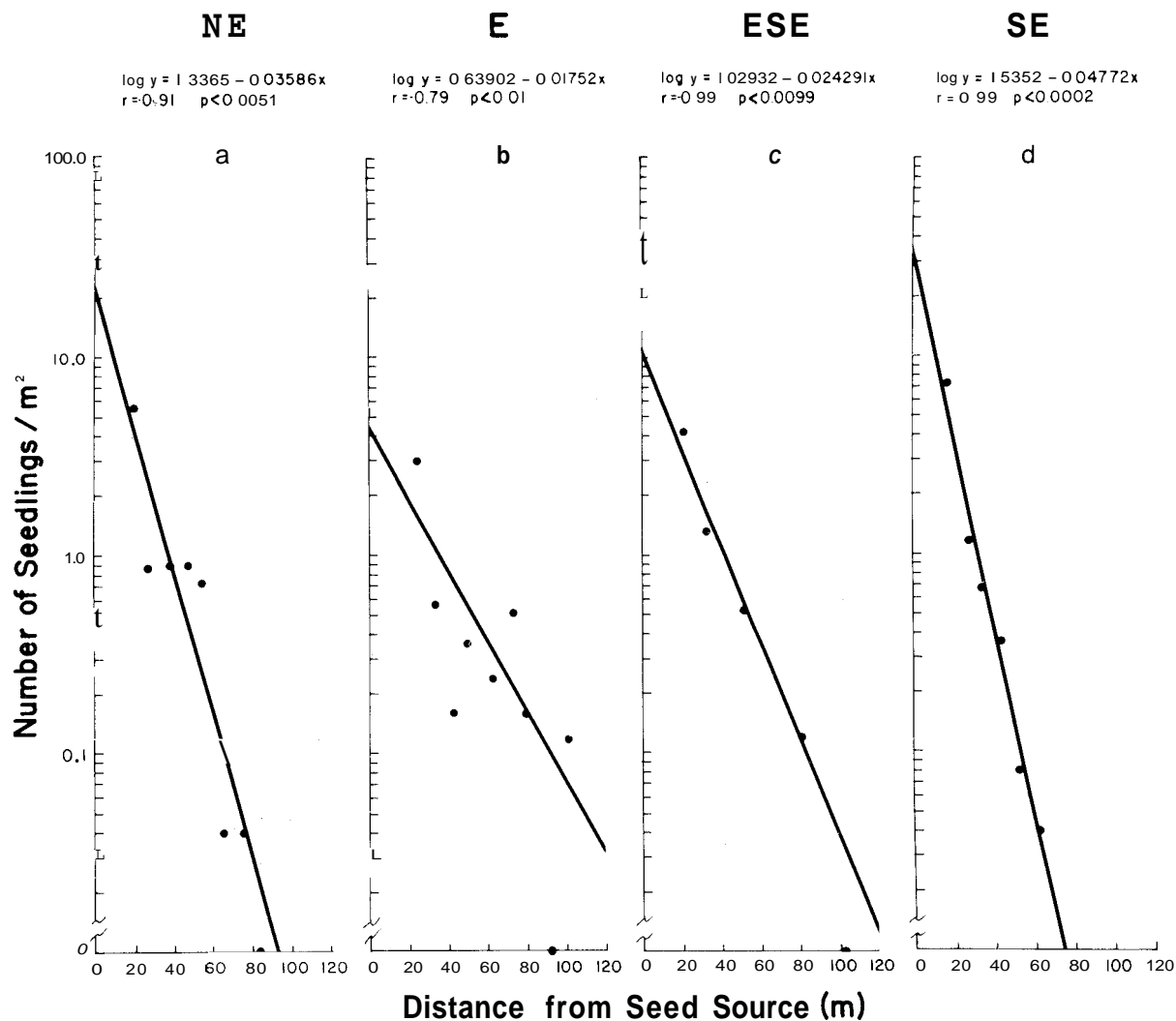


Fig. 2a-d. Density-distance distribution of one-year-old *Acer saccharum* seedlings along four compass directions (a-NE, b-E, c-ESE, d-SE) from an isolated tree. Y-axis scale is logarithmic.

single season (e.g., one-year-old cohort) because of the greater probability that the cumulative record would include stronger winds compared to any given year. The model for inter-specific comparisons should therefore be based on all-age data which integrate over a wider range of dispersal conditions.

Parallelism among the four regression lines (for both all-aged and one-year-old data) was rejected indicating that the slopes of regression were not statistically equivalent. Beta values correlated

strongly to wind speed parameters for corresponding wind directions. For example, a strong inverse relationship existed between β (one-year-old data) and average resultant wind speed ($r = -0.95$) and average wind speed of the fastest mile ($r = -0.97$) for NE, E and SE wind directions for October 1977 (NOAA 1977), the month when the bulk of the *Acer* seed was dispersed. Thus, as wind speed increased along a given vector, seeds were dispersed farther and computed β of the density of progeny increased.

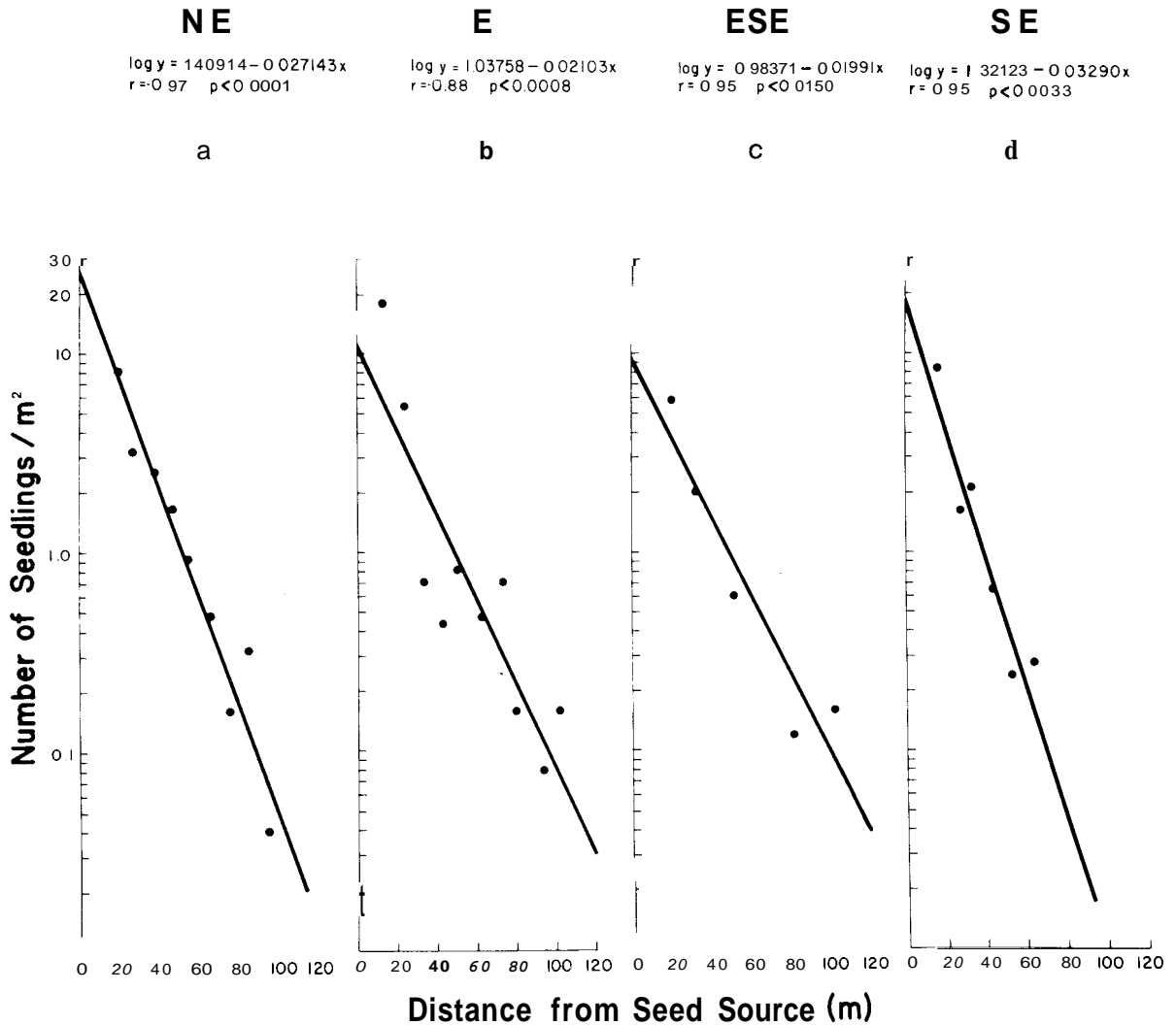


Fig. 3a-d. Density-distance distribution of all-aged *Acer saccharum* seedlings along four compass directions (a-NE, b-E, c-ESE, d-SE) from an isolated tree. Y-axis scale is logarithmic.

Fraxinus sile

Ash density ranged from 0–16 seedlings/m² with an average of approximately 3/m². A total of 1095 seedlings occurred in the sample quadrats. Densities were generally highest near the fencerow and decreased towards the distal ends of the transects. Seedling densities in the middle transects were roughly equivalent but were lower on transects nearest the edge of the sample area. These transects at the periphery of the seed shadow (transect nos. I, V, VI) were excluded from further analysis.

Transect nos. II, III, IV occurred well within the fencerow seed shadow and exhibited comparable total numbers of seedlings (219, 217, 152).

Data from the three transects were pooled because the transects were in effect sample replicates (parallel placement) rather than treatments (*i.e.*, different compass directions) as in *Acer*. Again as shown earlier for *Acer*, the untransformed data were arranged in linear fashion when graphed in logarithmic series (Fig. 4). The regression coefficient of -0.0102 was considerably larger than the pooled β for *Acer*, indicating a more gradual slope

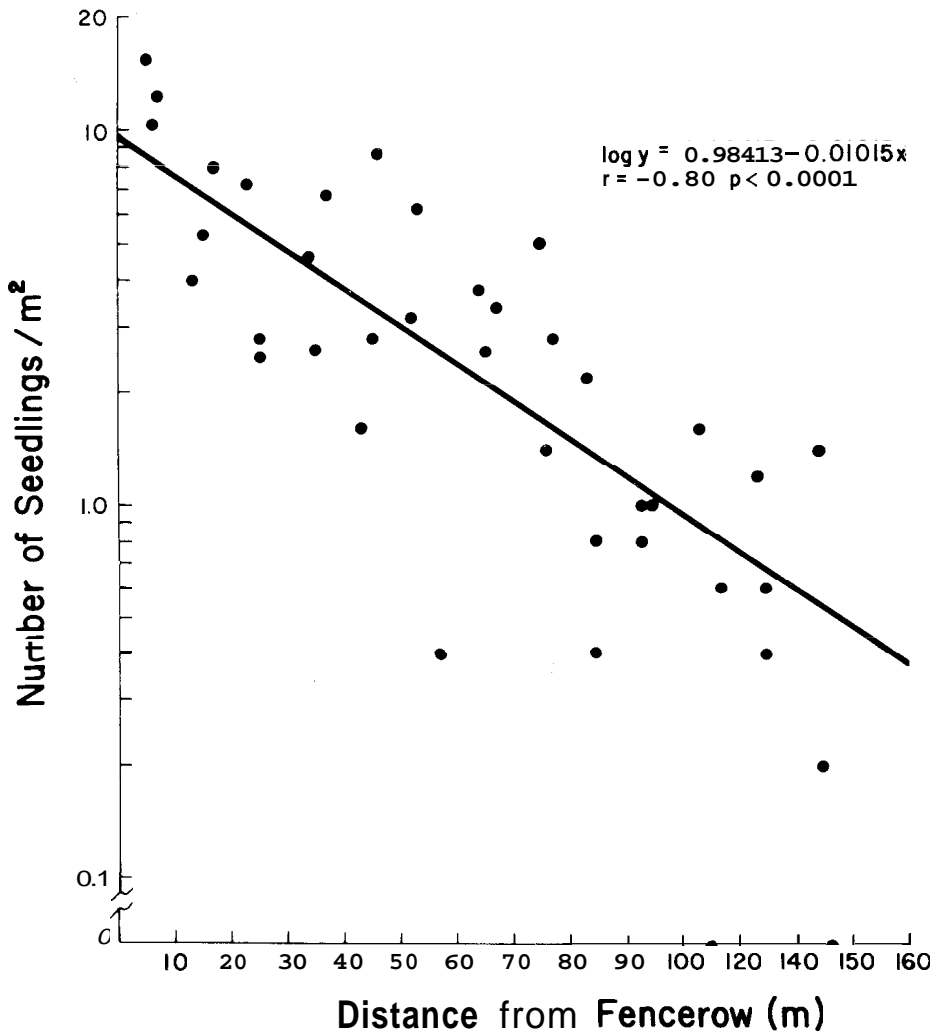


Fig. 4. Density-distance distribution of *Fraxinus* seedlings away from a fencerow. Pooled data are from three south-running parallel transects.

and therefore greater dispersibility for *Fraxinus*. The regression coefficient based on pooled data from the three middle transects was extremely similar to the regression coefficient from pooled data for all six transects (-0.0102 vs. -0.0107).

Tilia site

Data from the SE transect indicated interference from a young *Pinus* plantation located at the distal end of the transect. At 1 m distance, seedling density was $9/\text{m}^2$ dropping to near zero at 25 m, but then

increased to slightly less than $1/\text{m}^2$ along the portion of the transect occurring within the plantation. The upsurge in density was likely due to the decrease in wind speed associated with the plantation canopy and subsequent aggregation of seeds and seedlings at the leeward edge of the plantation. The S transect showed no interference because tree density in the plantation was far below that of the SE transect. Therefore data from the S transect were used to represent *Tilia* dispersibility.

Density of *Tilia* seedlings ranged from $0-10/\text{m}^2$ with a mean near $1/\text{m}^2$. No seedlings were recorded in quadrats beyond 21 m, although adjacent to the

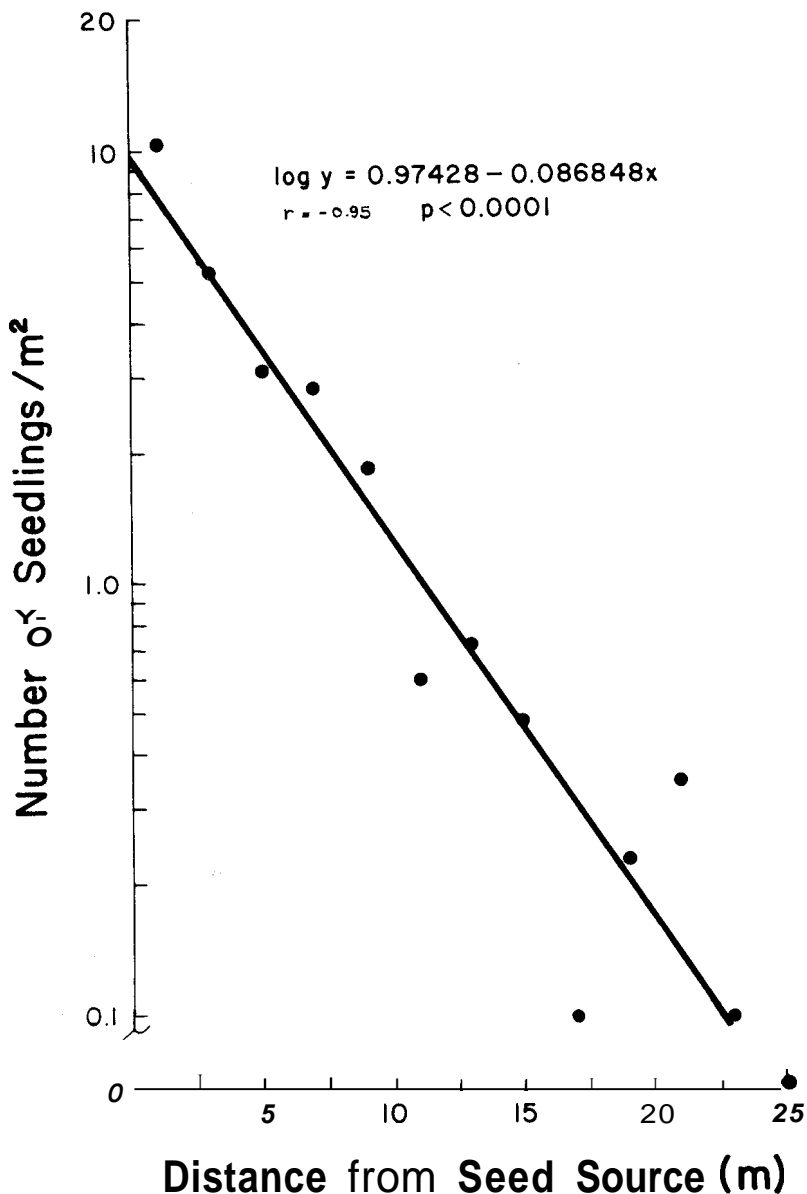


Fig. 5. Density-distance distribution of *Tilia* seedlings from a single seed source in a predominantly *Fraxinus* fencerow. Transect followed a SE compass direction.

transect a few seedlings occurred up to 26 m from the seed source. As was the case for *Acer* and *Fraxinus*, the *Tilia* data clearly approximated a straight line in logarithmic series (Fig. 5). The regression coefficient was small compared to those shown earlier indicating highly restricted dispersal. Again, there existed a strongly negative correlation with the log of y and x ($r = -0.95$, $p < 0.0001$).

Relative dispersibility

The regression lines (Figs. 2–5) reflect relative dispersibility when plotted together using the same intercept (Fig. 6). Curves for *Tilia* and *Fraxinus* represent dispersal by northerly winds. The most southerly transect available for *Acer* was SE (all-aged); the exact field conditions for south transects

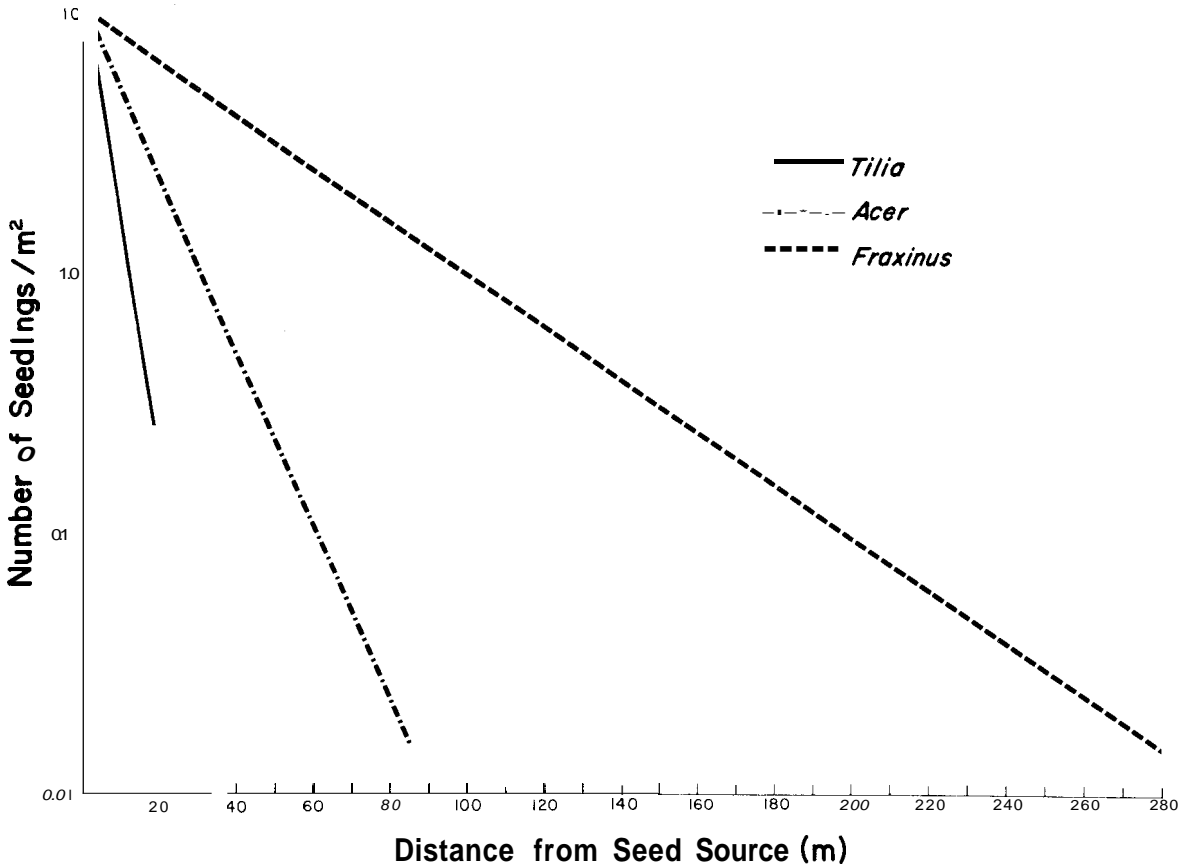


Fig. 6. Relative dispersibility of *Tilia*, *Acer* and *Fraxinus*. Linear regression equations for *Fraxinus* and *Tilia* are in Fig. 4 and Fig. 5, resp. *Acer* regression line is based on equation for SE compass direction (Fig. 3d). Regression lines to compare dispersibility are based on the same line intercept (10.0).

could not be found in the region. Mean wind speed of N and NW winds during the month of October 1977 (NOAA 1977) were nearly identical (5.2 vs. 5.1 m/sec, resp.).

The series of curves indicated the following relative order of dispersibility, from least to most: *Tilia*, *Acer*, *Fraxinus*. Quantitatively, β values indicated dispersibility ratios of 1:2.6:3.2, i.e., *Acer* exhibited a 2–3 fold greater dispersibility than *Tilia*, and *Fraxinus* exhibited about a three fold greater dispersibility than *Acer*. The ratio between *Acer* and *Tilia* may be a slight overestimate and between *Acer* and *Fraxinus* a slight underestimate because of the higher presumed release height for *Acer*. The dispersibility ratio between *Tilia* and *Fraxinus* was 1:8.3. The distance at which an order-of-magnitude decrease in density is reached would therefore be 12

m for *Tilia*, 31 m for *Acer* and 99 m for *Fraxinus*. Patches of vegetation farther than several hundred meters from sources of these relatively heavy, wind-dispersed seeds would have extremely low input of seeds.

Discussion

The β values reported represent near minima (i.e., maximum dispersibility) for each species under these field conditions. Slopes from relatively isolated seed sources should be flatter compared to forest interiors where wind speeds are reduced. Also, the β values were computed from seedling densities dispersed by northerly winds which exhibit the greatest average (1965–1974) wind speeds

(NOAA 1978). The ratios of dispersibility should remain relatively constant around the wind rose.

An important finding was the greater apparent dispersibility of *Fraxinus* than *Acer* (3.2: 1). The opposite would be predicted from fall rate; *Acer* has a lower terminal velocity (102 cm/sec) than *Fraxinus* (162 cm/sec) (Green 1980). McCutchen (1977) noted, however, that while the seeds of *Acer* should disperse farther in the low wind-speeds of forests, they are decidedly less stable in gusty, high-speed winds. *Acer* seeds descend like an autogiro, while *Fraxinus* seeds rotate about their long axis while also spinning around as they descend. Greater seed stability should produce greater dispersal of *Fraxinus* than *Acer* from isolated or fencerow trees exposed to the strongest winds in fragmented landscapes.

Differences between the species in dispersal phenology, not just in the samara plan, also help to explain the flatter seedling shadow for *Fraxinus*. To illustrate, the bulk of the *Acer* seed crop was dispersed in southern Wisconsin in late September through October before leaf abscission was complete. In northern Michigan, one-half of the seed crop had been dispersed by the end of September (Benzie 1959). *Fraxinus* seed, however, disperses after leaf abscission in November and continues through the winter months (Schopmeyer 1974). Average wind speed during *Acer* dispersal (Sept. – Oct.) was 7.0 m/sec and 8.1 m/sec during *Fraxinus* dispersal (Nov.–March) (NOAA 1978). The stronger winds during the dispersal of *Fraxinus* coupled with the greater average wind speed in the canopy due to the loss of foliage could have significantly increased dispersal relative to *Acer*. Moreover, the apparently poorly-formed abscission layer of *Fraxinus* samaras should have allowed release only during stronger winds, with the result that a larger portion of the seed crop was dispersed farther.

The results suggest that the relative dispersibility of species with different samara plans can shift substantially between forest conditions, where seed fall rate may be a good predictor, to the windier, more-turbulent conditions in highly-fragmented landscapes, where samara stability may be a more critical measure. While experimentally-derived mea-

asures of dispersibility based on seed morphology are of obvious value, they should be integrated with knowledge of the differences among species in dispersal phenology and in the meteorologic environment during the period of seed release.

Estimation of dispersibility using seedling shadows is time-efficient compared to seed trap studies. The approach also obviates the need to determine the amount of empty seed and germinability; the former can vary with dispersal distance (Stergios 1976 found greater dispersal of lighter, empty seeds of *Senecio*). It remains difficult in either approach to estimate dispersibility of very light wind-dispersed seeds (e.g., *Populus*) or dispersal of a small portion of the seed crop especially long distances under unusual meteorologic conditions. Measurement of dispersibility of animal-dispersed seeds requires special methods (Smith 1975, McDonnell and Stiles 1983; Johnson and Adkisson 1985; Holthuijzen 1985).

A drawback of the seedling shadow method to estimate plant vagility is that it requires finding seed trees next to spatially uniform sites which contain at least several cohorts of reproduction. In heavily-agriculturalized landscapes such as southeastern Wisconsin, however, few such sites untended by humans occurred. Replicate sites could not be found. The approach needs to be tried in landscapes where replicate, regenerating forests are more common. It is also difficult to determine the extent to which small, unapparent asymmetries in the environment or differences between line and single seed sources may have affected seedling shadows. Uniformity in seedling environment could be checked by sowing known number and quality of tree seeds in plots leading away from seed trees and monitoring predation, recruitment and seedling survival.

The ratios of dispersibility reported here can be used as coefficients in mathematical models of species' persistence in landscapes (e.g., DeAngelis *et al.* 1979; Johnson *et al.* 1981). Future use and refinement of these models in combination with improved parameter estimates from field experiments should improve our understanding of extinction potential in fragmented landscapes where propagule exchange among forest remnants has become

limited by the land use patterns imposed by humans. These results indicate that patches of vegetation farther than several hundred meters from sources of relatively heavy, wind-dispersed seed would have extremely low seed input.

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