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SEED DISPERSAL AND THE HOLOCENE MIGRATION OF WOODLAND HERBS

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Abstract. The distribution of many woodland herbs extends 1000–2000 km in a north–south direction, yet the majority of these species grow clonally, have little recruitment by seed, and possess no obvious mechanism for long-distance seed dispersal. Although aware that woodland herbs disperse poorly, ecologists have tacitly assumed that, given long periods of time, even small dispersal distances would allow woodland herbs to colonize the vast geographic region they now occupy. We examined this assumption for the understory herb *Asarum canadense.* To estimate long-term rates of spread by seed, we calibrated seed-dispersal diffusion models with life history data and with data on seed carries by ants. We supplemented our field observations and modeling results for *A. canadense* with a literature survey on the dispersal capabilities of other plant species.

Ants transported *A. canadense* seeds up to 35 m, the largest distance ants are known to move the seeds of any woodland herb. Empirically calibrated diffusion models indicated that over the last 16 000 yr *A. canadense* should only have traveled 10–11 km from its glacial refugia. In actuality, *A. canadense* moved hundreds of kilometers during this time. Models that examined the tail of *A. canadense*'s seed-dispersal curve indicated that occasional dispersal events had to have a high frequency ($\geq$0.001 on a per seed basis) and a large magnitude (dispersal distance $>$1 km) for *A. canadense* to have traveled over 200 km in 16 000 yr. The literature survey showed that most woodland herbs and many other forest, desert, coastal, and open-habitat plant species have limited seed-dispersal capabilities, similar to those in *A. canadense.* We conclude that woodland herbs, as well as many other plants, disperse so slowly that there is no documented mechanism by which most of these species could have reached their present geographical range since the last glacial maximum. This suggests that occasional events leading to long-distance dispersal dominate the Holocene colonization of northern temperate forest by woodland herbs, and this, in turn, has implications for issues ranging from the importance of genetic analyses to the structure of metapopulation models.

Key words: Asarum canadense; *diffusion models; Holocene migrations; long-distance dispersal; seed dispersal; woodland herbs.*

Introduction

Pollen records spanning the 16 000 yr since the last glacial maximum in North America and Eurasia indicate that tree species spread northward from refugia quickly and at different rates (Davis 1976, Delcourt and Delcourt 1987, Webb 1987, Birks 1989). As noted by Davis and others, these data have interesting ecological and evolutionary implications. For example, species-specific dispersal rates imply that the composition of tree communities has changed continually throughout the Holocene and that current communities may not have existed as recently as a few thousand years ago (Davis 1983). In contrast to the information on trees, little is known about how the distribution of herbaceous woodland species has changed over time. The relatively sparse, insect-borne pollen of woodland herbs appears much less reliably in pollen records than does the more abundant, wind-borne pollen of trees. Thus, our understanding of how woodland herbs colonized Northern temperate forests after the last glaciation remains sketchy even though these plants currently cover millions of hectares of understory habitat.

Investigations of the rate at which tree species moved northward following the retreat of the North American ice cap have revealed two discrepancies: the distances seeds move during standard dispersal events correlate poorly with estimated rates of migration, and only by assuming extreme, and presumably rare, seed movements can standard dispersal mechanisms account for the estimated rate of spread (Skellam 1951, Gleason and Cronquist 1964, Webb 1986, Johnson and Webb 1989, Greene and Johnson 1995, Wilkinson 1997; see also the round-table discussion in Bennett 1986). For the three genera of fagaceous trees (*Castanea*, *Fagus*, and *Quercus*), it has been suggested that unusually long-distance dispersal of nuts by Blue Jays (Johnson

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and Webb 1989) or Passenger Pigeons (Webb 1986) may help to resolve these discrepancies. We are not aware of comparable studies that examine the existence or magnitude of a discrepancy between known dispersal mechanisms and actual rates of long-term colonization in woodland herbs. Although it has been demonstrated that the spread of forest understory plants can be limited by dispersal (e.g., Peterken and Game 1984, Matlack 1994), such studies usually focus on small spatial and short temporal scales. We know of no papers that ask whether standard seed-dispersal mechanisms could have allowed temperate forest herbs to reach their present range over the course of the past 16 000 yr.

We find this question intriguing because the distribution of many woodland herbs extends 1000–2000 km in a north–south direction, yet the majority of these species grow clonally, have little recruitment by seed, and possess no obvious mechanism for long-distance seed dispersal (Bierzychudek 1982). As a result, the seeds of woodland herbs often move <1 m and only occasionally move more than a few tens of meters. In some instances, seeds of woodland herbs move such small distances that dispersal may serve primarily as a way of avoiding predators or locating suitable microhabitats rather than as a way of colonizing unoccupied habitat. For example, ant–plant mutualisms represent one of the most common modes of seed dispersal among woodland herbs (Handel et al. 1981). Although the transport of seeds by ants may provide plants with increased opportunities for germination (Handel 1978, Heithaus 1981, Kjellsson 1985*b*, Casper 1987, Levey and Byrne 1993), ants rarely move seeds more than a few meters. Hence, as dispersal agents ants move seed on a strictly local scale.

An examination of how woodland herbs reached their present range leads naturally to two additional issues. First, what is the importance of the tail of seed-dispersal curves, about which almost nothing is known (Portnoy and Willson 1993, Malanson and Armstrong 1996)? Ecologists usually ignore the tail of dispersal curves because long-distance dispersal events are by definition uncommon, and when they do occur, it is very difficult to follow them to completion. In the present study, we used movement models to examine the tails of dispersal curves. Specifically, we used models to test whether known mechanisms of seed dispersal in woodland herbs (such as ants or rodents) could reasonably account for actual, long-term rates of spread. Where standard mechanisms of seed dispersal could not account for observed rates of spread, we used models to estimate the frequency and distance of the occasional means of transport that must have occurred so that woodland herbs could colonize the vast geographic region that they now occupy. Second, if known dispersal mechanisms cannot explain the current distribution of woodland herbs, this opens the possibility that accidental, long-distance dispersal events, which may differ greatly from standard dispersal mechanisms, play a much more important role than is commonly thought. If true, this would have wide-ranging implications for a suite of ecological and evolutionary issues.

In this paper, we ask whether known dispersal mechanisms can account for the Holocene spread of the temperate woodland herb, *Asarum canadense* L. (wild ginger). To estimate long-term rates of spread by seeds, we calibrated seed-dispersal diffusion models with life history data and with detailed observations of individual seed movements. We supplement our results for *A. canadense* with a literature survey on the dispersal capabilities of other plants, and with results from models that examine the tail of dispersal curves for wild ginger and other herbs.

MATERIALS AND METHODS

Biology of Asarum canadense

A. canadense grows in the understory of deciduous forests extending from New Brunswick to southern Manitoba at the northern end of its range, and from North Carolina to eastern Kansas at the southern end of its range (Fernald 1970). *A. canadense* spreads vegetatively by rhizomes and produces geotropous, self-pollinated flowers. Seeds are produced in mid-June and weigh 13.7 mg (± 0.2 SE, $n = 50$). Like the seeds of many woodland herbs (Handel et al. 1981), *A. canadense* seeds bear elaisomes and are dispersed by ants. Heithaus (1986) reported that ants dispersed *A. canadense* seeds <1 m, a finding that agrees well with other ant-dispersal systems studied to date. More information about the biology of *A. canadense* can be found in Heithaus (1981, 1986), Muir (1995), Cain and Damman (1997), and Damman and Cain (1998).

Parameter estimation

We used demographic data and observations of seed carries by ants to calibrate diffusion models for the spatial spread of *A. canadense* over long periods of time. In particular, we needed to estimate two parameters from these data, r_m, the intrinsic rate of population increase, and D, the diffusion coefficient. Based on transition matrix analyses reported elsewhere (Damman and Cain 1998), we estimate the intrinsic rate of increase to be $r_m = 0.12$, which is the maximum value observed over 6 yr of study at four spatial locations. In the present paper, we estimated the diffusion coefficient (D) from data on the distance that ants transported *A. canadense* seeds. For this purpose, we observed 50 seed carries by ants at our study site in a sugar maple–beech–hemlock woodlot in Garreton, Ontario (latitude 44°50′ N, longitude 75°40′ W). We placed small piles of 10–20 *A. canadense* seeds on the forest floor in areas where *A. canadense* grew abundantly. We followed the movement of these seeds either directly by observing carries by ants during the day, or indirectly by noting the distance moved overnight by seeds marked with a fluorescent powder. The two approaches gave comparable results. From these data, we calculated the seed-dispersal diffusion coefficient (D) according to the relation $D = E[l^2]/4\tau$ (Okubo 1980), where $E[l^2]$ is the expected squared distance that ants carried *A. canadense* seeds and τ is the average time from the dispersal of a seed to its maturation as an adult ramet that itself can produce seeds. For *A. canadense,* Damman and Cain (1998) estimated τ = 10.1 yr.

Diffusion models

We used models of the long-term spread of woodland herbs to examine two questions: (1) is there a discrepancy between known dispersal capabilities and actual migration rates? And, if so, (2) how often and how far must unusual seed-dispersal events have carried the seeds of woodland herbs in order for these plants to have reached their present range? An answer to the first question could be obtained without resort to models, but a modeling approach is necessary to address the second question.

We modeled the long-term spread of *A. canadense* and other woodland herbs as a two-dimensional (homogeneous) diffusion process:

$$\frac{\partial n}{\partial t} = D\left(\frac{\partial^2 n}{\partial x^2} + \frac{\partial^2 n}{\partial y^2}\right). \tag{1}$$

In this formulation, $n(x, y, t)$ is the density of ramets that are located at coordinate position (x, y) at time t, and D is the diffusion coefficient (a measure of the long-term spread of populations) for dispersal by seed. Eq. 1 represents a reasonable method with which to model long-term displacements in *A. canadense* because there is no directional component to seed carries by ants over wild ginger's 10-yr generation time. Although the diffusion approach is reasonable, we cannot test its adequacy in detail because we lack time-profile data on the spread of *A. canadense* and other woodland herbs from known release points. Thus, in the discussion that follows we use diffusion models to illustrate general principles about the spread of woodland herbs rather than to predict in a precise way the movement of any particular species over long periods of time. Among various movement models that we could have used for this purpose, we selected diffusion models because they are biologically realistic (considerable backtracking in seed movement no doubt occurs) and because they provide a well-developed quantitative framework (see Okubo 1980 and Turchin 1998) with which to compare the movement of different species.

We also modified Eq. 1 to include a population growth term, $f(n)$:

$$\frac{\partial n}{\partial t} = D\left(\frac{\partial^2 n}{\partial x^2} + \frac{\partial^2 n}{\partial y^2}\right) + f(n). \tag{2}$$

The population growth term can take a variety of forms. For example, as populations expand into new habitat, it may be reasonable (Bennett 1986) to model population growth with a simple exponential growth term, $f(n) = r_m n$, or alternatively, with a logistic growth term, $f(n) = r_m n(1 - n/K)$. Our primary interest in this paper concerns the long-term rate of spread of woodland herb populations. With respect to Eq. 2, this means that we can ignore the functional form of $f(n)$ because similar results are obtained with exponential, logistic, and other population growth terms (Skellam 1951, Okubo 1980, Andow et al. 1990, Shigesada et al. 1995). In particular, under a variety of reasonable forms of $f(n)$, when time is large populations governed by Eq. 2 advance at an asymptotic rate of spread, c (with units of distance/time):

$$c = \sqrt{4r_m D} \tag{3}$$

where r_m is the intrinsic rate of increase of populations and D is the diffusion coefficient. Intuitively, it makes sense that the maximal rate of population advance (c) should depend not only on the rate of seed movement (D), but also on how rapidly populations grow (r_m) and hence disseminate large numbers of seeds.

Impact of occasional events

We incorporated occasional dispersal events into the diffusion-model approach described above in order to investigate the impact of unusual, long-distance dispersal events on the Holocene spread of woodland herbs. To do this, we specified the diffusion coefficient for local movements, the mean and variance of the distance that seeds were transported on occasional events, and the (per seed) frequency with which such occasional events occurred. We then recalculated the diffusion coefficient by weighting local and long-distance movements by the appropriate frequencies. Finally, we calculated an upper bound ($R_{\max}$) on the distance plants were likely to disperse by seed over long periods of time. Based on the asymptotic rate (c, defined in Eq. 3) of the spread of populations, we calculated $R_{\max}$ from the relation $R_{\max} = ct = \sqrt{4Dr_m}\,t$, where D is the diffusion coefficient weighted as just described. Advantages to this procedure include that it is simple to compute and that it allows ready comparison to results from diffusion models that do not include occasional dispersal events. A potential difficulty with this approach concerns its violation of the diffusion model assumption that movements consist of a large number of relatively homogeneous, small steps. In practice, however, violation of this assumption appears to make little difference. For example, when local movements have a mean (±1 SD) of 1.0 m (±1.0), and occasional, long-distance dispersal events occur with a frequency of 0.001 and have a mean (±1 SD) of 1000 m (±1000), the diffusion approximation described in this paragraph and a spatially explicit simulation of the movement process yield virtually identical net displacements over time (diffusion approximation: D =

482.3 m^2/yr, net displacement after 500 yr = 870.4 m; simulation: D = 481.8 m^2/yr, net displacement after 500 yr = 869.9 m).

We corroborated results from diffusion models with a spatially explicit simulation of the ‘‘scattered colony’’ model developed by Shigesada et al. (1995). In these simulations, local populations expanded radially at the rate c (defined by Eq. 3) and offspring colonies were established from the long-distance transport of seeds or other propagules. For each time step in the model, we kept track only of those offspring colonies that had dispersed the farthest from the refugia. We did this for two reasons: (1) our primary interest was in the maximum rate at which offspring colonies reached a given distance from the refugia, and (2) if this was not done the computer simulations ground to a halt due to the exponential production of offspring colonies. Relative to the diffusion approach described in the preceding paragraph, the ‘‘scattered colony’’ simulations have the advantage of directly modeling the spread of woodland herbs as a hierarchical movement process (local movements and occasional long-distance dispersal events). However, because of the extensive time period (16 000 yr) being modeled and the large number of offspring colonies produced, the simulations were very slow. In preliminary analyses, the two approaches gave similar results; thus, in this paper we relied on diffusion models because they were simpler to use.

Literature survey

A survey of the literature on distances dispersed by seeds provided an overview of the dispersal ability of woodland herbs as compared to plants of other growth forms and habitats. We included a study in our literature survey if it provided either an estimate of the mean or maximum distance from the parent plant over which seeds moved, or the data from which we could calculate such values. Dispersal distances reported for wind-dispersed plants usually represent estimates based on measurements of the rate at which seeds fall combined with assumptions about typical wind speeds in the plants’ natural habitat (e.g., Feekes 1936, Sheldon and Burrows 1973, Augspurger 1986, Matlack 1987). Because it is often difficult to document the long-distance movements that comprise the tail of a dispersal curve, the maximum distances in our literature survey represent underestimates of the true maximum distance that a seed can move. Many papers reported estimates of mean or maximum dispersal distances obtained under several different treatments. In such instances we selected the treatments that most closely mimicked natural conditions. When more than one treatment mimicked realistic conditions, we chose the conditions giving the longest dispersal distances. Because both the mean and maximum distances moved by the surveyed plant species showed highly skewed distributions, overall comparisons among plant classes and among modes of dispersal were made with the nonparametric Kruskal-Wallis test. Pairwise comparisons within the overall analysis were made with the nonparametric Mann-Whitney U test.

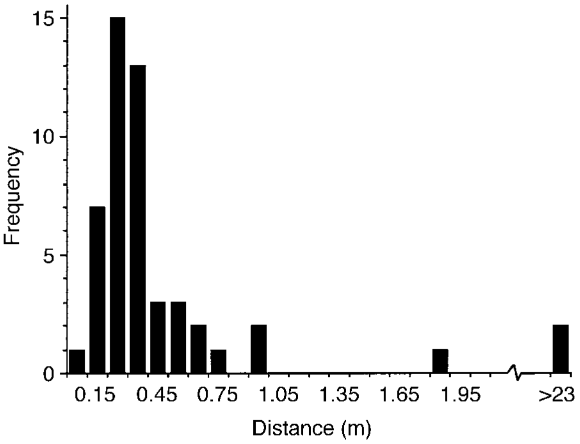

FIG. 1. Frequency distribution of the distance that ants carried *Asarum canadense* seeds. Except for the >23 m category, values on the x-axis are class midpoints.

RESULTS

Movement of Asarum canadense *seeds by ants*

Ants carried *A. canadense* seeds from 0.05 to 35 m (Fig. 1; mean ± 1 SD = 1.54 ± 5.84 m). The two long-distance carries that we observed (23.5 and 35 m) are the farthest we found reported for forest habitats and among the farthest we found reported for any ant–plant mutualism (Table 1; Appendix). Ants carried the seeds of two desert plants for distances greater than the maximum we observed for *A. canadense*: seeds in *Sclerolaena diacantha* (Davidson and Morton 1981) and *Datura discolor* (O’Dowd and Hay 1980) were dispersed by ants up to 77 and 39 m, respectively.

Long-term dispersal by seeds in Asarum canadense

We used the data on the distance ants moved seeds to calibrate diffusion models of dispersal in *A. canadense.* Our estimate for the diffusion coefficient ($D = E[l^2]/4\tau$ see *Materials and methods*) relied on detailed observations of individual behaviors (the distances ants carried seeds), not on mass-release or mark-recapture experiments. For ant-dispersed seeds in *A. canadense,* D = 0.89 m^2/yr.

We used field-calibrated diffusion models to calculate the distance *A. canadense* could spread by seed dispersal over long periods of time. In a simple diffusion process (Eq. 1), the probability (P) that at time t the net displacement (r) from a point of origin is greater than some value R is (Okubo 1980):

$$P = P\{r > R\} = e^{-R^2/4Dt} \qquad (4)$$

where t and D are as defined for Eq. 1. Eq. 4 may be rearranged to yield:

$$R = \sqrt{-4Dt\,\ln(P)}. \qquad (5)$$

TABLE 1. The effect of dispersal mechanism on the mean and maximum distances moved by the seeds of trees and herbs in woodland and open habitats. The 75th percentile and maximum values provide an estimate of the spread of the data around the median.

	Distance moved by seeds (m)							
	Mean distance				Maximum distance			
Dispersal mechanism	*n*	Median†	75th percentile	Max.	*n*	Median‡	75th percentile	Max.
Herbs								
Woodland								
Ant	15	1.38	1.96	9.00	12	4.00	5.25	35
Ballistic	3	1.50	2.64	3.02	4	3.40	4.03	4.55
Bird					1	33.0		
Wind	1	1.18			4	4.24	6.17	7.1
Water	1	275			1	400		
Open habitat								
Ant	1	0.0023			2	58.0		77
Ballistic	4	1.49	2.53	3.28	5	2.80	3.76	4.25
Adhesion	4	33.7	71.6	109	8	7.43	213	4423
Wind	25	1.37	2.50	25.7	83	12.0	137	10 000
None	13	0.500	2.04	7	39	7.00	34.0	380
Trees								
Ant	1	2.1			1	10.7		
Bat	2	56.3		75	2	185		270
Bird	9	23.73	850	14 300	11	200	3875	22 000
Rodent	5	10.3	13.8	20.6	5	51.5	89.5	151
Wind	5	16.9	33.7	45	72	165	319	3900

† Dispersal mechanism significantly affected the mean distance that seeds traveled: Kruskal-Wallis $\chi^2 = 33.3$, df = 9, $P < 0.0001$. Only dispersal mechanisms having more than one representative were included in the analysis.

‡ Dispersal mechanism significantly affected the maximum distance that seeds traveled: Kruskal-Wallis $\chi^2 = 89.7$, df = 11, $P < 0.0001$. Only dispersal mechanisms having more than one representative were included in the analysis.

For particular values of t and P, R represents an upper bound of the net displacement that is likely to occur by seed dispersal. We set $t = 16\,000$ yr and $P = 1/N(t)$, where $N(t) = N_0\exp(r_m t)$ was the size of a population that grew exponentially from time zero to time t (N_0 is the initial population size and r_m is the intrinsic rate of increase). By selecting t and P in this manner, over the last 16 000 yr only one plant from an exponentially growing population is likely to have traveled farther than R (Skellam 1951). Substitution of $P = 1/N(t)$ into Eq. 5 yields $R = \sqrt{4Dt(\ln N_0 + r_m t)}$. Note that for $N_0 = 1$, this equation reduces to $R = ct$, where c is defined by Eq. 3. Given the empirically observed values of $r_m = 0.12$/yr (see *Materials and methods*) and $D = 0.89$ m^2/yr, if we let $t = 16\,000$ yr and $N_0 = 1$, R equals 10.5 km. As discussed by Okubo (1980), the value of R varies little as N_0 is increased. For example, with r_m, D, and t held constant at the values just mentioned, R increases $<$0.1 km when N_0 is increased from one to 10^{12}. Because the value of N_0 has little practical effect, in results that follow we assume $N_0 = 1$, and thus, $R = R_{\max} = ct$, where $R_{\max}$ is as defined in *Materials and methods*: *Impact of occasional events.*

Our field-calibrated diffusion models indicate that *A. canadense* is likely to have dispersed a maximum of only 10–11 km during the past 16 000 yr. This estimate of the maximum distance moved depends on two empirically calibrated parameters: the intrinsic rate of population increase (r_m) and the diffusion coefficient (D). Because our estimate of r_m (0.12) may underestimate the true value, we examined the impact of r_m for a range of values that are reasonable for herbaceous plants (Silvertown et al. 1993). Even when $r_m = 1.2$, a value that is 10 times greater than our observed value and that exceeds all but one value reported in Silvertown et al. (1993), the maximum distance that *A. canadense* is likely to have dispersed is $<$35 km (Fig. 2A). Similarly, the diffusion coefficient (D) was estimated from dispersal data, and ants may disperse seeds farther than the longest carry (35 m) that we observed. We therefore calculated the upper bound for the distance *A. canadense* could disperse over long periods of time under a set of hypothetical, long-distance seed carries by ants. We assumed the hypothetical, long-distance carries occurred with a frequency of 0.001. On this basis we recalculated $R_{\max} = ct = \sqrt{4D_h r_m}\,t$, where D_h is a diffusion coefficient based on the (frequency-weighted) combination of empirical (Fig. 1) and hypothetical distances that ants could carry seeds. $R_{\max}$ was $<$100 km even for very unrealistic cases, such as hypothetical seed carries by ants on the order of 800–1200 m (Fig. 2B).

Literature survey

The relatively small mean and maximum dispersal distances that we report for *A. canadense* were typical of woodland herbs and herbs in general (Table 1; Appendix). The maximum dispersal distance reported for

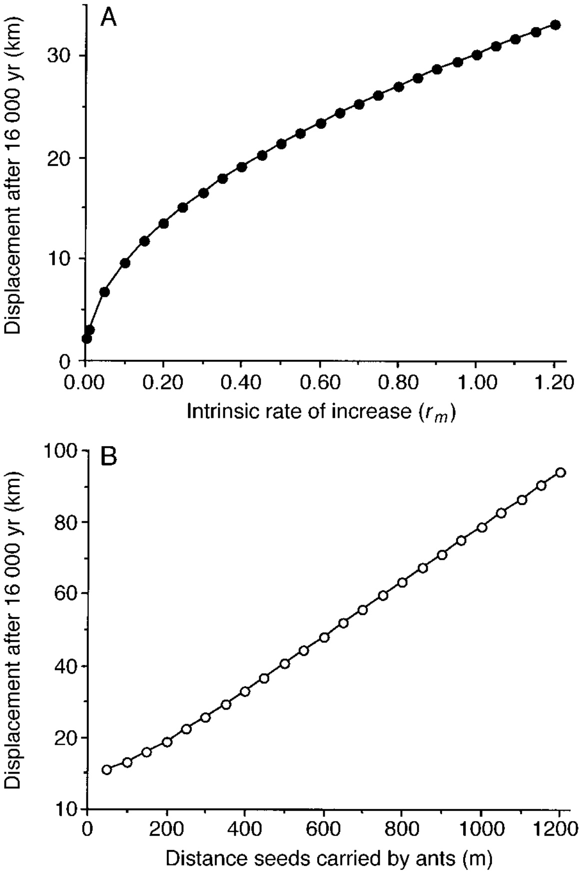

FIG. 2. The maximum displacement, $R_{\max}$ (km), traveled by *Asarum canadense* after 16 000 yr, as calculated from the relation $R_{\max} = \sqrt{4Dr_m}\,t$. (A) The impact of the intrinsic rate of population increase (r_m) on $R_{\max}$. The diffusion coefficient (D) was estimated from field data and equaled 0.89 m^2/yr. (B) The impact of hypothetical, long-distance seed carries by ants on $R_{\max}$. Values on the x-axis are the mean hypothetical long distance (m) that ants transport *A. canadense* seeds. For each of these values, the standard deviation in the distance that ants carried seeds was set equal to the mean, and the diffusion coefficient (D) was then estimated as described in *Materials and methods*: *Impact of occasional events.* The intrinsic rate of increase (r_m) was estimated from field data and equaled 0.12.

any woodland herb is 400 m for the water-dispersed seeds of *Mimulus guttatus* (Waser et al. 1982). After this species, the maximum dispersal distances reported for other woodland herbs are 35 m for the ant-dispersed seeds of *A. canadense* (this study), 33 m for the bird-dispersed seeds of *Phytolacca americana* (Hoppes 1988), and 17 m for the ant-dispersed seeds of *Sanguinaria canadensis* (Pudlo et al. 1980).

The mean dispersal distances of woodland herbs (median = 1.39 m, N = 20) were statistically indistinguishable from those of herbs growing in open habitats (median = 1.07 m, N = 47) (Mann-Whitney U test: Z = 0.93, P = 0.17). However, maximum dispersal distances were lower among woodland herbs (median = 4.0 m, N = 22) than among herbs growing in open, and presumably windier, habitats (median = 10.0 m, N = 137) (Mann-Whitney U test: Z = 1.94, P = 0.026). When pooled across seed-dispersal mechanisms, trees had greater mean (median = 16.1 m, N = 22) and maximum (median = 150 m, N = 91) dispersal distances than did herbs (mean: median = 1.20 m, N = 67; maximum: median = 7.59 m, N = 159) (Mann-Whitney U test: Z = 4.80, $P < 0.0001$ for mean distance, and Z = 8.19, $P < 0.0001$ for maximum distance).

Mean and maximum dispersal distances usually are collected within fairly homogeneous habitat, and hence, do not include the influence of barriers to dispersal. An alternative approach that does incorporate the impact of barriers to dispersal is to record the rate at which plants colonize recently available habitat. For example, Matlack (1994) measured the distance traveled from nearby source populations by woodland species that had migrated into second growth forests of known age. From these data Matlack calculated maximum yearly rates of spread for a variety of herbs, shrubs, and vines; these maximum migration rates represent a parameter similar to c (see Eq. 3). For *A. canadense,* Matlack reports a maximum yearly rate of spread of 0.59 m/yr. Extrapolated to 16 000 yr, this rate implies *A. canadense* would move 9.4 km, a figure in close agreement with the 10.5 km calculated from our diffusion models. If we take the largest rate of spread reported by Matlack (2.5 m/yr for *Potentilla canadensis*), in 16 000 yr a woodland herb moving at this (maximal) rate would disperse 40 km.

Impact of occasional events

We know of no data that address the frequency and distance of occasional dispersal events in woodland herbs. We used diffusion models to provide a preliminary assessment of the frequencies and distances that would allow woodland herbs to colonize Northern temperate forests over the past 16 000 yr. For models calibrated with data for *A. canadense,* occasional dispersal events had to have a high frequency ($\geq$0.001 on a per seed basis) and a large magnitude (dispersal distance $>$1 km) in order for *Asarum* to have traveled over 200 km in 16 000 yr (Fig. 3). Our literature survey (Appendix) indicates that *A. canadense* disperses as well as or better than most herbaceous plants; thus, the results in Fig. 3 may apply to most herbs. There are, however, exceptions: models consistent with published seed dispersal data for *Tussilago farfara* show that even in the absence of occasional dispersal events, *T. farfara* could have dispersed over 900 km in 16 000 yr (Fig. 4). For species with dispersal capabilities similar to *Tussilago,* occasional dispersal events have little impact unless they occur with high frequency and have a large magnitude; this is because the standard dispersal process already includes long-distance events.

As shown above for *A. canadense* (Fig. 2A), long-term displacements calculated from our diffusion mod-

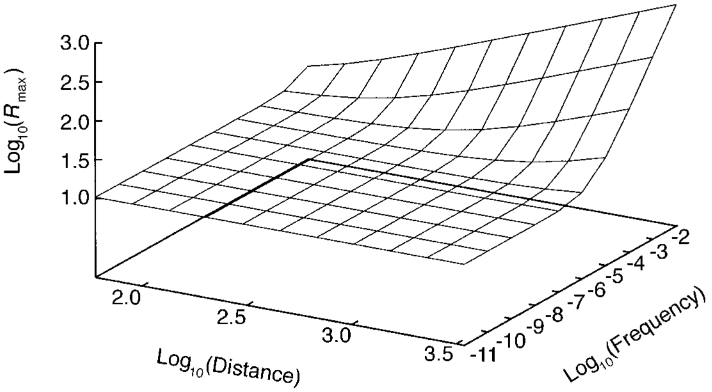

FIG. 3. The maximum displacement [$\log_{10}(R_{\max})$] traveled by *Asarum canadense* after 16 000 yr as a function of the frequency ($\log_{10}$) and distance (m; $\log_{10}$) that seeds are transported in long-distance dispersal events. $R_{\max}$ (km) was calculated as in Fig. 2; for these calculations, the intrinsic rate of increase (r_m) was estimated from field data and equaled 0.12.

els depend on the magnitude of the intrinsic rate of increase, r_m. This is evident from the relation $R_{\max} = \sqrt{4Dr_m}\,t$, where, on a logarithmic scale, r_m, D, and t have an additive effect on $R_{\max}$. When occasional dispersal events are incorporated into the estimate of the diffusion coefficient, D, it can be shown that

$$\ln(R_{\max}) = \ln\left(\frac{t}{\sqrt{\tau}}\right) + \frac{1}{2}\ln(r_m) + \frac{1}{2}\ln[(1 - f)(\sigma^2 + \mu^2) + f(\sigma_r^2 + \mu_r^2)] \quad (6)$$

where t is time, τ is the average time from the dispersal of a seed to its maturation as a seed-producing adult, f is the frequency of occasional dispersal events, μ and σ^2 are the mean and variance of the distance of standard dispersal events, and μ_r and σ_r^2 are the mean and variance of the distance of occasional dispersal events. Eq. 6 indicates that the population growth rate (r_m) and the frequency (f) and magnitude (μ_r) of occasional dispersal events exert complex, nonlinear effects on $R_{\max}$. For example, a graph of $R_{\max}$ vs. r_m has a characteristic shape: $R_{\max}$ increases with the square root of r_m. However, the relative impact of r_m, f, and μ_r varies greatly, depending on the value of these and other parameters in Eq. 6 (e.g., compare curves 1–3 in Fig. 5). Overall, results in Eq. 6 and Figs. 2–5 demonstrate that demographic parameters (e.g., those that determine r_m), the mean and variance of standard dispersal events, and the frequency, mean, and variance of occasional dispersal events have an individual and a joint impact on how rapidly plants colonize new geographic regions.

DISCUSSION

Holocene migration of Asarum canadense *and other woodland herbs*

Of the seed-dispersal mechanisms reported in the literature, wind dispersal, adhesion, bat dispersal, and bird dispersal appear to be the most likely to move seeds far enough to account for the postglacial recolonization of North America and Eurasia by plants (Table 1; Appendix). However, bird and wind dispersal, both of which have the potential to carry seeds long distances, can only rarely account for the estimated rate of spread of trees during the Holocene (e.g., Skellam 1951, Wells 1983, Chambers and Elliott 1989). In addition, long-distance dispersal events may be quite rare in some instances, even for bird- or wind-dispersed trees. For example, Webb (1987) presented evidence that the crossing of Lake Michigan by *Fagus grandifolia,* a tree with bird- or rodent-dispersed nuts, took almost 2000 yr and required jumps of between 25 and 130 km. Similarly, Greene and Johnson (1995) estimated that, even with their relatively mobile seeds, wind-dispersed trees growing in woodlots separated by

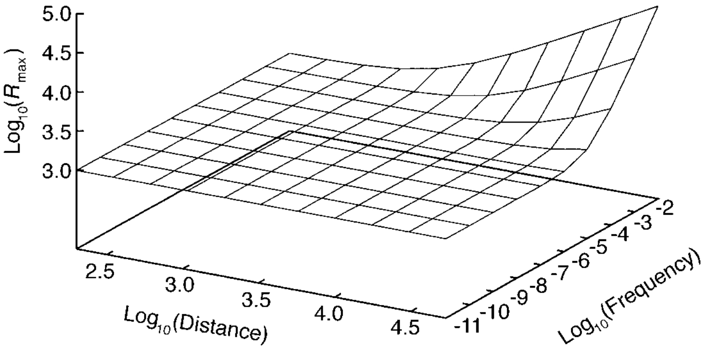

FIG. 4. The maximum displacement [$\log_{10}(R_{\max})$] traveled after 16 000 yr by plants with dispersal capabilities similar to *Tussilago farfara,* plotted as a function of the frequency ($\log_{10}$) and distance (m; $\log_{10}$) that seeds are transported in long-distance dispersal events. $R_{\max}$ (km) was calculated as in Fig. 2, with the exception that the intrinsic rate of population increase (r_m) equaled 0.225, the average value found in the literature review of Silvertown et al. (1993).

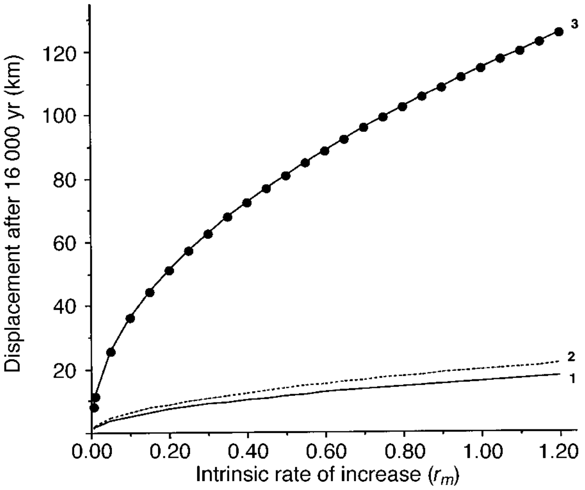

FIG. 5. The impact of the intrinsic rate of population increase (r_m) on $R_{\max}$ (calculated as in Fig. 2). The mean ± 1 SD of standard dispersal events in curves 1–3 was 1.4 ± 2.8 m; 1.4 m was selected as equal to the median value of mean dispersal distances reported for woodland herbs (see Appendix). The frequency and mean ± 1 SD of occasional, long-distance dispersal events in the three curves were as follows: 10^{-6} and 250 ± 500 m in curve 1; 10^{-6} and 1000 ± 2000 m in curve 2; 10^{-4} and 1000 ± 2000 m in curve 3.

>1 km would be effectively isolated for thousands of years.

Because of the lack of fossil pollen data for most woodland herbs, the minimum distance that *Asarum canadense* moved since the glacial maximum 16 000 yr ago is best estimated from the pollen record for trees that presently occupy the same habitats as *Asarum.* During the glacial maximum, refugia for trees that currently form the canopy of forests in which *A. canadense* grows (e.g., *Acer saccharum* and *Fagus grandifolia*) lay along the Gulf Coast of the southeastern United States (Watts and Stuiver 1980, Bennett 1985, Delcourt and Delcourt 1987). Delcourt (1979) provides evidence that *Fagus* may have had isolated refugia as far north as Tennessee. However, pollen records also clearly indicate that areas as far south as northern Georgia and the coastal plain of North Carolina were covered with boreal forest, a vegetation type indicating climates too severe for *A. canadense* today (Watts 1970, Ritchie 1987).

How far did *A. canadense* travel in the late-Glacial and Holocene? If its refugia coincided with those of *Acer saccharum, A. canadense* must have moved 700 km to reach the southern edge of its current range and 1900 km to reach the northern edge of its current range. Alternatively, if its refugia coincided with the isolated *F. grandifolia* refugia located in Tennessee, then wild ginger must have moved 100 and 1300 km to reach the current southern and northern edges of its range, respectively. It is possible that scattered *A. canadense* populations existed farther north than the isolated *Fagus* refugia. However, no refugia for *A. canadense* existed within 100 km of our study site: our study site and the surrounding area within at least 100 km were first covered by ice for up to 40 000 yr, then submerged under the saltwater Champlain Sea until ~12 000–10 000 yr ago (Terasmae and Mott 1959, Flint 1971). *A. canadense* exhibits little or no seed dormancy (Baskin and Baskin 1986). The lack of dormancy and the severity of the climate suggest that neither any seed nor any populations of *A. canadense* could have persisted north of the glacial front. Therefore, we estimate that during the past 16 000 yr *A. canadense* must have traveled a minimum of 450 km from the southern edge of the glacier to the northern edge of its current range.

Because ants cannot reasonably be posited to move *A. canadense* seeds as far as 100–450 km in 16 000 yr (Fig. 2), we infer that *A. canadense* reached our study site and the northern edge of its range by other means. This conclusion is strengthened by the fact that *Asarum* may have taken much less than 16 000 yr to arrive at our study site. For example, woodland herbs in the genus *Viola,* many of which rely on ants for dispersal and currently grow with *A. canadense,* arrived in southern Ontario at the same time as *Acer saccharum* (~8000 yr before present) (Schwert et al. 1985). If *A. canadense* reached southern Ontario as rapidly as *Viola,* this would make it all the more unlikely that wild ginger's northward migration was mediated by ants.

To generalize from *A. canadense* to the northward migration of other species, the majority of woodland herbs do not have morphological adaptations for long-distance dispersal by wind, adhesion, or ingestion. With very few exceptions, even the woodland herbs with such adaptations have low seed-dispersal distances (Appendix) and low yearly migration rates (Matlack 1994). Seed-eating birds rarely forage in the forest understory, and, in any case, most woodland herbs do not produce seeds until after migratory birds fly north (e.g., migrants pass through our study site in late April to early May, yet seeds are not available until mid-June or later). Although rodents cache seeds, they move seeds relatively short distances (<100 m) before burying them (Vander Wall 1993). Rodents eat the seeds of *A. canadense* and other woodland herbs, but in so doing destroy them. It is extremely unlikely that rodents would remove seeds, travel long distances, and then excrete or cache viable seeds. Finally, as the glaciers retreated most rivers flowed from north to south (Pielou 1991); hence, transport by water is not a plausible explanation of the Holocene migration of forest herbs. Thus, there are no documented dispersal mechanisms that account for long-distance dispersal in most woodland herbs.

To summarize, woodland herbs, even those with viable seed banks or refugia populations located just south of the glacial maximum, must have traveled 450 km or more in the past 16 000 yr. Thus, our results and literature review present a paradox: seed-dispersal data and yearly migration rates (Matlack 1994) indicate that most woodland herbs should have moved far less than 100 km over the past 16 000 yr, yet these species actually moved from 450 to 2000 km during this period. Given that there are no documented dispersal mechanisms that can account for this discrepancy, we conclude that occasional events leading to long-distance dispersal were of critical importance in the Holocene colonization of northern temperate forests by woodland herbs (see also Wilkinson 1997, who reached a similar conclusion for the postglacial migration of trees). Such occasional events could include meteorological accidents like tornadoes (Webb 1986) and hurricanes (Campbell 1983), and biotic accidents like the transport of seeds in mud clinging to the feet of vertebrates or the ingestion and subsequent excretion of viable seeds by birds that fly long distances (e.g., Darwin 1859, Webb 1986, Wilkinson 1997).

Implications of occasional, long-distance dispersal events

Our conclusion that occasional, long-distance dispersal events were necessary for the colonization of forest-understory habitat by woodland herbs highlights the importance of the tail of seed dispersal curves (see also Portnoy and Wilson 1993) and has several implications.

1) Population biologists long have argued for the importance of genetics in documenting unusual, long-distance dispersal events. Our results support this argument since they suggest that occasional dispersal events play a critical role. Genetics also may be very useful in discriminating between island and stepping stone models of dispersal; this distinction has considerable relevance for metapopulation models (see point 4 below). Furthermore, in principle genetic data could be used to disentangle the present-day frequency and magnitude of occasional dispersal events. To do this would require two steps. First, ecological data would be used to quantify seed dispersal and plant demography; this would allow estimation of parameters such as the intrinsic rate of population increase (r_m) and the diffusion coefficient (D), as we have done for *A. canadense.* Second, genetic techniques would be used to estimate the frequency with which alleles are transferred between widely separated populations. With such genetic and demographic data, it should then be possible to estimate both the frequency and distance of occasional dispersal events.

2) Several authors have noted that the limited dispersal of seeds in woodland herbs increases the likelihood that these species will adapt to local conditions (Levin and Kerster 1974, Waser et al. 1982). More generally, Ehrlich and Raven (1969) argued strongly that there was so little gene flow between populations that it was not useful to think of species as panmictic. Our results imply that occasional, long-distance dispersal events may be far more important than previously thought. Our diffusion-model results for *Asarum canadense* suggest that accidental, long-distance dispersal events occurred with a frequency of 0.001 or more (on a per seed basis). There are ∼30 000 *Asarum* ramets located at our study site; on average, 8% of these ramets flower each year and 11 seeds/flower are produced (Damman and Cain 1998). Assuming the frequency of long-distance dispersal events suggested by diffusion models applies to present-day populations, these data indicate that a minimum of 26 *Asarum* seeds are transported long distances from our study site each year by unusual means. Nothing is known, for *Asarum* or other woodland herbs, about the percentage of such distantly dispersed seeds that establish at new locations. In addition, there is little information on whether selection for locally adapted genotypes is strong enough to overwhelm the disruptive influence of gene flow. Overall, it remains an open question whether occasional, long-distance transport of seeds prevents the adaptation of woodland herbs to local conditions.

3) Previous studies suggest that dispersal can limit the range of many rare plant species (Peterken and Game 1984, Whitney and Foster 1988, Primack and Miao 1992). Our results support this contention because they indicate that even over long periods of time, rare woodland herbs would be unlikely to reach new habitat patches on their own. In addition, because it would take herbs a hopelessly long period of time to move long distances via the standard processes of seed dispersal, our results suggest that at large spatial and temporal scales, corridors may be of little consequence for the direct (unaided) dispersal of woodland herbs. Consistent with this suggestion, Helliwell (1975) and Fritz and Merriam (1994) found few forest-understory plants growing in hedgerows that could act as dispersal corridors. However, corridors may be of critical importance in allowing the movement of vertebrates, which in turn may act as important, if accidental, long-distance dispersal agents for woodland herbs. In general, because we cannot at present separate the frequency and magnitude of occasional dispersal events, we do not know whether such events would (a) allow rapid recolonization of regions in which local herb populations went extinct (Primack and Miao 1992), or (b) provide woodland herbs with a means of dispersal rapid enough to track projected global climate change (Davis 1989).

4) When occasional, long-distance dispersal events play an important role in colonization of habitat, then distance to the seed source and details of the dispersal mechanism may predict patterns of colonization poorly. For example, the equally rapid northward migration of some trees and herbs in the wake of the retreating glaciers (e.g., Schwert et al. 1985) suggests that typical seed-dispersal distances may tell us little about long-distance dispersal (see also Webb 1986). At a very different spatiotemporal scale, Dale (1989) reported that the density of wind-dispersed herb seeds arriving on a large debris avalanche bore no relationship to the

distance from the nearest seed source (where the distance was at least 100 m). In general, once the critical dispersal events involve improbable circumstances, distance from source populations may no longer effectively predict patterns of seed movement (unless the distances are very large). While studies of the colonization of oceanic islands long have accepted the importance of accidental dispersal (e.g., Carlquist 1967, Sorenson 1986), studies at smaller scales and investigations of dispersal within a continuous habitat emphasize more predictable events (e.g., seed-dispersal curves: Ribbens et al. 1994, Lavoral et al. 1995). Studying adaptations for seed dispersal probably allows us to understand how plants fill space within a colonized habitat, but not how plants first colonized the habitat patch. Because the majority of plant species rarely move distances >100 m, at intermediate spatial scales (e.g., 200 m to 20 km) the isolation-by-distance terms incorporated into many metapopulation models (Perry and Gonzalez-Andujar 1993, Hanski 1994, Thrall and Antonovics 1995, Malanson and Armstrong 1996) may distort rather than clarify predictions about colonization patterns for plants. However, at very large spatial scales (e.g., hundreds to thousands of kilometers), it is likely that the degree of movement between populations will decrease with distance. Overall, the spread of plant species and the extent to which isolated populations interact may perhaps best be modeled as a hierarchical movement process (dispersal curves at local spatial scales, ''island models'' at intermediate spatial scales, ''stepping-stone models'' at large spatial scales). The stratified diffusion model introduced by Shigesada et al. (1995) provides a recent example of such a model.

5) Most analyses in this paper focused on woodland herbs. However, our results probably apply to many other plant species. For example, even though maximum seed-dispersal distances for herbs that live in open habitats such as grasslands, montane meadows, deserts, and old fields can equal 10 km, our literature survey revealed that 74% of 137 herb species that lived in open habitats had a maximum dispersal distance that was <60 m (Appendix; see also Cheplick 1998). Given such limited dispersal distances, we suspect that occasional, accidental transport of seeds may be important in these plant communities as well.

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APPENDIX

Maximum and mean seed-dispersal distances as reported in the literature.

Species	Habitat	Growth form	Dispersal mechanism
Plants of forest understory and canopy			
Asarum canadense L.	forest	herb	ant
A. canadense L.	forest	herb	ant
Calathea ovandensis Matuda	forest	herb	ant
Carex pilulifera L.	forest	herb	ant
Sanguinaria canadensis L.	forest	herb	ant
Trillium ovatum Pursh.	forest	herb	ant
Viola blanda Willd.	forest	herb	ant
Viola cucullata Ait.	forest	herb	ant
Viola eriocarpa Schwein	forest	herb	ant
Viola odorata L.	forest	herb	ant
Viola papilionacea Pursh.	forest	herb	ant
Viola pedata L.	forest	herb	ant
Viola rostrata Pursh.	forest	herb	ant
Viola spp.	forest	herb	ant
Cnidoscolus stimulosus (Michx.) Engelm. & Gray	forest	herb	ant + ballistic
Crotalaria rotundifolia (Walt.) Poir.	forest	herb	ant + ballistic
Stillingia sylvatica (Muell. Arg.) Small	forest	herb	ant + ballistic
Carex pauciflora Lightf.	forest	herb	ballistic
Geranium maculata L.	forest	herb	ballistic
Impatiens capensis Meerb.	forest	herb	ballistic
I. capensis Meerb.	forest	herb	ballistic
Viola striata Ait.	forest	herb	ballistic
V. striata Ait.	forest	herb	ballistic
Phytolacca americana L.	forest	herb	bird
Mimulus guttatus Fisch. ex D. C.	forest	herb	water
Aster acuminatus Michx.	forest	herb	wind
A. acuminatus Michx.	forest	herb	win
Aster prenantoides Muhl.	forest	herb	wind
Eupatorium rugosum Houtt.	forest	herb	wind
Piper amalgo	forest	shrub	bat
Alnus crispa (Ait.) Pursh	forest	shrub	wind
Halesia monticola Sarg.	forest	shrub	wind
Purshia tridentata (Pursh) DC.	forest	shrub	rodent
P. tridentata (Pursh) CD.	forest	shrub	rodent
Acacia suaveolens (Sm.) Willd.	forest	tree	ant
Dipteryx panamensis (Pitt.) Rec. & Mell	forest	tree	bat
Casearia corymbosa H. B. K.	forest	tree	bird
Cornus controversa Hemsl.	forest	tree	bird
Fagus grandifolia Ehrh.	forest	tree	bird
Ficus stupenda Miq.	forest	tree	bird
Ficus subtecta Corner	forest	tree	bird
Pinus albicaulis Engelm.	forest	tree	bird
Pinus edulis Engelm.	forest	tree	bird
Pinus sp. & *Thuja* sp.	forest	tree	bird
Quercus palustris Muenchh.	forest	tree	bird
Virola surinamensis (Rol.) Warb.	forest	tree	bird
Fagus silvatica L.	forest	tree	rodent
Juglans nigra L.	forest	tree	rodent
Pinus jeffreyi Murr.	forest	tree	rodent
Quercus macrocarpa Michx.	forest	tree	rodent
Quercus muehlenbergii Engelm.	forest	tree	rodent
Acer palmatum Thunb.	forest	tree	wind
Acer pseudoplatanus L.	forest	tree	wind
Acer rubrum L.	forest	tree	wind
A. rubrum L.	forest	tree	wind
A. rubrum L.	forest	tree	wind
Acer saccharum Marsh.	forest	tree	wind
Acer cappadocicum	forest	tree	wind
Acer griseum Pax	forest	tree	wind
Acer platanoides L.	forest	tree	wind
Ailanthus altissima (Mill.) Swingle	forest	tree	wind
Albizzia julibrissum Durazzini	forest	tree	wind
Alseis blackiana Hemsl.	forest	tree	wind
Aspidosperma cruenata Woods	forest	tree	wind
Astronium graveolans Jacq.	forest	tree	wind
Betula papyrifera Marsh.	forest	tree	wind
Bombacopsis quinata (Jacq.) Dug.	forest	tree	wind
Bombacopsis sessilis (Benth.) Pitt.	forest	tree	wind
Carpinus caroliniana Walt.	forest	tree	wind

APPENDIX. Extended.

Treatment†	Dispersal distance (m)		References
	Maximum	Mean	
	35	1.54	present study
	0.94‡	0.8‡	Heithaus (1986)
with aril	3.25	1.14	Horvitz and Schemske (1994)
	1.4	0.4	Kjellsson (1985*a*)
	17	1.38	Pudlo et al. (1980)
	1.8	0.395	Mesler and Lu (1985)
	3.8	1	Beattie and Lyons (1975)
	2.1	1.5	Beattie and Lyons (1975)
	5.4	1.2	Beattie and Lyons (1975)
	0.02	0.01	Beattie and Lyons (1975)
	4.8	2.1	Beattie and Lyons (1975)
	5.1	1.4	Beattie and Lyons (1975)
	4.2	1.2	Beattie and Lyons (1975)
	1.5	0.75	Culver and Beattie (1978)
		9	Stamp and Lucas (1990)
		9	Stamp and Lucas (1990)
		9	Stamp and Lucas (1990)
		1	Hutton (1976)
	4.55	3.02	Stamp and Lucas (1983)
	1.7‡	0.24	Stamp and Lucas (1983)
	3.5		Primack and Miao (1992)
	3.3	0.79‡	Stamp and Lucas (1983)
	3‡	1.5	Beattie and Lyons (1975)
	33		Hoppes (1988)
water	400	275	Waser et al. (1982)
field data, open	5.25	1.18	Hughes et al. (1988)
10 km/h	5.08‡		Matlack (1987)
10 km/h	3.11		Matlack (1987)
10 km/h	7.1		Matlack (1987)
	700	37.8	Fleming (1981)
10 km/h	6.65		Matlack (1987)
10 km/h	18.5		Matlack (1987)
1° + 2° dispersal	20.96	9.55	Vander Wall (1994)
	16‡	6.21‡	Vander Wall (1995)
	10.75	2.1	Andersen (1988)
	100	75	Morrison (in DeSteven and Putz 1985)
	200		Howe (1977)
birds	42.5	15.32	Masaki et al. (1994)
	4000		Johnson and Adkisson (1985)
from trunk	75	6.67	Laman (1996)
from trunk	75	5.36	Laman (1996)
	3500	100	Hutchins and Lanner (1982)
	22 000	14 300	Vander Wall and Balda (1977)
	15 000		Reimers (in Vander Wall and Balda 1977)
	1900	1100	Darley-Hill and Johnson (1981)
	49		Howe et al. (1985)
	13	4.13	Jensen (1985)
	151	11.6	Stepanian and Smith (1986)
chipmunk	68.94	20.58	Vander Wall (1993)
	51.5	10.3	Stepanian and Smith (1986)
	45.3	6.4	Stepanian and Smith (1986)
10 km/h	11.6		Matlack (1987)
10 km/h	60.1		Matlack (1987)
	160‡		Green (1980)
10 km/h	98.7‡		Matlack (1987)
field	475		Greene and Johnson (1995)
	100		Green (1980)
10 km/h	48.2		Matlack (1987)
10 km/h	29.2		Matlack (1987)
10 km/h	50.3		Matlack (1987)
10 km/h	111.6		Matlack (1987)
10 km/h	16.2		Matlack (1987)
12.6 km/h	377		Augspurger (1986)
12.6 km/h	258		Augspurger (1986)
12.6 km/h	184		Augspurger (1986)
field	475		Greene and Johnson (1995)
12.6 km/h	324		Augspurger (1986)
12.6 km/h	88		Augspurger (1986)
10 km/h	19.4		Matlack (1987)

APPENDIX. Continued.

Species	Habitat	Growth form	Dispersal mechanism
Catalpa bignonioides Walt.	forest	tree	wind
Cavanillesia platanifolia (H. & B.) H. B. K.	forest	tree	wind
Cedrela odorata L.	forest	tree	wind
Ceiba pentandra (L.) Gaertn.	forest	tree	wind
Cespedizia macrophylla Seem.	forest	tree	wind
Chamaecyperis thyoides (L.) BSP.	forest	tree	wind
Cochlospermum vitifolium (Willd.) Spreng.	forest	tree	wind
Cordia alliodora (R. & P.) Cham.	forest	tree	wind
Couratari panamensis Standl.	forest	tree	wind
Dalbergia retusa Hemsl.	forest	tree	wind
Eucalyptus regnans F. Muell.	forest	tree	wind
Fraxinus americana L.	forest	tree	wind
F. americana L.	forest	tree	wind
Fraxinus excelsior L.	forest	tree	wind
Jacaranda copaia (Aubl.) D. Don	forest	tree	wind
Juniperus virginiana L.	forest	tree	wind
Lafoensia punicifolia DC.	forest	tree	wind
Larix laricina (DuRoi) K. Koch	forest	tree	wind
Liriodendron tulipifera L.	forest	tree	wind
L. tulipifera L.	forest	tree	wind
Lonchocarphus pentaphyllus (Poir.) DC.	forest	tree	wind
Lonchocarpus velutinus Seem.	forest	tree	wind
Luehea seemannii Tr. & Planch.	forest	tree	wind
Luehea speciosa Willd.	forest	tree	wind
Macrocnemum glabrescens (Benth.) Wedd.	forest	tree	wind
Myroxylon balsamum (L.) Harms	forest	tree	wind
Ochroma pyramidale (Cav. ex Lam.)	forest	tree	wind
Picea glauca (Moench) Voss	forest	tree	wind
Picea engelmannii Parry *ex* Engelm.	forest	tree	wind
Pinus contorta Loud.	forest	tree	wind
Pinus resinosa Ait.	forest	tree	wind
Pinus strobus L.	forest	tree	wind
Platanus occidentalis L.	forest	tree	wind
Platymiscium pinnatum (Jacq.) Dug.	forest	tree	wind
Platypodium elegans J. Vogel	forest	tree	wind
P. elegans J. Vogel	forest	tree	wind
Pseudobombax septenatum (Jacq.) Dug.	forest	tree	wind
Pseudotsuga menziesii (Mirb.) Franco	forest	tree	wind
Pterocarpus rohrii Vahl	forest	tree	wind
Tabebuia guayacan (Seem.) Hemsl.	forest	tree	wind
Tabebuia rosea (Bertol.) DC.	forest	tree	wind
Tachigalia versicolor Standl. & L. O. Wms.	forest	tree	wind
Terminalia amazonica (J. E. Gmel.) Excell in Pulle	forest	tree	wind
Terminalia oblonga	forest	tree	wind
Tilia americana L.	forest	tree	wind
Trichospermum mexicanum (DC.) Baill.	forest	tree	wind
Triplaris cumingiana Fisch. & C. Meyer	forest	tree	wind
Tsuga canadensis (L.) Carr.	forest	tree	wind
Vatairea erythrocarpa Ducke	forest	tree	wind
Parthenocissus quinquefolia (L.) Planch.	forest	vine	bird
Toxicodendron radicans Ktze.	forest	vine	bird
Vitis vulpina L.	forest	vine	bird
Clematis virginiana L.	forest	vine	bird
Plants of open habitats			
Cardamine resedifolia L.	montane	herb	ballistic
Achillea moschata Wulfen	montane	herb	none
Achillea nana L.	montane	herb	none
Agrostis rupestris All.	montane	herb	none
Arabis alpina L.	montane	herb	none
Cerastium arvense L.	montane	herb	none
Cerastium pedunculatum Gaudin	montane	herb	none
Poa alpina L.	montane	herb	none
Poa nemoralis L.	montane	herb	none
Sagina linnaei Pressl.	montane	herb	none
Saxifraga sp.	montane	herb	none
Sempervivum sp.	montane	herb	none
Silene rupestris L.	montane	herb	none
Trifolium dubium Sibth	montane	herb	none
Trifolium pallescens Schreber	montane	herb	wind

APPENDIX. Extended.

	Dispersal distance (m)		
Treatment†	Maximum	Mean	References
10 km/h	16.8		Matlack (1987)
12.6 km/h	224		Augspurger (1986)
12.6 km/h	410		Augspurger (1986)
12.6 km/h	314		Augspurger (1986)
12.6 km/h	775		Augspurger (1986)
10 km/h	68.8		Matlack (1987)
12.6 km/h	96		Augspurger (1986)
12.6 km/h	140		Augspurger (1986)
12.6 km/h	229		Augspurger (1986)
12.6 km/h	117		Augspurger (1986)
	150	30	Cremer (1965 in Harper 1977)
	70.71		Green (1980)
10 km/h	70.1‡		Matlack (1987)
10 km/h	40.3		Matlack (1987)
12.6 km/h	538		Augspurger (1986)
field	1200		Greene and Johnson (1995)
12.6 km/h	192		Augspurger (1986)
	80	4.54	Brown et al. (1988)
10 km/h	111.9		Matlack (1987)
	86.6‡		Green (1980)
one-seeded fruits	93	16.87	Augspurger and Hogan (1983), Augspurger (1986)
12.6 km/h	239		Augspurger (1986)
12.6 km/h	350		Augspurger (1986)
12.6 km/h	181		Augspurger (1986)
12.6 km/h	340		Augspurger (1986)
12.6 km/h	159		Augspurger (1986)
12.6 km/h	228		Augspurger (1986)
field	475		Greene and Johnson (1995)
field	200		Green and Johnson (1996)
	40	4.84	Greene and Johnson (1989)
field	475		Greene and Johnson (1995)
field	475		Greene and Johnson (1995)
10 km/h	62.8		Matlack (1987)
12.6 km/h	191		Augspurger (1986)
	110‡	45	Augspurger (1983*a*, *b*)
	137		Augspurger (1986)
12.6 km/h	139		Augspurger (1986)
field	800		Greene and Johnson (1995)
12.6 km/h	268		Augspurger (1986)
12.6 km/h	223		Augspurger (1986)
12.6 km/h	246		Augspurger (1986)
12.6 km/h	141		Augspurger (1986)
12.6 km/h	335		Augspurger (1986)
12.6 km/h	276		Augspurger (1986)
10 km/h	15		Matlack (1987)
12.6 km/h	147		Augspurger (1986)
12.6 km/h	211		Augspurger (1986)
field	1600		Greene and Johnson (1995)
12.6 km/h	176		Augspurger (1986)
	24	9	Hoppes (1988)
	33		Hoppes (1988)
	24		Hoppes (1988)
10 km/h	3.23		Matlack (1987)
	<1		Stöcklin and Bäumler (1996)
	<1		Stöcklin and Bäumler (1996)
	4		Stöcklin and Bäumler (1996)
	<1		Stöcklin and Bäumler (1996)
	<1		Stöcklin and Bäumler (1996)
	<1		Stöcklin and Bäumler (1996)
	<1		Stöcklin and Bäumler (1996)
	<1		Stöcklin and Bäumler (1996)
	50		Stöcklin and Bäumler (1996)
	10		Stöcklin and Bäumler (1996)
	40		Stöcklin and Bäumler (1996)
	<1		Stöcklin and Bäumler (1996)
	10		Stöcklin and Bäumler (1996)
	10		Stöcklin and Bäumler (1996)
	6		Stöcklin and Bäumler (1996)

APPENDIX. Continued.

Species	Habitat	Growth form	Dispersal mechanism
Adenostyles leucophylla (Willd.) Reichenb.	montane	herb	wind
Carex frigida All.	montane	herb	wind
Cirsium spinosissimum (L.) Scop.	montane	herb	wind
Epilobium fleischeri Hochst.	montane	herb	wind
Erigeron angulosus Gaudin	montane	herb	wind
Geum reptans L.	montane	herb	wind
Hieracium murorum L.	montane	herb	wind
Hieracium staticifolium All.	montane	herb	wind
Linaria alpina (L.) Miller	montane	herb	wind
Oxyria digyna (L.) Hill	montane	herb	wind
Ranunculis adoneus Gray	montane	herb	wind
Rumex scutatus L.	montane	herb	wind
Solidago aplestris Waldst. & Kit. ex Willd.	montane	herb	wind
Taraxacum officinale Weber.	montane	herb	wind
Tussilago farfara L.	montane	herb	wind
Rhododendron ferrugineum L.	montane	shrub	none
Alnus viridis (Chaix) DC.	montane	shrub	wind
Myricaria germanica (L.) Desv.	montane	shrub	wind
Salix spp.	montane	shrub	wind
Larix decidua Mill.	montane	tree	wind
Datura discolor Bernh.	desert	herb	ant
Sclerolaena diacantha (Nees) Benth.	desert	herb	ant
Sporobolus airoides Torr.	desert	herb	none
Artemesia herba-alba Asso	desert	herb	none
Cryptantha flava (A. Nels.) Payson	desert	herb	wind
Happlopappus squarrosus Hook. & Arn.	desert	shrub	ant
*Bursera graveolen*s	desert	shrub	bird
Lithospermum caroliniense (Walt.) MacMill.	dune	herb	none
Vulpia fasciculata (Forskål) Samp.	dune	herb	none
Geranium carolinianum L.	field	herb	ballistic
Geranium molle L.	field	herb	ballistic
Phlox drummondii Hook.	field	herb	ballistic
Achyranthes aspera L.	field	herb	adhesion
Bidens sp.	field	herb	adhesion
Petiveria alliaceae L.	field	herb	adhesion
Abutilon theophrasti Medic.	field	herb	none
Agropyron repens (L.) Beauv.	field	herb	none
Atriplex patula var. *hastata* L.	field	herb	none
Bromus inermis Leyss.	field	herb	none
Capsella bursa-pastoris (L.) Medic.	field	herb	none
Carex extensa Good.	field	herb	none
Carex sp.	field	herb	none
Dipsacus sylvestris Huds.	field	herb	none
Hypericum gentianoides (L.) BSP.	field	herb	none
Panicum miliaceum L.	field	herb	none
P. miliaceum L.	field	herb	none
Plantago aristata Michx.	field	herb	none
Plantago major L.	field	herb	none
Poa annua L.	field	herb	none
Poa pratensis L.	field	herb	none
Ranunculus scleratus L.	field	herb	none
Salicornia herbacea L.	field	herb	none
Stipa comatat Trin & Rupr.	field	herb	none
Suaeda maritima (L.) Dumort.	field	herb	none
Vulpia ciliata (Le Gall) Stace & Auquier	field	herb	none
Agrostis stolonifera L.	field	herb	wind
Andropogon glomeratus (Walt.) B. S. P.	field	herb	wind
Andropogon gyrans Ashe	field	herb	wind
Andropogon longiberbis Hackel	field	herb	wind
Andropogon virginicus L.	field	herb	wind
Apocynum cannabinum L.	field	herb	wind
Apocynum sibiricum Jacq.	field	herb	wind
Artemesia frigida Willd.	field	herb	wind
Asclepias syriaca L.	field	herb	wind
A. syriaca L.	field	herb	wind
A. syriaca L.	field	herb	wind
Apera spica-venti	field	herb	wind
Aster tripolium L.	field	herb	wind
Carduus tenuiflorus Curt.	field	herb	wind
Carlina vulgaris L.	field	herb	wind

APPENDIX. Extended.

Treatment†	Dispersal distance (m) Maximum	Mean	References
	85		Stöcklin and Bäumler (1996)
	<1		Stöcklin and Bäumler (1996)
	30		Stöcklin and Bäumler (1996)
	50		Stöcklin and Bäumler (1996)
	85		Stöcklin and Bäumler (1996)
	4		Stöcklin and Bäumler (1996)
	10		Stöcklin and Bäumler (1996)
	75		Stöcklin and Bäumler (1996)
	12		Stöcklin and Bäumler (1996)
	1		Stöcklin and Bäumler (1996)
		0.25	Scherff et al. (1994)
	12		Stöcklin and Bäumler (1996)
	4		Stöcklin and Bäumler (1996)
	50‡		Stöcklin and Bäumler (1996)
	20‡		Stöcklin and Bäumler (1996)
	25		Stöcklin and Bäumler (1996)
	70		Stöcklin and Bäumler (1996)
	100		Stöcklin and Bäumler (1996)
	100		Stöcklin and Bäumler (1996)
	15		Stöcklin and Bäumler (1996)
	39		O'Dowd and Hay (1980)
	77		Davidson and Morton (1981)
	15.2	3.33	Knipe and Springfield (1972)
0.25 m height	0.5	0.16	Friedman and Orshan (1975)
field data	31.3	2.36	Casper (1987)
	3		Louda (1982)
	35	7	Clark and Clark (1981)
	199	58.8	Westelaken and Maun (1985)
	0.21	0.07	Watkinson (1978)
	4.25	3.28	Stamp and Lucas (1983)
	2.8	1.78	Stamp and Lucas (1983)
	1.5	0.78	Stamp and Lucas (1983)
	4423.4	34.4	Bullock and Primack (1977)
		108.8	Bullock and Primack (1977)
	156.6	32.9	Bullock and Primack (1977)
	1.04		Primack and Miao (1992)
field		7	Hume and Archbold (1986)
20 km/h	55		Feekes (1936)
field	7	1.72	Hume and Archbold (1986)
20 km/h	35		Feekes (1936)
20 km/h	31		Feekes (1936)
field	3	1.07	Hume and Archbold (1986)
	1.5	0.2	Werner (1975)
	0.5		Primack and Miao (1992)
	1.5‡	0.5	McCanny and Cavers (1989)
	3		McCanny and Cavers (1987)
	18		Primack and Miao (1992)
20 km/h	38		Feekes (1936)
20 km/h	180		Feekes (1936)
20 km/h	25		Feekes (1936)
20 km/h	35		Feekes (1936)
20 km/h	36	0.13	Feekes (1936)
field	100	3	Hume and Archbold (1986)
20 km/h	380	0.10	Feekes (1936)
disturbed by walking	1.1	0.19	Carey and Watkinson (1993)
20 km/h	61		Feekes (1936)
10 km/h, 1 m height	13.8		Campbell (1983)
10 km/h, 1 m height	10.3		Campbell (1983)
	7.35		Campbell (1983)
10 km/h, 1 m height	8.6		Campbell (1983)
10 km/h	83.3		Matlack (1987)
field data		25.7	Platt and Weis (1977)
field	25	3	Hume and Archbold (1986)
10 km/h	18.1		Matlack (1987)
field data		13.8	Platt and Weis (1977)
field data, 1 m		11‡	Morse and Schmidt (1985)
20 km/h	140		Feekes (1936)
20 km/h	1500		Feekes (1936)
16.41 km/h	2.12		Sheldon and Burrows (1973)
16.41 km/h	1.47		Sheldon and Burrows (1973)

APPENDIX. Continued.

Species	Habitat	Growth form	Dispersal mechanism
Centaurea scabiosa L.	field	herb	wind
Cirsium arvense (L.) Scop.	field	herb	wind
Cirsium palustre (L.) Scop.	field	herb	wind
Cirsium undulatum (Nutt.) Spreng.	field	herb	wind
Cirsium vulgare (Savi) Ten. [=*Cirsium lanceolatum* Scop.]	field	herb	wind
C. vulgare (Savi) Ten.	field	herb	wind
C. vulgare (Savi) Ten.	field	herb	wind
Crepis biennis L.	field	herb	wind
Crepis virens L.	field	herb	wind
Epilobium angustifolium L.	field	herb	wind
E. angustifolium L.	field	herb	wind
Epilobium hirsutum L.	field	herb	wind
Epilobium palustre L.	field	herb	wind
Erigeron acer L.	field	herb	wind
Erigeron canadensis L.	field	herb	wind
Eupatorium cannabinum L.	field	herb	wind
E. cannabinum L.	field	herb	wind
Gentianella germanica (Willd.) Börner	field	herb	wind
Heterotheca latifolia Buckl.	field	herb	wind
Hieracium umbellatum L.	field	herb	wind
Holcus lanatus L.	field	herb	wind
Hypochoeris radicata L.	field	herb	wind
H. radicata L.	field	herb	wind
Juncus bufonius L.	field	herb	wind
Leontodon autumnalis L.	field	herb	wind
L. autumnalis L.	field	herb	wind
Liatris aspera Michx.	field	herb	wind
L. aspera Michx.	field	herb	wind
Liatris cylindrica Michx.	field	herb	wind
Mirabilis hirsuta (Pursh) MacM.	field	herb	wind
Oenothera biennis L.	field	herb	wind
Phragmites sp.	field	herb	wind
Physalis subglabrata Mackenz. & Bush	field	herb	wind
Rorippa islandica (Oeder) Borbás	field	herb	wind
Rumex obtusifolius L.	field	herb	wind
Scabiosa columbaria L.	field	herb	wind
Schizachyrium scoparium (Michx.) Nash	field	herb	wind
Senecio jacobaea L.	field	herb	wind
Senecio congestus var. *palustris* (L.) Fern.	field	herb	wind
Senecio squalidus L.	field	herb	wind
Senecio viscosus L.	field	herb	wind
Senecio vulgaris L.	field	herb	wind
S. vulgaris L.	field	herb	wind
Solidago altissima L.	field	herb	wind
Solidago missouriensis Nutt.	field	herb	wind
Solidago rigida L.	field	herb	wind
Sonchus arvensis L.	field	herb	wind
S. arvensis L.	field	herb	wind
Sonchus oleraceus L.	field	herb	wind
Spergularia media (L.) C. Presl. [=*S. marginata* (DC.) Kittel)]	field	herb	wind
Spergularia marina (L.) Griseb. [=*S. salina* J. & C. Presl.]	field	herb	wind
Taraxacum officinale Weber.	field	herb	wind
T. officinale Weber.	field	herb	wind
T. officinale Weber.	field	herb	wind
Tragopogon porrifolius L.	field	herb	wind
T. porrifolius L.	field	herb	wind
Tragopogon pratensis L.	field	herb	wind
Trifolium arvense L.	field	herb	wind
Tussilago farfara L.	field	herb	wind
Verbascum thapsus L.	field	herb	wind
Verbena stricta Vent.	field	herb	wind
Salix alba L.	field	shrub	wind
Salsola iberica	field	shrub	wind
Ulmus cprocera Salisb. [=*U. campestris*]	field	tree	wind
Andira inermis (W. Wright) H. B. K.	field	tree	bat
Prunus serotina Ehrh.	field	tree	bird
P. serotina Ehrh.	field	tree	bird
Acer negundo L.	field	tree	wind
Betula lenta L.	field	tree	wind

APPENDIX. Extended.

Treatment†	Dispersal distance (m) Maximum	Mean	References
16.41 km/h	1.56		Sheldon and Burrows (1973)
16.41 km/h	11.35		Sheldon and Burrows (1973)
16.41 km/h	6.81		Sheldon and Burrows (1973)
field data		18.4	Platt and Weis (1977)
20 km/h	900		Feekes (1936)
10 km/h	11.6‡		Matlack (1987)
field data	32	1	Klinkhamer et al. (1988)
20 km/h	350		Feekes (1936)
20 km/h	650		Feekes (1936)
20 km/h	10 000		Feekes (1936)
10 km/h	35.7‡		Matlack (1987)
20 km/h	3800		Feekes (1936)
20 km/h	7300		Feekes (1936)
16.41 km/h	3.61		Sheldon and Burrows (1973)
20 km/h	2500		Feekes (1936)
10 km/h	7.81		Matlack (1987)
16.41 km/h	5.89‡		Sheldon and Burrows (1973)
field	1.1	0.3	Verkaar et al. (1983)
disk seeds	5	1.65	Venable and Levin (1985)
10 km/h	3.03		Matlack (1987)
20 km/h	340		Feekes (1936)
20 km/h	1900		Feekes (1936)
16.41 km/h	2‡		Sheldon and Burrows (1973)
20 km/h	100		Feekes (1936)
20 km/h	610		Feekes (1936)
16.41 km/h	1.64‡		Sheldon and Burrows (1973)
	9.5	2.49‡	Levin and Kerster (1969)
	9‡	2.5	Levin and Kerster (1974)
10 km/h, 1 m height	9	2.5	Levin and Kerster (1974)
field data	2	0.41	Platt and Weis (1977), Platt (1976)
field data		1.83	Platt and Weis (1977)
20 km/h	2500		Feekes (1936)
10 km/h	1.47		Matlack (1987)
20 km/h	80		Feekes (1936)
10 km/h	2.48		Matlack (1987)
field	1.3	0.3	Verkaar et al. (1983)
10 km/h, 1.5 m height	4.11		Campbell (1983)
	36	2.5	Poole and Cairns (in Harper 1977), McEvoy and Cox (1987)
20 km/h	8800		Feekes (1936)
16.41 km/h	2.53		Matlack (1987)
16.41 km/h	2.57		Sheldon and Burrows (1973)
20 km/h	1200		Feekes (1936)
16.41 km/h	2.9‡		Sheldon and Burrows (1973)
10 km/h	14.9		Matlack (1987)
field	45		Hume and Archbold (1986)
field data		4.9	Platt and Weis (1977)
20 km/h	1100		Feekes (1936)
16.41 km/h	10‡		Sheldon and Burrows (1973)
16.41 km/h	6.56		Sheldon and Burrows (1973)
20 km/h	130		Feekes (1936)
20 km/h	340		Feekes (1936)
20 km/h	620		Feekes (1936)
16.41 km/h	2.27‡		Sheldon and Burrows (1973)
10 km/h	1.49‡		Matlack (1987)
10 km/h	5.77		Matlack (1987)
16.41 km/h	1.8‡		Sheldon and Burrows (1973)
20 km/h	1900		Feekes (1936)
10 km/h	0.75		Matlack (1987)
	4000		Bakker (in Harper 1977)
	13	4	Salisbury (in Harper 1977)
field data		1.03	Platt and Weis (1977)
20 km/h	6500		Feekes (1936)
tumbleweed, field data	4069	3050	Stallings et al. (1995)
20 km/h	330		Feekes (1936)
	104.4	37.63	Janzen et al. (1976)
	35	7.06	Smith (1975)
	9‡	1‡	Hoppes (1988)
10 km/h	41.1		Matlack (1987)
	85		Matlack (1989)

APPENDIX. Continued.

Species	Habitat	Growth form	Dispersal mechanism
Betula populifolia Marsh.	field	tree	wind
Populus sp.	field	tree	wind
Typha latifolia L.	marsh	herb	wind
T. latifolia L.	marsh	herb	wind
Phlox pilosa L.	prairie	herb	ballistic
Agrostis hiemalis (Walt.) B. S. P.	prairie	herb	wind
Andropogon gerardi Vitman	prairie	herb	wind
Andropogon scoparius Michx.	prairie	herb	wind
Festuca paradoxa Desv.	prairie	herb	wind
Setaria geniculata (Lam.) Beauv.	prairie	herb	wind
Silphium laciniatum L.	prairie	herb	wind
Sorghastrum nutans (L.) Nash	prairie	herb	wind
Sphenopholis obtusata (Michx.) Scribn.	prairie	herb	wind
Aristida congesta Roem & Scholt.	savanna	herb	adhesion
Cenchrus ciliaris L.	savanna	herb	adhesion
Schmidtia pappaphoroides Stend.	savanna	herb	adhesion
Setaria verticillata (L.) Beauv.	savanna	herb	adhesion
Tragus berteronianus Schult.	savanna	herb	adhesion
Eragrostis rigidior Pilger	savanna	herb	none
Panicum maximum Jacq.	savanna	herb	none
Urochloa mosambicensis Schult.	savanna	herb	none
Urochloa panicoides (Hack) Dandy	savanna	herb	none
Chloris virgata Sm.	savanna	herb	wind
Enneapogon cenchroides (Licht) C. E. Hubbard	savanna	herb	wind
Zostera marina L.	marine	herb	water
Z. marina L.	marine	herb	water
Z. marina L.	marine	herb	water

† When measured under more than one condition, we selected the seed-dispersal treatment that led to the greatest dispersal distance. Estimates of dispersal distances for plants bearing wind-dispersed seeds often depended on combining a measured rate of fall with typical infructescence heights and assumed wind speeds.

‡ Because we used only the largest mean or maximum dispersal distances, these values were excluded from the analyses.

APPENDIX. Extended.

Treatment†	Dispersal distance (m) Maximum	Mean	References
10 km/h	64.1		Matlack (1987)
20 km/h	3900		Feekes (1936)
20 km/h	5400		Feekes (1936)
10 km/h	46.9‡		Matlack (1987)
	3.6	1.2	Levin and Kerster (1974)
tumbling	11	2.22	Rabinowitz and Rapp (1979)
	0.19	0.06	Rabinowitz and Rapp (1981)
	0.11	0.03	Rabinowitz and Rapp (1981)
	0.29	0.08	Rabinowitz and Rapp (1981)
	0.39	0.11	Rabinowitz and Rapp (1981)
field data	2.75	1.09	Pleasants and Jurik (1992)
	0.24	0.06	Rabinowitz and Rapp (1981)
with glumes	0.46	0.08	Rabinowitz and Rapp (1981)
10 m/s	2.31		Ernst et al. (1992)
10 m/s	7.26		Ernst et al. (1992)
10 m/s	7.59		Ernst et al. (1992)
10 m/s	3.28		Ernst et al. (1992)
10 m/s	2.24		Ernst et al. (1992)
10 m/s	10.19		Ernst et al. (1992)
10 m/s	7.95		Ernst et al. (1992)
10 m/s	4.46		Ernst et al. (1992)
10 m/s	3.16		Ernst et al. (1992)
10 m/s	5.56		Ernst et al. (1992)
10 m/s	13.11		Ernst et al. (1992)
	200		Churchill et al. (1985)
	4.5‡		Orth et al. (1994)
	50‡	1.27	Ruckelshaus (1996)