

DISPERSAL OF *TRILLIUM* SEEDS BY DEER: IMPLICATIONS FOR LONG-DISTANCE MIGRATION OF FOREST HERBS

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Abstract. Theoretical models of plant range expansion require the assumption of occasional long-distance seed-dispersal events to explain post-glacial migration rates. For the many forest herbs whose seeds are dispersed primarily by ants, there are few documented mechanisms of occasional long-distance dispersal, so models of forest-herb migration have been largely phenomenological. Here we show that viable seeds of *Trillium grandiflorum*, an ant-dispersed forest herb in eastern North America, are dispersed via ingestion and defecation by white-tailed deer. We also use data from the literature on movement patterns and gut retention times to model a deer-generated seed shadow, showing that most seeds dispersed by deer should travel at least several hundred meters from parent plants, and occasionally >3 km. Our results provide a mechanism of long-distance dispersal that has likely contributed to rates of post-glacial migration and post-agricultural forest colonization.

Key words: ant dispersal; climate change and plant migration; deer, white tailed; dispersal biology; forest herbs, long-distance migration of; herbivore; migration; seed dispersal, long distance; seed shadow, deer generated; Trillium.

INTRODUCTION

The ability of plant species to track rapid climate change and to persist in highly fragmented landscapes depends critically on dispersal of seeds into suitable habitats. For temperate forest plants, an apparent paradox exists in that observed seed dispersal distances seem unable to explain post-glacial migration rates of up to several hundred meters per year as indicated by pollen records (Delcourt and Delcourt 1991) and consideration of current distributions in relation to the maximum extent of glaciers (Cain et al. 1998). This has been dubbed “Reid’s paradox” (Clark et al. 1998) after Reid (1899). A theoretical resolution of Reid’s paradox invokes rare, long-distance dispersal events that are unlikely to be observed in typical studies of seed dispersal, but that can produce realistic migration rates in models of post-glacial range expansion (Clark et al. 1998). The occasional migration of ant-dispersed herbs across hundreds of meters of open habitat into post-agricultural forests in less than a century (Matlack 1994) also requires long-distance dispersal. The consequences of long-distance dispersal have been the subject of numerous recent theoretical studies (e.g., Clark

1998, Clark et al. 2001), and are of intense interest given the implications for invasion dynamics, population genetic structure, and vegetation response to future climate change (Pitelka et al. 1997, Cain et al. 2000). However, while rare, long-distance dispersal events may resolve Reid’s paradox at a theoretical level, consideration of actual *mechanisms* by which seeds are occasionally dispersed long distances remains largely speculative and anecdotal.

The challenge posed by Reid’s paradox is particularly acute for the many forest herbs whose seeds have no known mechanisms of long-distance dispersal (Cain et al. 1998). For many forest herbs, ants are the primary means of seed dispersal (Handel et al. 1981), but most ant-dispersed seeds move only a few meters, and the longest recorded dispersal distance for a forest herb via ants is only 70 m (Sernander 1906). Vespid wasps have been observed dispersing seeds of ant-dispersed *Trillium* species in eastern North American forests (Zettler and Spira 2001), though not further than 30 m. Possible mechanisms of longer-distance dispersal for otherwise ant-dispersed species include mud on the feet of animals, tornados and hurricanes, or occasional ingestion and defecation by vertebrates (Cain et al. 1998). However, documented examples of such mechanisms are limited to only a few anecdotal reports for some European species (Ridley 1930, Müller-Schneider 1986), and there is a general lack of quantitative information

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TABLE 1. Locations, times, and numbers of *Trillium grandiflorum* seeds retrieved and germinated from feces of white-tailed deer.

Site†	Year	Range of dates of collection	No. pellet groups		No. <i>Trillium</i> seeds	
			Total collected	With <i>Trillium</i> seeds	Retrieved	Germinated
McGowan's Woods	2000	20 Jul–12 Aug	34	6	17	2
McGowan's Woods	2001	23–31 Jul	10	4	8	3
Schoolhouse Hill	2001	19–25 Jul	7	0	0	0
Bundy Road	2001	9–27 Jul	6	0	0	0
Trillium Woods	2001	12–18 Jul	9	4	11	2
Novak Woods	2001	13–27 Jul	7	0	0	0
Reynolds Woods	2001	13 Jul	1	1	1	0
Total			74	15	37	7

† All sites are in forests in the Ithaca, New York (USA), area.

on the distribution of dispersal distances such mechanisms can be expected to generate (Cain et al. 2000). Pakeman (2001) suggested that seed dispersal via ingestion by large mammalian herbivores is a likely candidate for long-distance dispersal of many temperate herbs, but at first consideration this seems an unlikely prospect for most ant-dispersed forest herbs in that their seeds are generally quite large relative to the small hard seeds typically found in mammalian herbivore feces (Janzen 1984). Large seeds without a hard seed coat are less likely than small hard seeds to pass undamaged through the chewing and digestive tract of a large herbivore.

In this paper we report the dispersal of viable seeds of *Trillium grandiflorum* (Michx.) Salisb., an ant-dispersed forest herb of eastern North America, via ingestion and defecation by white-tailed deer (*Odocoileus virginianus* Zimm.). In addition, we use data from the literature on movement patterns and gut retention times of white-tailed deer to model a deer-generated seed shadow. To our knowledge this is the first documented mechanism of long-distance seed dispersal (>1 km) for an apparently ant-dispersed forest herb in eastern North America.

METHODS

Field methods and germination trials

The impetus for this study came in July 2000 when, in a forest near Ithaca, New York, USA (McGowan's Woods), *Trillium grandiflorum* plants were found clipped below the sepals, suggesting frugivory by an unknown animal; the presence of a peduncle indicated that these had been reproductive individuals. Normally, in late July and early August, ripe fruits (slightly fleshy, whitish-green capsules) of *T. grandiflorum* split open from the bottom and fall to the ground, leaving behind three green sepals and three withered petals on a peduncle attached to the rest of the plant. White-tailed deer are abundant in central New York, as they are in

much of eastern North America (Halls 1984), and we hypothesized that the observed damage had been caused by browsing deer.

To investigate the possibility that white-tailed deer disperse *Trillium* seeds, we examined deer pellets collected from several forests. Thirty-four white-tailed deer pellet groups that appeared freshly deposited were collected from McGowan's Woods over eight different days during the fruiting period of *T. grandiflorum* between 19 July and 12 August 2000. An additional 39 pellet groups were collected from six forest stands (including McGowan's Woods) in the Ithaca area during 9–31 July 2001, with 1–10 pellet groups collected per stand (Table 1). *Trillium grandiflorum* was present in all stands, and abundance was particularly high in one stand, Trillium Woods. Pellet groups were washed individually by hand in a 0.5-mm sieve, and all *Trillium* seeds were retrieved. Seeds were also collected from ripe fruits in the field as germination controls; 10 control seeds were tested in 2000 and 50 seeds in 2001. All seeds were rinsed and placed on moist filter paper in petri dishes at 4°C for four months prior to germination trials. *Trillium grandiflorum* seeds are ellipsoidal, approximately 2 × 2 × 3 mm in size, and lack hard seed coats.

To test for germination (radicle emergence), seeds collected in 2000 were initially placed in a growth chamber and exposed to daily cycles of 15 h of light (10 μmol·m⁻²·s⁻¹) at 25°C and 9 h of darkness at 15°C. None of the deer-collected seeds or the 10 control seeds germinated in these conditions, and all of these seeds were subsequently placed at 4°C for an additional four months prior to the second germination trial. In this and subsequent trials, seeds were held at a constant 20°C in darkness, optimal germination conditions for *T. grandiflorum* (Solt 1996). Deer-collected seeds and the 50 control seeds collected in 2001 were placed directly into these optimal conditions following a 4-mo stratification period. Germination was scored weekly for three months.

Because *Trillium* seeds found in deer scat may be either *T. grandiflorum* or *T. erectum* L. (a less common species in the area), tissue extracts were made from all germinated seeds, and these extracts were run on starch gels to score phenotypes at two allozyme loci. As part of another study, loci that showed diagnostic banding patterns distinguishing *T. grandiflorum* from *T. erectum* were determined by scoring allozyme phenotypes for >400 individuals of *T. grandiflorum* from forests throughout central New York, including McGowan's Woods, and 30 individuals of *T. erectum* collected from McGowan's Woods (M. Vellend, unpublished data). Tissues were extracted in buffer 1 from Werth (1985) and absorbed onto filter paper wicks prior to electrophoresis. Phenotypes were scored for the diagnostic loci glutamate dehydrogenase (GDH) and phosphoglucuronate dehydrogenase (PGD) using a morpholine-citrate buffer system (see Wendel and Weeden [1989] for methods).

Seed shadows generated by deer

The seed shadow an animal can be expected to generate via endozoochorous dispersal will be a function of its gut retention times and movement patterns. We used literature data to estimate a deer-generated seed shadow by first calculating the following two matrices. **RT** is a $T \times 1$ matrix whose elements are the proportions of seeds defecated in each of T time intervals. **MOV** is a D (distance) $\times T$ (time) matrix whose elements represent the probability that a deer is within a given distance interval at a given time interval following ingestion of seeds; the columns of this matrix sum to 1. We used 100-m distance intervals, and 1-h time intervals. **MOV** \times **RT** gives a probability distribution for the distances that deer-dispersed seeds can be expected to move (i.e., a seed shadow). This seed shadow pertains only to the fraction of seeds dispersed by deer without specifying what this fraction is.

Several studies have investigated the retention time of chemically labeled foods in white-tailed deer digestive tracts (Mautz and Petrides 1971, Jenks and Leslie 1989, Barnes et al. 1992). The distribution of retention times after the first appearance of label is approximately log normal, and the compartment models of Pond et al. (1988) for passage through ruminant digestive tracts provide excellent fits to data (Jenks and Leslie 1989, Barnes et al. 1992). However, there is tremendous variation in retention time among trials. In 78 feeding trials for 22 different deer on a variety of diets in these studies, the time between feeding and first appearance of label in feces ranged from 9 h to 41 h, and the mean retention time from 12 h to 79 h.

Using a relatively "rapid" distribution of gut retention times is the most conservative approach to estimating a deer-generated seed shadow. This approach

is also realistic for *Trillium* in that its seeds are relatively large and heavy, and such seeds pass most rapidly through ruminant digestive tracts (Gardener et al. 1993). To estimate **RT**, we first fit the G2 two-compartment model of Pond et al. (1988) to a data set in Barnes et al. (1992) reporting the concentration of chemical label defecated over time ($r^2 = 0.99$). The G2 two-compartment model combines a gamma distribution of residence times in one digestive compartment, and an exponential distribution in a second digestive compartment (Pond et al. 1988). In order to have a distribution of retention times that could be combined with movement data (movement data are generally available only for 24-h periods—see next paragraph), we rescaled this distribution such that defecation begins 9 h after ingestion, and all seeds are excreted within 24 h. In the rescaled distribution, the proportion of seeds defecated was maximum between 11 h and 12 h following ingestion. This distribution was then used to calculate **RT** with 15 1-h time intervals.

Though the literature abounds with studies of deer movement in different regions and seasons (Marchinton and Hirth 1984), relatively few studies provide information on deer locations at a temporal scale that is comparable to gut retention times. We found nine studies that collectively provided diagrams of 87 movement pathways for 22 different white-tailed deer during time periods of 21–24 h (Progulske and Baskett 1958, Jeter and Marchinton 1964, Heezen and Tester 1967, Bridges 1968, Marshall and Whittington 1968, Byford 1969, Smith 1970, Kammermeyer 1975, Ivey and Causey 1981). These diagrams represent all seasons of the year, and five different states (Alabama, Florida, Georgia, Missouri, and Minnesota), with most diagrams consisting of lines connecting dots that represent locations determined hourly or every two hours by radio telemetry.

For each of the 87 movement diagrams we calculated the Euclidean distance from the first recorded location at hourly intervals in the following way. (Our assumption is that seeds are eaten at the first location, and defecated through time along the traveled path.) If exact times were not provided for each radio location, we assumed that locations were determined at equal intervals between 0 and 24 h. In Progulske and Baskett (1958), movement pathways were provided with no discrete locations indicated; for these diagrams, we assumed a constant rate of movement over each 24-h period. All times were then rounded to the nearest hour. If more than one location was provided for a given hour-long interval, we calculated the mean distance from the start. If no locations were provided for a given interval, we assumed a constant rate of movement between observed locations. Using the combined data

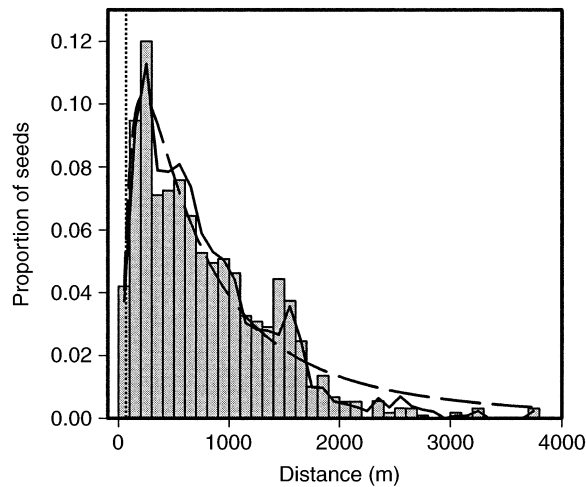


FIG. 1. Estimated distribution of distances expected for seeds dispersed by white-tailed deer. The bars represent the seed shadow estimated using literature data on movement patterns and gut retention times. The dashed line is the best-fit log-normal distribution to these data (Proportion of seeds = $0.1 \times \exp\{-0.5[\ln(\text{Distance}/219.8)/1.1]^2\}$); the solid line is the frequency distribution of all distances moved after an initial 9-h time delay (i.e., ignoring the distribution of retention times). The dotted vertical line shows the maximum observed seed dispersal distance via ants for a forest herb (70 m; Sernander 1906).

sets, we then calculated the elements of the **MOV** matrix with 100-m distance intervals up to 3800 m.

RESULTS

Across the 74 pellet groups examined, we found 37 *Trillium* seeds: 17 from McGowan's Woods in 2000, and 20 from the six sites in 2001 (Table 1). Two of the 17 seeds in 2000, and 5 of the 20 seeds in 2001 germinated, and were confirmed as *Trillium grandiflorum* based on their phenotypes at the two allozyme loci. Germination occurred for 9 of the 10 control seeds in 2000 and 46 of the 50 control seeds in 2001.

Virtually all seeds dispersed by white-tailed deer are expected to move further from the parent plant than the longest reported dispersal distance (70 m) via ants for a forest herb (Sernander 1906; Fig. 1). Most deer-dispersed seeds should move at least several hundred meters from parent plants, with <5% moving <100 m, and >25% moving >1 km (Fig. 1). The furthest distance observed in the data sets used here was 3730 m. The distribution of dispersal distances was approximately log normal ($r^2 = 0.92$), though the best-fit log-normal distribution overestimated the proportion of seeds moving the longest distances (>2 km). An excellent approximation to the seed shadow was provided by ignoring the distribution of retention times, and sim-

ply calculating the distribution of distances moved after the initial 9-h time delay (Fig. 1).

DISCUSSION

For fruits with no obvious morphological adaptations for dispersal by highly mobile animals or wind, there are numerous possible mechanisms of occasional long-distance dispersal (see *Introduction*). For temperate-zone plants, many of these mechanisms have been documented in a range of habitats, with examples coming almost exclusively from Europe (Ridley 1930, Müller-Schneider 1986). However, such documentations have been largely anecdotal, and rarely verified or quantified, likely due to the difficulty of repeatedly observing relatively rare events (Cain et al. 2000). To our knowledge, dispersal of viable *Trillium grandiflorum* seeds by white-tailed deer represents the first documented mechanism of long-distance dispersal (>1 km) for a primarily ant-dispersed forest herb in eastern North America.

We found *T. grandiflorum* seeds dispersed by deer in multiple sites (each separated by ~10 km) over two years in central New York, and our result is likely to hold in much of the range of *T. grandiflorum* in eastern and midwestern North America. Studies in Illinois (Anderson 1994), Minnesota (Augustine and Frelich 1998), and Wisconsin (Rooney 2000) have all demonstrated intense herbivory by white-tailed deer on *Trillium* species, and while plants are mostly eaten prior to seed ripening, herbivory continues through the period when seeds are ripe. Removal of *T. grandiflorum* fruits has been reported in Michigan by Kalisz et al. (1999), who attributed the removal to deer, and in southern Québec by Lubbers and Lechowicz (1989), who attributed it to an unknown animal. Jacobs and Jacobs (1997) hypothesized that deer may facilitate *Trillium* migration via seed dispersal, and Don Jacobs (*personal communication*) has retrieved germinable seeds of *T. cuneatum* Raf. from deer feces in Georgia.

The seed shadow based on movement patterns and gut retention times was closely approximated by the frequency distribution of all distances traveled between 9 and 24 h from the start of each pathway, without including information on the distribution of gut retention times (Fig. 1). This suggests that gut retention times do not exert an important influence over the seed shadow, apart from specifying minimum and maximum times for defecation following ingestion. The approximately log-normal shape of the distribution of movement distances is supported by at least two additional data sets. Hartless (2000) presented frequencies of movement distances over 5-d intervals for white-tailed deer in the Florida Everglades; the combined distribution for males and females was log normal ($r^2 = 0.99$) with a tail that extended farther (up to 10 km)

than in the data sets used here (as expected given the longer time intervals). The distribution of movement distances for white-tailed deer fawns over 15-h periods in Oklahoma was also approximately log normal ($r^2 = 0.94$), with movements up to a maximum of 1.2 km (Garner and Morrison 1977). Thus, the shape of the seed shadow presented in Fig. 1 is likely to apply quite generally to deer-dispersed seeds. The scaling of the distance axis is almost certain to vary both regionally and seasonally, but given that movement distances are often greater in summer than winter (Marchinton and Hirth 1984), the seed shadow estimated here is likely conservative for summer-dispersed seeds (i.e., *Trillium*). The tail of the distribution is also likely to extend considerably further than shown in Fig. 1, given that white-tailed deer have been reported moving >10 km in less than 24 h (Marchinton and Hirth 1984).

A full appreciation of the role of deer in plant migration will require additional studies on the range of species dispersed by deer, the proportion of fruits of particular species eaten, and the proportion of ingested seeds that are defecated intact and germinable (Pakeman 2001). Preliminary results of a detailed survey of seeds found in white-tailed deer feces (J. A. Myers, unpublished data) indicates that many herbaceous species with no obvious means for long-distance dispersal are also dispersed by white-tailed deer (no additional ant-dispersed species have been found). Numerous studies on other large herbivores also report viable seeds in feces (Pakeman 2001), but because seeds of many forest herbs (including *Trillium*) are relatively large, lack hard seed coats, and are produced in relatively small numbers (Bierzychudek 1982), they are unlikely to be found without intensive sampling efforts. *Trillium grandiflorum* is one of the more abundant forest herbs in central New York, and a preferred food of white-tailed deer. If other ant-dispersed forest herbs are also dispersed by deer, a sample size of pellet groups on the order of hundreds is likely to be required to demonstrate this. However, theoretical models make clear that even very occasional long-distance dispersal events can strongly influence rates of migration (Cain et al. 2000), so finding even small numbers of seeds is of great significance.

Trillium grandiflorum has been used as a model system in several population genetic studies (Kalisz et al. 1999, 2001, Irwin 2001), and seed dispersal by deer provides a mechanistic basis for interpreting large-scale patterns of genetic structure. While ant dispersal has important implications for genetic structure of *T. grandiflorum* at a small spatial scale (~0.02 ha, Kalisz et al. 1999, 2001), ants do not move the seeds much more than 10 m from parent plants (Kalisz et al. 1999), and cannot explain apparently high gene flow among more distant populations (>1 km apart, Irwin 2001).

Deer are clearly implicated in gene flow over large distances in *T. grandiflorum*, and perhaps in other ant-dispersed forest herbs as well.

In conclusion, seed dispersal via ingestion and defecation by deer provides a mechanism of long-distance dispersal that has likely contributed to rates of post-glacial migration (Cain et al. 1998, Pakeman 2001) and post-agricultural forest colonization (Matlack 1994). Seed dispersal by deer is amenable to quantification, and can therefore be used to model migration under different scenarios of future climate change. Seeds dispersed by deer represent the tail of *T. grandiflorum*'s seed shadow, but even this tail appears to have a tail of its own.

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