

Empirical Evidence of Long-Distance Dispersal in *Miscanthus sinensis* and *Miscanthus* × *giganteus*

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Many perennial bioenergy grasses have the potential to escape cultivation and invade natural areas. We quantify dispersal, a key component in invasion, for two bioenergy candidates: *Miscanthus sinensis* and *M. × giganteus*. For each species, approximately 1×10^6 caryopses dispersed anemochorously from a point source into traps placed in annuli near the source (0.5 to 5 m; 1.6 to 16.4 ft) and in arcs (10 to 400 m) in the prevailing wind direction. For both species, most caryopses (95% for *M. sinensis* and 77% for *M. × giganteus*) were captured within 50 m of the source, but a small percentage (0.2 to 3%) were captured at 300 m and 400 m. Using a maximum-likelihood approach, we evaluated the degree of support in our empirical dispersal data for competing functions to describe seed-dispersal kernels. Fat-tailed functions (lognormal, Weibull, and gamma (Γ)) fit dispersal patterns best for both species overall, but because *M. sinensis* dispersal distances were significantly affected by wind speed, curves were also fit separately for dispersal distances in low, moderate, and high wind events. Wind speeds shifted the *M. sinensis* dispersal curve from a thin-tailed exponential function at low speeds to fat-tailed lognormal functions at moderate and high wind speeds. *M. sinensis* caryopses traveled farther in higher wind speeds (low, 30 m; moderate, 150 m; high, 400 m). Our results demonstrate the ability of *Miscanthus* caryopses to travel long distances and raise important implications for potential escape and invasion of fertile *Miscanthus* varieties from bioenergy cultivation.

Nomenclature: Eulaliagrass, *Miscanthus sinensis* Anders.; giant miscanthus, *Miscanthus* × *giganteus* Anders.

Key words: Biofuel; bioenergy; dispersal kernel; fat-tailed; invasiveness; probability density function.

The giant miscanthus hybrid (*Miscanthus* × *giganteus* Anders.) and eulaliagrass (*Miscanthus sinensis* Anders.) are large perennial grasses being considered for bioenergy production in the United States (Heaton et al. 2008; Lewandowski et al. 2003; Stewart et al. 2009) and Europe (Clifton-Brown et al. 2001; Deuter and Abraham 1998). These species are capable of producing large biomass yields on marginal land (Zub and Brancourt-Hulmel 2010), allowing farmers to reserve their most productive land for food crops (Heaton et al. 2008). Although these species may represent a boon for the bioenergy industry, it is

important to evaluate their potential environmental impacts before widespread release (Barney and DiTomaso 2008; Buddenhagen et al. 2009; Davis et al. 2010; Quinn et al. 2010). For example, many second-generation biofuel crops have a suite of traits in common with known invaders (Raghu et al. 2006). The variety of *M. × giganteus* currently being evaluated as a biofuel in the United States is considered noninvasive, principally because this triploid hybrid is thought to be sterile (Barney and DiTomaso 2008). However, triploid sterility can break down during rare recombination events, resulting in fertile allopolyploid and diploid gametes (Ramsey and Schemske 1998). In fact, although they are thought to be produced quite rarely, fertile seeds of *M. × giganteus* have been reported (Linde-Laursen 1993). Conversely, some varieties of *M. sinensis* are known to produce copious quantities of viable seed (Meyer and Tchida 1999), a trait that confers a practical advantage for propagation and breeding in bioenergy systems (Christian et al. 2005; Yu et al. 2009). However, this trait has led to the escape of *M. sinensis* from ornamental plantings into natural areas in the eastern United States (Meyer et al. 2010; Quinn et al. 2010). Several of these

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Interpretive Summary

Eulaliagrass (*Miscanthus sinensis*) has already escaped from ornamental plantings to form large naturalized populations hundreds of meters from original planting locations (Quinn et al. 2010). Our results suggest that these new populations could have established following long-distance seed dispersal. Because the potential for long-distance dispersal and subsequent establishment has been demonstrated, it is important to take preventive measures to avoid further propagule pressure and gene flow into naturalized populations. As has been pointed out, breeders of bioenergy and ornamental varieties can take steps to minimize the potential for escape by selecting for nonshattering seedheads, engineering glabrous seeds, and inducing sterility (Quinn et al. 2010). Our results indicate a strong effect of wind speed on dispersal distance in *M. sinensis*. Growers should be aware of the need to monitor for escaped plants, particularly if producing fertile varieties. Because we show that most giant miscanthus (*Miscanthus* × *giganteus*) and *M. sinensis* seeds were trapped near the source, exhaustive monitoring efforts should be conducted on a regular basis within 50 m of production fields. In addition, because we know that a small proportion of seeds can disperse several hundred meters from a source, growers should also coordinate efforts with local land managers to ensure early detection and control of escaped plants in nearby natural areas.

invasive populations have established hundreds of meters to several kilometers from original plantings within short periods (Quinn et al. 2010). This pattern indicates that seeds may be capable of dispersing long distances. To address scenarios in which fertility is retained in *M. sinensis* or returned to *M.* × *giganteus* (Yu et al. 2009) in bioenergy production systems, it is important to quantify their ability for long-distance dispersal as a component of escape, establishment, and invasion risk for these species.

Wind dispersal has been correlated with invasion success in many plant species (Gasso et al. 2009; Lloret et al. 2005). *Miscanthus* fruits (caryopses) are known to be dispersed by wind in native grasslands (Ohtsuka et al. 1993), likely because of the presence of silky hairs (i.e., *fluff*) on the caryopses. A previous study of *M. sinensis* wind dispersal in native grasslands showed an exponential decline in the number of seeds caught as distance from the seed source increased (Nishiwaki and Sugawara 1993). However, the maximum distance investigated in that study was 20 m from the seed source. The ability of *Miscanthus* spp. to travel long distances is, therefore, unknown. If we are to explain previous escapes and predict the potential for new colonization events, we must characterize long-distance dispersal more accurately. This information, along with knowledge of population growth rates, is critically important for estimating potential rates of spread for escaped populations (Neubert and Parker 2004). It has been suggested that *M. sinensis* has not reached the limit of its distribution in the United States (L.D. Quinn, T. M. Culley, and J.R. Stewart, unpublished data); if production

of fertile (seeds or pollen) *Miscanthus* varieties expands, spread of invasive varieties could expand in tandem.

Empirical estimation of long-distance dispersal by wind can be challenging for several practical reasons. In seed capture studies using entire plants, it is necessary to simultaneously maximize the sampling area and the seed source (Nathan et al. 2003; Skarpaas et al. 2005). Potential dispersal is usually estimated from the number of seeds produced on plants used as point or patch sources in capture studies. These estimates range from a few hundred thousand seeds, e.g., thistles (*Carduus* spp.) (Skarpaas and Shea 2007) to several million seeds, e.g., heather [*Calluna vulgaris* (L.) Hull] (Bullock and Clarke 2000), or horseweed [*Coryza canadensis* (L.) Cronq.] (Dauer et al. 2007). However, few studies estimate the actual number of seeds that disperse during the experiment period, and reliance on predispersal seed-source estimates may overestimate the source strength. Seeds can fail to abscise because of low wind speeds (Schippers and Jongejans 2005) and a variety of other environmental or genetic factors. Optimization of trap design and arrangement has been the subject of considerable study and discussion (Bullock et al. 2006; Cousens et al. 2008; Kollmann and Goetze 1998; Page et al. 2002; Wiese et al. 1998). Although various methods are used, many researchers agree that the proportional sampling area should be held constant at increasing distances from a seed source (Bullock and Clarke 2000; Skarpaas et al. 2004) and that the prevailing wind direction should be considered in placement of traps in sectors or annuli around the source (Skarpaas et al. 2005; Skarpaas and Shea 2007). Few studies of wind-dispersed seeds have sampled traps at distances substantially greater than 100 m from a seed source (but see Dauer et al. 2007). Sampling greater distances requires more materials and greater effort, but may capture rare, long-distance dispersal events, which could have a disproportionately large influence on population spread rates (Cain et al. 2000). In this study, we quantified dispersal distances for *M.* × *giganteus* and *M. sinensis* across 400 m in field-based trials to provide empirically based dispersal kernels for these species. Knowledge of long-distance dispersal behavior for these species can prepare farmers, gardeners, and land managers for the risks of escape into adjacent landscapes. This information can also be used in mechanistic models predicting spread at larger scales.

Materials and Methods

Experimental Design. Our experiment was conducted in a soybean [*Glycine max* (L.) Merr] field in the 405-ha (1,001 acre) South Farms agricultural research property of the University of Illinois at Urbana-Champaign (UIUC). The 320 m by 405 m field (40°4'4.4034"N, 88°12'22.359"W) was harvested in early autumn 2009,

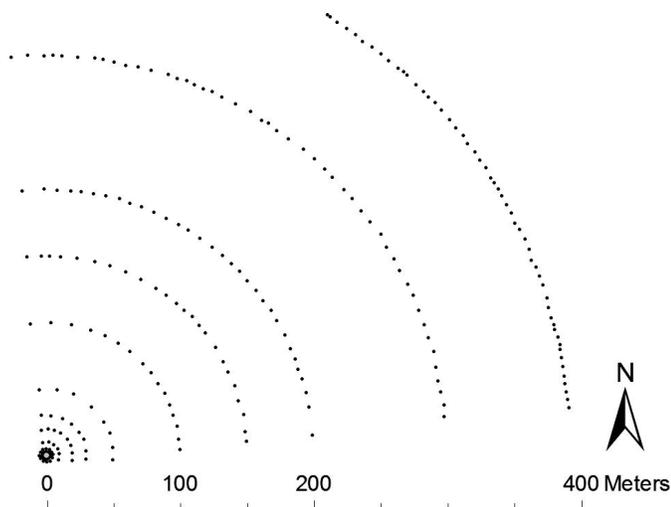


Figure 1. Schematic map showing trap locations across sampling area.

leaving bare soil during the trials. Most of the surrounding area is dedicated to traditional agricultural research, but both *Miscanthus × giganteus* and *M. sinensis* are grown in bioenergy test plots approximately 1.5 km (0.9 mi) to the east and approximately 4 km to the southwest. To minimize potential for seed contamination from these external sources, we conducted our dispersal trials after most of the caryopses had abscised (approximately November to December). Sticky traps were also placed in the field directly before our dispersal trials (November 2009 to February 2010) to detect background seed capture rates. No grass seeds were caught in these traps.

Wind speed and direction data were obtained from a weather station located approximately 4 km to the southwest of experimental field. Previous years' weather station data and expert opinion (T. Mies, personal communication) were used to predict predominant wind directions during the experimental period in 2010. Because wind typically originated from the south and west in past winters (and during the two trials; see Supplementary Figure 1), we erected a dispersal structure (point source) in the southwest corner of the field (see Figure 1, showing trap setup). Seed traps were placed at regular intervals (approximately equidistant) in north to east (90°) arcs at 300, 200, 150, 100, 50, 30, 20, and 10 m from the point source. Traps were also placed at 400 m, but because of the spatial constraints of the field, the entire north to east arc could not be sampled. Instead, traps at 400 m were restricted to the east to northeast quadrant (approximately 52°). Traps were set up in annuli (concentric rings) at 5, 3, 2, 1, and 0.5 m from the point source to capture seed rain in all directions during low wind events (Skarpaas and Shea 2007). The number of traps increased with distance from the point source to keep the sampling area consistent at



Figure 2. The dispersal source, comprising 600 *Miscanthus sinensis* or *Miscanthus × giganteus* panicles, and seed trap (inset), with trapped caryopses circled in black ink.

each distance (Bullock et al. 2006). Although greater sampling area provides greater accuracy, sampling large areas at long distances (e.g., 400 m) can be logistically intractable. In this case, it was feasible to sample 2.5% of the total possible area of each sampling distance (arc or annulus).

Seed traps (Figure 2) were assembled from 7.6 cm by 12.7 cm (3 in by 5 in) sticky insect traps,¹ stapled to thin, wooden strips. These units were screwed onto wooden stakes that, once inserted into the soil, held the traps approximately 10 to 50 cm from the soil surface. The number of stakes and sticky traps per stake varied at each sampling distance to keep proportional sampling area constant at each distance (2.5% of area = arc length × height of sticky traps). For example, 48 stakes with four traps stake⁻¹ were placed at 300 m, whereas 10 stakes with 0.5 traps stake⁻¹ (sticky traps were cut in half) were used at 2 m. There were 835.5 sticky traps in place for each trial. The location of each stake was recorded with a handheld Global Positioning System device.²

Miscanthus × giganteus panicles were collected from a 2-yr-old planting at the UIUC Energy Farm (40°3'51.696"N, 88°11'25.1514"W) in early November 2009 when caryopses were beginning to abscise. *Miscanthus sinensis* panicles were collected in early November 2009 from a naturalized population in the Red River Gorge Geological Area in Daniel Boone National Forest in Kentucky (37°48'12.24"N, 83°39'46.08"W) and from an ornamental variety collection at the UIUC Energy Farm. All *M. sinensis* panicles were sterilized by γ -irradiation³ to prevent germination after dispersal. Intact panicles of both species were stored in open bins in ambient conditions indoors for approximately 2 mo before trials.

To estimate the number of caryopses that dispersed during the experiment, 20 panicles from each species were sampled randomly from storage before trials began and from the dispersal structure after each trial ended. One hundred caryopses were counted and weighed from each panicle before all remaining caryopses were stripped and weighed. This provided an estimate of the total number of caryopses on each panicle and allowed us to compare caryopsis mass between species. Predispersal *M. × giganteus* panicles contained an average of 3,732 caryopses panicle⁻¹, whereas *M. sinensis* panicles contained an average of 1,764 caryopses panicle⁻¹. The number of caryopses remaining on panicles after dispersal trials will be given in the “Results and Discussion” section. Average weight ($n = 20$ per species) of 100-caryopsis lots was 3.5×10^{-2} g for *M. × giganteus* and 6.48×10^{-2} g for *M. sinensis*.

Panicles were attached to the dispersal structure (Figure 2) by gluing peduncles between two 2.4 m by 2.5 cm by 7.6 cm boards, which were bolted together. Each set of two boards held 100 panicles. Although the density of the panicles in our dispersal structure was greater than on typical plants, it was desirable to introduce a very large number of caryopses in a small (point) structure to maximize trapping likelihood and to simplify analyses. Six sets were used to create the dispersal structure (or point source), resulting in 600 panicles for potential dispersal. According to predispersal estimates explained above, the point source introduced approximately 2.3×10^6 *M. × giganteus* caryopses and 1.1×10^6 *M. sinensis* caryopses for potential dispersal. Racks of panicles were mounted on steel fence posts approximately 1.75 m from the ground to mimic the height of *Miscanthus* plants.

The point source for *M. × giganteus* was set in the field on January 12, 2010, and removed, along with the sticky traps, after approximately 5 wk; 1 wk was allowed to elapse between trials so that any remaining *M. × giganteus* seeds would be likely to disperse from the area. The *M. sinensis* point source and new sticky traps were set in the field on February 24, 2010, and removed after approximately 6 wk. For both trials, trapped seeds were censused twice per week. When a new seed was detected on a sticky trap, it was circled with marker (Figure 2) to avoid counting it as a new seed on the following census date.

Data Analysis. The distances of all traps with > 0 caryopses at the conclusion of each trial were plotted in histograms, and density by distance curves were generated by first converting the total number of caryopses caught at each distance to a density value by dividing into the total trapping area at each distance. Both expressions of dispersal data are useful in further analysis of population spread because the former provides the probability of a propagule dispersing to a given distance, and the latter provides an estimate of the density of propagules spreading to a given

distance (Cousens et al. 2008). However, development of population spread models is outside the scope of this article, the aim of which is to describe empirically derived dispersal patterns. Probability density functions (PDFs) were fitted to frequency distributions of dispersal distances (distance PDFs) (Cousens et al. 2008), and density by distance patterns for both species using the maximum-likelihood function `fitdistr()` in the MASS library in R (R Development Core Team 2008).⁴ This function returns parameter estimates and Akaike’s Information Criterion (AIC) values for 15 built-in distributions, five of which (lognormal, gamma (Γ), Gaussian (normal), exponential, and Weibull) are commonly used to describe dispersal distributions (Cousens et al. 2008). A routine for an additional distribution (inverse Gaussian) was also developed for `fitdistr()` (A. Adler, personal communication). Akaike weights (w_i) were calculated from AIC scores and used to determine the amount of support in the data for the best-fitting models of seed dispersal for both species.

Weather station data allowed us to derive the maximum recorded wind speed in the time interval between any two census dates. If the maximum speed in the days preceding a particular census date was < 7 m s⁻¹ (mean = 5.7 for both trials), that census date was categorized as *low wind*. *Moderate wind* census dates were characterized by wind speeds ranging from 7 to 10 m s⁻¹ (mean = 8.8 for *M. sinensis* trial and 8.2 for *M. × giganteus* trial), and *high wind* census dates were characterized by wind speeds > 11 m s⁻¹ (mean = 12.0 for *M. sinensis* trial and 18.1 for *M. × giganteus* trial). These categories were determined by examining natural breakpoints in the distribution of maximum wind speeds on all dates in both trials. Dispersal distances were grouped by wind category to allow PDFs to be fit for each wind speed category using the method described above.

Average and maximum wind speeds were compared between the two trials, using Wilcoxon rank sum tests. Relationships between wind speed and dispersal patterns were determined using general linear models (GLM) in R, with number of new caryopses captured and average trap distance used as response variables, and average and maximum wind speed (m s⁻¹) used as a predictor. Average and maximum wind speeds were taken from the period between census events. Census dates were treated as independent replicates. It was necessary to square-root transform the response variables to meet GLM assumptions of normality and constant error variance.

Results and Discussion

Approximately 1.03×10^6 *M. × giganteus* and 1.08×10^6 *M. sinensis* caryopses dispersed during the trials, representing 45 and 99.7% of the caryopses available for dispersal at the beginning of each trial. Despite the large

Table 1. Total number of *Miscanthus × giganteus* and *Miscanthus sinensis* caryopses caught at each trapping distance throughout 5 and 6 wk, respectively. *Potential dispersal* = *Proportion of caryopses caught at each distance* × *the number of caryopses dispersed*. Density values are based on total sampling area at each distance.

Trap distance m	<i>Miscanthus × giganteus</i>				<i>Miscanthus sinensis</i>			
	Caught		Potential dispersal	Density	Caught		Potential dispersal	Density
	No.	% of total	No.	caryopses m ⁻²	No.	% of total	No.	caryopses m ⁻²
0.5	4	5.3	54,688	210.53	18	4	42,740	947.37
1	3	4	41,016	125.00	15	3.3	35,617	625.00
2	9	12	123,048	183.67	31	6.8	73,608	632.65
3	7	9.3	95,704	90.91	69	15.2	163,837	896.10
5	11	14.7	150,391	94.83	87	19.1	206,577	750.00
10	9	12	123,048	155.17	62	13.6	147,216	1068.97
20	12	16	164,063	103.45	86	18.9	204,203	741.38
30	2	2.7	27,344	9.39	51	11.2	121,097	239.44
50	1	1.3	13,672	3.23	14	3.1	33,242	45.16
100	5	6.7	68,360	8.05	12	2.6	28,493	19.32
150	6	8	82,032	6.44	6	1.3	14,247	6.44
200	3	4	41,016	2.42	2	0.4	4,749	1.61
300	2	2.7	27,344	1.07	1	0.2	2,374	0.54
400	1	1.3	13,672	0.41	1	0.2	2,374	0.41
Total	75	100	1,025,396		455	100	1,080,375	

number of caryopses that dispersed from the panicles, only 75 *M. × giganteus* caryopses and 455 *M. sinensis* caryopses were caught in the traps. Although most caryopses were captured within the first 50 m (95% for *M. sinensis*; 77% for *M. × giganteus*), caryopses were detected at all trapping distances (to 400 m) for both species (Table 1).

Aside from single-seed tracking studies, few seed-trapping studies report the number of seeds that actually disperse. Using this value, we can extrapolate from the proportion of seeds caught at each location to the number of seeds that could have been caught if all dispersed seeds behaved similarly (and trapping area was unlimited). For example, the proportion of trapped *M. sinensis* caryopses that traveled to 400 m was very low (0.002 or 0.2%) (Table 1). However, that proportion would be equal to 2,374 caryopses at 400 m if all dispersed caryopses displayed the same behavior as those that were trapped (Table 1). The number of caryopses released at our point source was much greater than most other seed trapping studies and simulations (e.g., Saura-Mas and Lloret 2005; Skarpaas and Shea 2007; Skarpaas et al. 2004, 2005) (but see Bullock and Clarke 2000), but still represents an extremely small proportion of the number of seeds that might be produced by a production field of *M. sinensis*. *M. sinensis* seed production has been estimated from 6,500 to 140,000 seeds m⁻² in the native range (Stewart et al. 2009), and a single plant can produce more than 100 panicles (L. Quinn, unpublished data). Thus, *M. sinensis* could produce 6.5×10^7 to 1.4×10^9 seeds ha⁻¹. If 0.2%

of those seeds dispersed to 300 m and 400 m, as in our study, this would equate to a propagule load between 1.3×10^5 and 2.8×10^6 at those distances. Unfortunately, in situ germination studies have not yet been conducted. As such, we cannot predict the proportion of dispersed seeds that could successfully germinate under field conditions. However, controlled germination tests have shown germination rates up to 72% (mean ± standard error [SE] = 27% ± 4.2) for ornamental *M. sinensis* individuals setting large quantities of seed (> 3,000 3+ panicles⁻¹) (Meyer and Tchida 1999). Thus, even by conservative estimates, a large quantity of potentially germinable seed could be dispersed long distances if unimproved (fertile) *M. sinensis* were planted for large-scale production. Of course, we cannot be certain that dispersed seeds not caught by traps behaved similarly to those that were trapped. Further modeling and validation studies should be conducted to verify this prediction.

Neither average nor maximum wind speeds differed during the two trials ($P > 0.05$). Average speed was 3.6 (± 0.39 SE) m s⁻¹ during the *M. × giganteus* trial and 4.2 (± 0.34 SE) m s⁻¹ during the *M. sinensis* trial. Maximum wind speed was 12.6 (± 5.0 SE) m s⁻¹ during the *M. × giganteus* trial and 8.4 (± 0.73 SE) m s⁻¹ during the *M. sinensis* trial. Wind speed significantly affected *M. sinensis* dispersal behavior, with greater maximum wind speeds correlating with greater numbers of caryopses caught ($R^2 = 0.47$, $P \leq 0.01$) and with greater distances traveled ($R^2 = 0.44$, $P \leq 0.01$). Average wind speed affected *M. sinensis*

Table 2. Fit of six probability density functions commonly used to describe the frequency distribution of seed dispersal distance (distance PDF) and the density by distance curve. For both *Miscanthus × giganteus* and *Miscanthus sinensis*, the distribution that fit best for the distance PDF was the lognormal. For density by distance, the Weibull distribution showed the best fit for *M. sinensis*, whereas the gamma (Γ)-distribution was best for *M. × giganteus*.^a Best-fit distributions are shown in bold.

Distance PDF	AIC			w_i		
	Model	<i>M. sinensis</i>	Model	<i>M. × giganteus</i>	<i>M. sinensis</i>	<i>M. × giganteus</i>
Function						
Lognormal	1	726.64	1	431.37	0.77	0.70
InvGaussian	2	729.30	2	434.02	0.20	0.19
Weibull	3	733.96	3	435.51	0.02	0.09
Γ	4	739.25	4	438.69	0.001	0.02
Exponential	5	769.48	5	470.85	< 0.001	< 0.001
Normal (Gaussian)	6	911.92	6	552.19	< 0.001	< 0.001
Density by distance						
Weibull	1	189.61	2	145.67	0.83	0.32
Lognormal	2	192.84	3	147.12	0.16	0.16
Exponential	3	199.57	4	149.37	0.01	0.05
Γ	4	203.26	1	144.96	< 0.001	0.46
InvGaussian	5	209.17	5	152.05	< 0.001	0.01
Normal (Gaussian)	6	211.59	6	163.99	< 0.001	< 0.001

^aAbbreviations: PDF, probability density function; AIC, Akaike Information Criterion obtained from maximum-likelihood distribution-fitting method `fitdistr()` in R; InvGaussian, inverse Gaussian distribution; W_i , Akaike weights for each function, approximating the probability that each model is the best.

similarly (number caught: $R^2 = 0.40$, $P \leq 0.05$; distance traveled: $R^2 = 0.31$, $P \leq 0.05$). No significant patterns were detected for *M. × giganteus* for average or maximum wind speed. *Miscanthus sinensis* panicles lost a much greater percentage of caryopses (99.7%) than *M. × giganteus* did (45%) during the trials. If release thresholds of seeds from mother plants are defined as a function of wind speed (Jongejans and Telenius 2001; Schippers and Jongejans 2005), it follows that *M. sinensis* abscission rates are more sensitive to variation in wind speed than *M. × giganteus*. There is no indication in the literature that *M. × giganteus* has been specifically bred for nonshattering panicles. However, nonshattering lines have been successfully selected in agricultural crops for centuries (Doebley 2006). If *Miscanthus* species are introduced for large-scale bioenergy production, it may be advantageous for breeders to develop nonshattering varieties before release (Quinn et al. 2010).

Distance PDFs were described best by the lognormal distribution for both *M. × giganteus* ($w_i = 0.70$) and *M. sinensis* ($w_i = 0.77$) (Table 2; Figure 3), whereas the density by distance curves were described best by the Weibull distribution for *M. sinensis* ($w_i = 0.83$) and the Γ -distribution for *M. × giganteus* ($w_i = 0.46$) (Table 2; Figure 4). The lognormal distribution fit nearly as well for

M. × giganteus ($w_i = 0.32$), however (Table 2). Several other seed dispersal studies indicate strong support for the fit of lognormal and Weibull distributions to distance and density by distance patterns (Greene and Johnson 1989; Greene et al. 2004; Martinez and Gonzalez-Taboada 2009; Stoyan and Wagner 2001). Both the lognormal and the Weibull functions decline slowly at distances far from the source (i.e., fat-tailed). This can be contrasted with thin-tailed functions, like normal or exponential functions, which decline sharply at far distances (Cousens et al. 2008; Kot et al. 1996). Fat-tailed dispersal patterns have been linked with rapid population spread and invasion of new territories (Kot et al. 1996), but others point out that long-distance dispersal can be an erratic process and successful spread by individual propagules does not guarantee establishment of viable populations (Clark et al. 2003). More work is necessary to quantify seed germination rates and seedling establishment success of *Miscanthus* in habitats into which seeds may disperse, but the evidence provided here indicates that both species have the potential to disperse long distance by wind. If fertile seeds are retained or induced (Yu et al. 2009) in *Miscanthus* species for bioenergy production, farmers and land managers should expect a large influx of propagules in areas surrounding production fields.

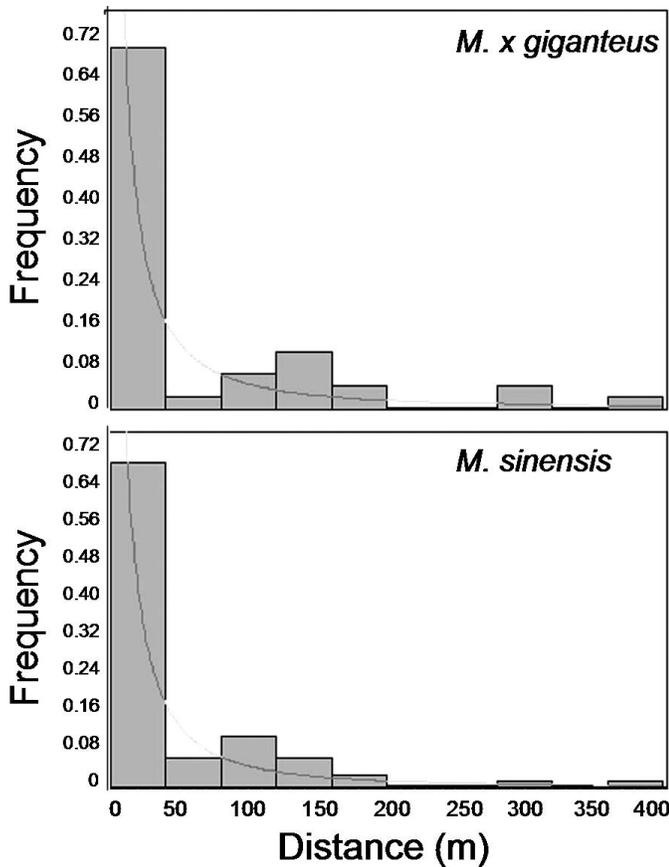


Figure 3. Frequency distributions of dispersal distances (distance PDFs) for (A) *Miscanthus* × *giganteus* and (B) *Miscanthus sinensis* caryopses. Curves represent the fit of the lognormal distribution to the data for both species.

Because *M. sinensis* dispersal was significantly affected by wind speed, distributions were fitted to distance frequencies under three wind types for this species. In low wind conditions, an exponential function was the best model ($w_i = 0.42$), whereas lognormal functions fit best for moderate winds ($w_i = 0.62$) and high winds ($w_i = 0.90$) (Table 3). It is not surprising that low winds produced a thin-tailed dispersal kernel. In all three wind conditions, most seeds were clustered near the source, and in low winds, *M. sinensis* caryopses traveled a maximum of 30 m (Figure 5). Under stronger wind conditions, the tail became fatter and shifted to the right (maximum distance = 150 m in moderate winds; maximum distance = 400 m in high winds; Figure 5). Because fat-tailed dispersal distributions predict greater probabilities of seeds dispersing beyond the sampling area than thin-tailed distributions, this suggests that caryopses in our experiment are likely to have traveled farther than 400 m in high-wind conditions. This is particularly noteworthy given that our experimental design sampled much greater distances than most other empirical dispersal studies.

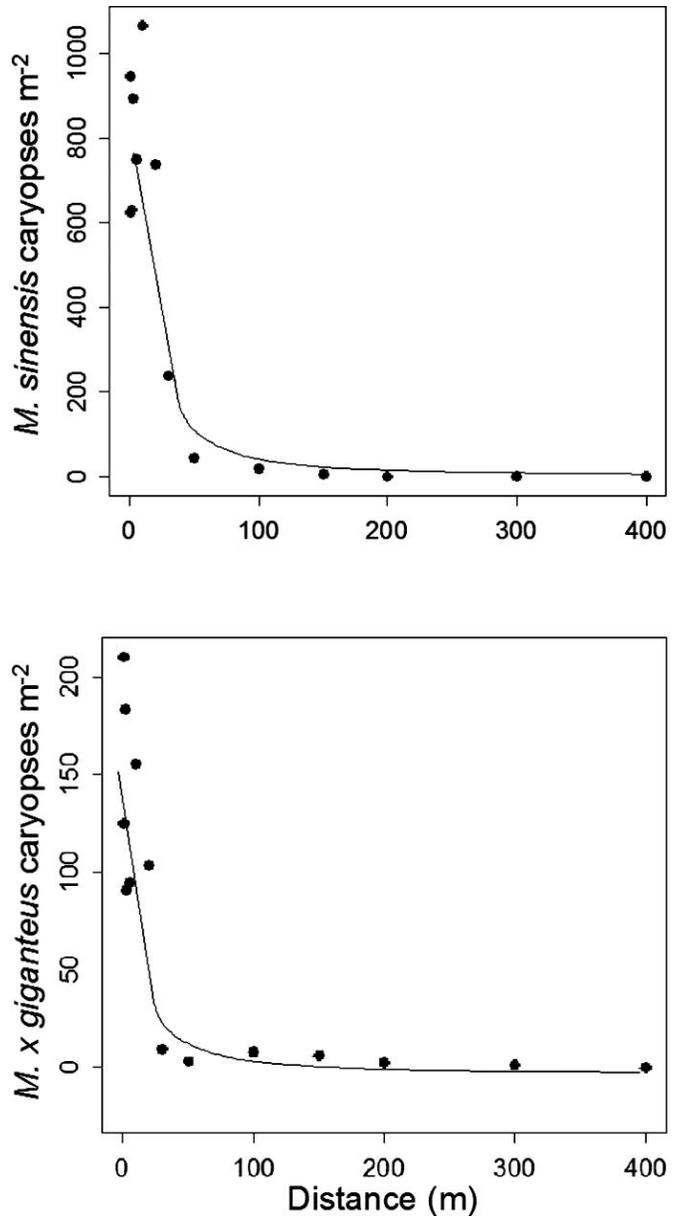


Figure 4. Density of trapped caryopses for *Miscanthus sinensis* (top panel) and *Miscanthus* × *giganteus* (bottom panel) at each trapping distance based on area of traps at each distance. The best-fitting function for *M. sinensis* is the Weibull distribution, while the γ -distribution fits the *M. x giganteus* density pattern best.

It should be noted that our experiment was conducted across a bare, flat surface and that direct comparisons between seed dispersal distances in bare fields and in natural vegetation have yielded substantially different results (Marushia and Holt 2006). This is most likely due to differences in boundary layers, turbulence, and other wind patterns generated by vegetated surfaces (Cousens et al. 2008; Lowry and Lowry II 1989). However, because

Table 3. Fit of six probability density functions for frequency of dispersal distances on low, moderate, and high wind days for *M. sinensis*. For low wind days, the best-fitting distribution was exponential, but on moderate and high wind days, the distribution that fit best was the lognormal.^a Best-fit distributions are shown in bold.

Function	Low wind			Moderate wind			High wind		
	Model	AIC	w_i	Model	AIC	w_i	Model	AIC	w_i
Lognormal	4	63.51	0.14	1	525.07	0.62	1	493.54	0.90
InvGaussian	5	64.01	0.11	2	526.15	0.36	3	499.77	0.04
Weibull	2	63.22	0.16	3	531.62	0.02	2	499.26	0.05
Γ	3	63.23	0.16	4	535.53	0.003	4	503.68	0.01
Exponential	1	61.35	0.42	5	551.33	< 0.001	5	517.32	< 0.001
Normal (Gaussian)	6	70.94	< 0.001	6	655.32	< 0.001	6	622.13	< 0.001

^a Abbreviations: AIC, Akaike Information Criterion obtained from maximum-likelihood distribution-fitting method `fitdistr()` in R; InvGaussian, inverse Gaussian distribution; W_i , Akaike weights for each function, approximating the probability that each model is the best.

production of *Miscanthus* species for bioenergy will likely occur in relatively uniform agricultural landscapes similar to our experimental location, our results may be reasonably realistic. Of course, local factors must be taken into account in each location. Our results provide the first empirical evidence of potential dispersal distance for *M. sinensis* and *M. × giganteus* and strongly suggest that care should be taken in planting fertile varieties near sensitive habitats.

Sources of Materials

¹ Sensor yellow monitoring cards, Whitmire Micro-Gen Research Laboratories Inc., 3568 Tree Court Industrial Blvd. St. Louis, MO 63122.

² eTrex Vista, Garmin, 1200 E. 151st Street, Olathe, KS 66062-3426.

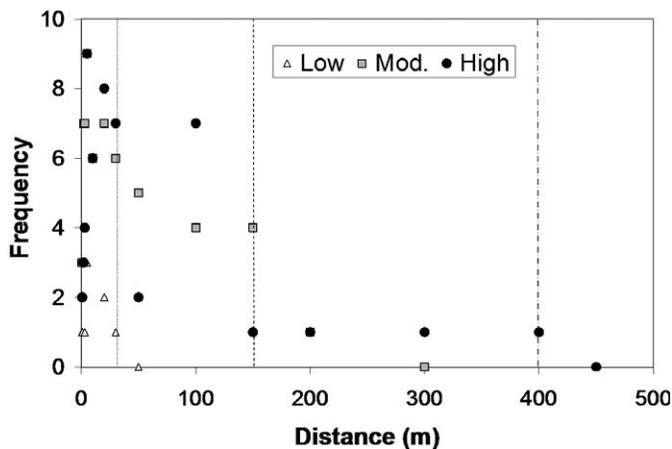


Figure 5. Frequency distribution of dispersal distances in *Miscanthus sinensis* on low (unfilled triangles), moderate (grey squares), and high (black circles) wind days. Vertical dashed lines are drawn at the last positive value for each wind speed group (e.g., 30 m for low wind, 150 m for moderate wind, and 400 m for high wind).

³ γ -irradiation service, Steris Isomedix Co., 1880 Industrial Drive, Libertyville, IL 60048-9439.

⁴ R statistical software, R: A Language and Environment for Statistical Computing, Version 2.6.0. R Foundation for Statistical Computing, Vienna, Austria.

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