

95% of basidiospores fall within 1 m of the cap: a field- and modeling-based study

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Abstract: Plant establishment patterns suggest that ectomycorrhizal fungal (EMF) inoculant is not found ubiquitously. The role of animal vectors dispersing viable EMF spores is well documented. Here we investigate the role of wind in basidiospore dispersal for six EMF species, *Inocybe lacera*, *Laccaria laccata*, *Lactarius rufus*, *Suillus brevipes*, *Suillus tomentosus* and *Thelephora americana*. Basidiospores adhered to microscope slides placed on three 60 cm transects radiating from sporocarps. Morphological characteristics of species as well as average basidiospore volume were recorded. Number of basidiospores was quantified at specific distances to produce actual dispersal gradients. We found a negative exponential decay model using characteristics for each species fit the field data well. The 95% modeled downwind dispersal distance of basidiospores was calculated for each species. The 95% modeled downwind dispersal distance increased with increasing cap height and decreasing basidiospore volume for the species sampled, with 95% of basidiospores predicted to fall within 58 cm of the cap. Differences in anatomical characteristics of EMF species influence how far basidiospores are dispersed by wind. We discuss the role of wind dispersal leading to patterns of EMF establishment during primary succession.

Key words: dispersal model, ectomycorrhizal establishment, primary succession, wind dispersal

INTRODUCTION

A common misconception regarding EMF basidiospores is that “everything is everywhere, but the environment selects” (Baas-Becking 1934). This

means that environmental factors, not dispersal limitations, influence the observed range of EMF species (Finlay 2002). However studies have shown that this is not always the case (Dickie and Reich 2005, Peay et al. 2007, Nunez et al. 2009, Peay et al. 2010) (see Dickie et al. 2010 for details) and colonization of host tree species by basidiospore inoculum is difficult to achieve. For EMF species to be successful in basidiospore-based reproduction they need to effectively disperse their basidiospores. Two dominant vectors of EMF basidiospore dispersal are animals (Maser and Maser 1988, Cázares and Trappe 1994, Johnson 1996, Lilleskov and Bruns 2005, Ashkannejhad and Horton 2006) and wind (Allen 1987). This study focuses on the importance of wind dispersal for EMF basidiospores.

Most EMF basidiospores are under 10 μm long, and sporocarp production is in the range of 1×10^9 basidiospores per sporocarp (Buller 1909). Their size and abundance should allow for long distance dispersal by wind to other habitats (Buller 1909, Lacey 1996). But EMF species differ in their ability to produce and disperse basidiospores. In an island biogeography study it was shown that species that invest heavily in dispersal are more likely to colonize small and distant tree islands, but as the tree islands begin to grow and develop other, presumably more competitive species, are able to establish and replace the initial colonizers (Peay et al. 2007). These results are driven initially by differences in dispersal ability of the fungi. Borchers and Perry (1990) and Dickie and Reich (2005) corroborate this idea by reporting that increasing distance from the forest edge reduced the amount of EMF inoculum available.

Much of the work done on basidiospore dispersal thus far either has been inferred through genet studies (Dahlberg and Stenlid 1994, Kretzer et al. 2004, Dunham et al. 2006) on pathogenic species (Fitt and McCartney 1986) or on arbuscular mycorrhizal fungi (Warner et al. 1987, Allen et al. 1989). A significant amount of work has been done on saprotrophic fungal basidiospore dispersal (Gregory et al. 1961, Haard and Kramer 1970, McCracken 1972, Rockett and Kramer 1974, Kay and Vilgalys 1992, Nordén and Larsson 2000). While saprotrophs are probably the most similar to EMF in dispersal patterns, there are differences in dispersal height and growth habit (on standing or prone trees) as well as length of the dispersal period, with many conks producing basidiospores over an entire season. Because of these differences there is a need for more study of EMF basidiospore dispersal.

Submitted 30 Nov 2010; accepted for publication 19 Apr 2011.

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Currently in the literature these types of studies are limited. Allen (1987) reported that in the primary successional tephra zone deposited after the 1980 Mount St Helens eruption only one ectomycorrhizal *Thelephora* basidiospore was captured from the airstream per 24 trap h. While this is important in showing that EMF basidiospores are present in the airstream and available for establishment, it is unknown how far these basidiospores traveled and why *Thelephora* was the only EMF species with basidiospores found in the airstream. Another study by Li (2005) found that less than 5% of basidiospores released from the ectomycorrhizal species *Amanita muscaria* var. *alba* dispersed as far as 5.2 m from the sporocarp. Li (2005) does a good job in quantifying basidiospore amounts at distances from a sporocarp but addresses only one cluster of fruiting bodies from one species and does not measure dispersal immediately adjacent to the caps. These studies, especially those on saprotrophic and EMF species, have been seminal in improving our understanding of basidiospore dispersal. The purpose of the present study was to investigate EMF basidiospore deposition within 1 m of the sporocarps of six species in five genera.

We investigated wind dispersal on the Oregon coastal sand dunes in the Oregon Dunes National Recreation Area in the Siuslaw National Forest, Oregon, USA. Research by Ashkannejhad and Horton (2006) showed that the dominant fungi on seedlings in isolated areas of the sand dunes without existing EMF networks were suilloid fungi (*Suillus* and *Rhizopogon* spp.). These were also the dominant EMF inoculant found in deer feces in the area, leading to the conclusion that deer are one of the main long distance dispersal agents of primary successional epigeous and hypogeous basidiomycetes on the sand dunes. The role of wind in the dispersal of the epigeous basidiomycetes was not addressed.

The objective of the present study was to investigate EMF basidiospore dispersal by wind. These six species of EMF were selected based on their putative role in early successional habitats, variation in basidiospore morphology and variation in cap height: *Suillus brevipes*, *Suillus tomentosus*, *Lactarius rufus*, *Inocybe lacera*, *Laccaria laccata* and *Thelephora americana*. We used basidiospore dispersal field data to develop an exponential decay model that demonstrates a general pattern of basidiospore dispersal by wind and how morphological characteristics of the species affect dispersal distances.

MATERIALS AND METHODS

Study area.—This study was conducted in the Tahkenitch Creek area in the Oregon Dunes National Recreation Area,

Siuslaw National Forest, Oregon, USA. Mild temperatures and abundant precipitation characterize the climate of the area with little or no seasonal moisture deficiency (Wiedemann et al. 1999). Weather reports generated 1971–2000 show an average yearly high of 15.5 C, an average low of 6.9 C, and an average yearly precipitation of 162.8 cm (45.472°N, 124.267°W) (©2010, PRISM Climate Group, Oregon State University). Wind speeds recorded at the Newport, Oregon, marine buoy (Station 46050), roughly 80 km north of the study site indicated that velocity is highest in Nov–Feb and lowest in Jun–Aug (National Oceanic and Atmospheric Administration, www.wr.noaa.gov). The summer winds generally originate from N–NW, the winter winds from S–SW, and the fall and spring winds are transitional between the two (Wiedemann et al. 1999).

The study ecosystem is composed of four zones: a foredune that parallels the ocean, the deflation plain forest, the dune system and the original stable forest to the east (see Ashkannejhad and Horton 2006 for details). This work was done on the edge of the deflation plain forest adjacent to the open dune system. The dominant ectomycorrhizal (EM) tree species is *Pinus contorta* var. *contorta*. Other EM host trees include *Picea sitchensis* Bong. Carr., *Pseudotsuga menziesii* Mirb. Franco and *Tsuga heterophylla* Raf. Sarg.

Sporocarp selection.—Six EMF species were chosen for sampling: *Suillus brevipes*, *Suillus tomentosus*, *Inocybe lacera*, *Laccaria laccata*, *Thelephora americana* and *Lactarius rufus*. These species were chosen based on their abundant fruiting in the area and potential for establishment in early successional settings. Five healthy individuals with expanded pilei from each species were selected opportunistically over 5 d, and all other sporocarps within a 5 m radius were removed to reduce background spore noise.

Data collection.—Dispersal sampling occurred from 22–27 Oct 2008 (TABLE I). For each individual three transects were set up, running 0–60 cm from the sporocarp and oriented radially around the sporocarp at 0°, 120°, 240°, with 0° oriented in the prevailing downwind direction (toward the southeast during summer months). Each transect had five microscope slides on it at 1–5, 10–15, 25–30, 40–45, and 55–60 cm from the sporocarp for a total of 15 slides/sporocarp (FIG. 1a). Slides were dipped into a hot solution of 90% petroleum jelly, 10% paraffin wax and allowed to cool to a thin, even surface that would trap impacting basidiospores. Petroleum jelly was used because it is an adhesive that is easy to work with and readily available. Paraffin wax was added to harden the petroleum jelly so it would not melt in the sun (Galán and Domínguez-Vilches 1997). Slides were left outside 24 h then returned to the lab for analysis.

Average wind speeds were obtained from the Newport, Oregon, marine buoy (Station 46050) for each collection period (National Oceanic and Atmospheric Administration, www.wr.noaa.gov). After the collection period the sporocarp cap area and height of the fertile surface were recorded. For *Thelephora* individuals cap area and height was not recorded due to the multilayered and irregular shape of the sporocarps. All the individuals were collected, the dry weight recorded and sporocarps saved for voucher specimens (TABLE I).

TABLE I. Physical measurements of EMF sporocarps and average wind speed (m/s) (± 1 SD) during collection period for individuals of the six species analyzed

Specimen number	Species	Date initiated	Data used (y/n)	Dry weight (mg)	Area (cm ²)	Height (cm)	Av wind (m/s) (SD)
1	<i>I. lacera</i>	10/22/08	y	12.5	0.8	1.5	5.6 (1.6)
2	<i>I. lacera</i>	10/22/08	y	18.7	0.6	2.3	5.6 (1.6)
10	<i>I. lacera</i>	10/23/08	y	36.2	1.6	3.7	8.1 (1.8)
11	<i>I. lacera</i>	10/23/08	n	75.1	0.95	1	8.1 (1.8)
26	<i>I. lacera</i>	10/25/08	y	92.6	4.7	3.6	5.5 (2.0)
17	<i>L. laccata</i>	10/24/08	n	20.8	0.33	2.2	6.6 (1.6)
18	<i>L. laccata</i>	10/24/08	n	25.5	0.86	1.7	6.5 (1.6)
21	<i>L. laccata</i>	10/25/08	n	262.4	2.3	4	5.8 (1.8)
22	<i>L. laccata</i>	10/25/08	y	132.4	3.9	3.7	5.8 (1.8)
30	<i>L. laccata</i>	10/26/08	y	214.7	5.2	5.2	3.2 (0.6)
12	<i>L. rufus</i>	10/23/08	n	402.1	7.5	4	8.1 (1.8)
13	<i>L. rufus</i>	10/24/08	n	1341.1	16.6	4.3	6.3 (1.7)
14	<i>L. rufus</i>	10/24/08	n	855.3	11.9	3.5	6.3 (1.7)
23	<i>L. rufus</i>	10/25/08	y	1042	19.9	4.9	5.8 (1.8)
31	<i>L. rufus</i>	10/26/08	y	810.8	16.9	5.3	3.2 (0.6)
7	<i>S. brevipes</i>	10/23/08	y	810.8	12.9	4.5	8.4 (1.5)
9	<i>S. brevipes</i>	10/23/08	y	330.9	7.3	2.6	8.4 (1.5)
20	<i>S. brevipes</i>	10/25/08	y	6892.4	83.2	3	6.0 (1.7)
25	<i>S. brevipes</i>	10/25/08	y	1677.9	25.9	3.4	5.6 (1.9)
29	<i>S. brevipes</i>	10/26/08	y	2647.5	30.6	3.1	3.2 (0.6)
3	<i>S. tomentosus</i>	10/22/08	y	1780.6	2.6	3	5.7 (1.7)
8	<i>S. tomentosus</i>	10/23/08	y	1065	18	4	8.4 (1.5)
16	<i>S. tomentosus</i>	10/24/08	y	2331.3	34.2	2.5	6.5 (1.7)
27	<i>S. tomentosus</i>	10/26/08	y	1720.8	18.4	4.5	3.2 (0.6)
28	<i>S. tomentosus</i>	10/26/08	y	1319.7	13.5	2.4	3.2 (0.6)
5	<i>T. americana</i>	10/22/08	y	4265.2	n/a	n/a	5.8 (1.9)
6	<i>T. americana</i>	10/22/08	y	1890	n/a	n/a	5.8 (1.9)
15	<i>T. americana</i>	10/24/08	y	3066.7	n/a	n/a	6.5 (1.7)
19	<i>T. americana</i>	10/25/08	y	2177.6	n/a	n/a	6.0 (1.7)
24	<i>T. americana</i>	10/25/08	y	3663.3	n/a	n/a	6.0 (1.7)

Microscope measurements.—A Nikon Eclipse E600 phase contrast microscope with attached SPOT camera and SPOT basic analysis software 4.0.1 was used for counting basidiospores (Diagnostic Instruments Inc., Sterling Heights, Michigan). Slides were viewed by putting them directly under the microscope with no cover slip with the exception of *Lactarius rufus* where Meltzer's reagent and a cover slip were used to increase visibility of the basidiospores. Each centimeter on the slide was sampled by photographing five views at that centimeter then counting all basidiospores present in the image. Each image covered a distance 610 μ m long by 460 μ m wide with a resulting area of 0.28 mm². Basidiospores in each view were summed to give an overall number of basidiospores in 1.4 mm² at each centimeter on the slide (FIG. 1b). When basidiospore slides were viewed under the microscope it was evident that some of the individuals were not sporulating at the time of collection and these were discarded from further analysis. This reduced the number of sporocarps used for three of the sampled species, *Inocybe lacera*, *Laccaria laccata* and *Lactarius rufus*. Also backwind transects were discarded for three individuals sampled (one each for *Suillus brevipes* and *Lactarius rufus* and two for *Inocybe lacera*) due to sticky

microscope slides being placed upside down or disturbed by animals. This reduction in sporocarps and transects resulted in the number of data points, 125–375, collected for each species (TABLE II).

For each of the six species studied basidiospore length and width measurements were taken for five basidiospores from each of the five sampled individuals and the results averaged (TABLE II). This was used to obtain average basidiospore volume using the formula for volume of an ellipsoid [$V = (4/3)\pi a \cdot b \cdot c$] where a, b, and c represent radii in x, y and z directions.

Negative exponential model.—A negative exponential model was employed to estimate basidiospore dispersal from the different species of ectomycorrhizal mushrooms. Such descriptive empirical models are used to fit mathematical formulas to measured deposition data (as reviewed in Fitt and McCartney 1986) to estimate model parameter values consistent with the data. These data tend to fit relatively simple, unimodal leptokurtic distributions characterized by a peak at the source followed by a rapid decline and relatively long, "fat" tail (as reviewed in Levin et al. 2003). In plant-dispersal studies two commonly used empirical

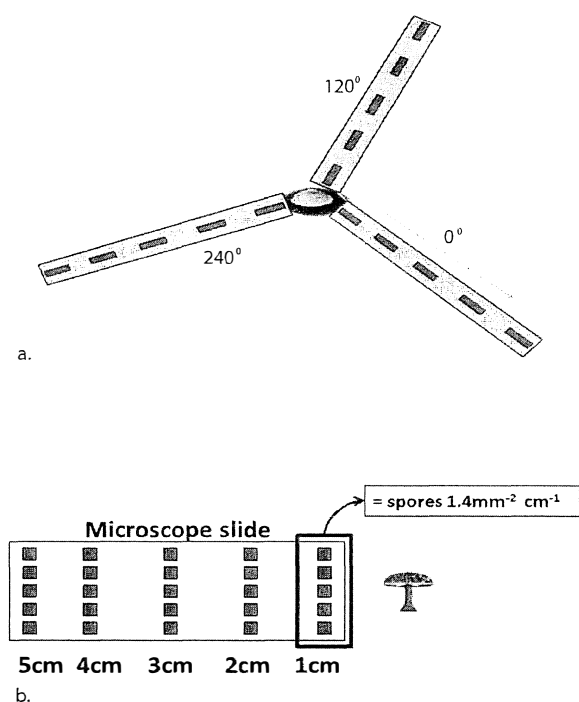


FIG. 1. a. Sampling design of microscope slides arranged around a fruiting body. The downwind transect is oriented at 0° and the two backwind are at 120° and 240° respectively. Five microscope slides are placed on each transect from 1–5, 10–15, 25–30, 40–45 and 55–60 cm for a total of 15 slides per sporocarp. b. Expanded diagram of a slide in a. Each microscope slide was divided into 5 cm and at each centimeter five views were taken. The number of basidiospores were counted within each image then summed to give an overall number of basidiospores $1.4 \text{ mm}^{-2} \text{ cm}^{-1}$.

models are the power law model and the negative exponential model (Bullock et al. 2006). When 124 dispersal gradients were compared to determine which model fit the data better, it was determined that both work equally well with this type of data (as reviewed in Fitt and McCartney 1986). For this study the negative exponential

model was used because the y axis (proportion of basidiospores) remains finite as the x axis (distance from sporocarp) tends to zero as opposed to the inverse power law where the y axis is infinite as the x axis tends to zero (Okubo and Levin 1989).

The basic equation for this model is $Y = ae^{-bx}$ where “a” is the source strength and e^{-bx} represents the negative exponential decline at distance “x” that is controlled by the parameter “b”. This basic model was modified to incorporate potential effects of morphological factors, such as cap area, dry weight, cap height and basidiospore volume, as well as the environmental factors of wind speed and direction. We initially attempted to fit models to all data from all species. This approach was rejected due to large amounts of variation between species causing poor model fits. As a result each species was modeled separately so that the individual models were better fit for each species and to allow for comparison between species.

Parameters were evaluated with the model in Microsoft Office Excel 2007 with the SOLVER function to fit the model to dispersal data. Initial model validation procedures excluded the cap area, dry weight and wind speed parameters from further evaluation. Akaike information criteria (AIC) were used to determine which combination of the remaining parameters would most correctly fit the observed basidiospore dispersal data for each of the six species (Akaike 1974). The best model was determined for each species as the model with the lowest AIC value that was also > 3 points lower than any other model within that species (Burnham and Anderson 2002).

Combined analyses.—The distance, x_{95} , at which 95% of basidiospores fell on the transect in the prevailing downwind direction was estimated for each species with the formula $x_{95} = 3/b$ where b represents the parameter which describes the radial decline in basidiospore dispersal in the dominant wind direction. The 90% confidence interval of the 95% downwind dispersal distance was determined for all species studied (FIG. 3). To produce this the model was evaluated for each individual of a species independently and the 95% dispersal distance determined. Using these values, a mean over all individuals of the species and the corresponding 90% confidence interval around the mean were produced. Also plotted on this graph is the 95%

TABLE II. Number of sporocarps, number of data points, mean spore volume and mean cap height for each of the six species; standard deviations are indicated in parentheses

Species ^a	Number of sporocarps	Number data points	Mean spore volume (μm^3)	Mean cap height (cm)	95% dispersal distance
<i>Inocybe lacera</i>	4	250	208 (85)	2.8 (1.1)	3 cm
<i>Thelephora americana</i>	5	375	211 (45)	ND ^b	7 cm
<i>Laccaria laccata</i>	2	150	279 (59)	4.5 (1.1)	14 cm
<i>Suillus tomentosus</i>	5	375	84 (19)	3.3 (0.9)	16 cm
<i>Suillus brevipes</i>	5	350	65 (19)	3.3 (0.7)	25 cm
<i>Lactarius rufus</i>	2	125	171 (49)	5.1 (0.3)	58 cm

^aSpecies are arranged in order of shortest to longest dispersal distance for 95% of basidiospores.

^bCap height was not determined (ND) for *Thelephora americana*.

dispersal distance of a species using all individuals to make the aggregate estimate.

RESULTS

Using AIC model selection criteria, the model including cap height, basidiospore volume and wind direction parameters was determined to best fit the observed basidiospore dispersal data for all species except *Thelephora americana*, which does not have a height variable, where the best fitting model includes basidiospore volume and wind direction parameters (TABLE III) (Akaike 1974, Burnham and Anderson 2002). These models represent individual species' basidiospore dispersal data well with relatively high r^2 values of 0.71–0.88 ($r^2 = 1 - SS_{\text{residuals}}/SS_{\text{Total}}$, where $SS_{\text{residuals}}$ is the sum of squared differences between modeled and observed values and SS_{Total} is the sum of squared differences between observed values and their mean).

The equation that incorporates these factors is $Y = \frac{abc}{\pi(b+c)} (\cos^2(\theta)e^{-br} + \sin^2(\theta)e^{-cr})e^{+dh+fs}$ where "a", the spore source strength parameter, is determined by taking the sum of all basidiospores counted on all slides for an individual sporocarp, " θ " represents the direction angle measured relative to the prevailing downwind direction, "r" represents radial distance from the sporocarp, "h" represents height and "s" is the basidiospore volume. An estimate of total number of basidiospores deposited over all radial distances is given by a $\exp(dh + fs)$. The variables "b, c, d, f" are parameters that are estimated by the model to obtain the best value of r^2 within models and the lowest AIC between models.

Actual and modeled dispersal gradients and the distance within which 95% of dispersed basidiospores are expected to fall along the downwind transect for *Suillus brevipes* are graphed (FIG. 2) as an illustration of the dispersal curves (figures for other species were similar). Observed and modeled data indicated that most of the basidiospores are deposited close to the cap, and this number decreases quickly with increasing distance (FIG. 2) (SUPPLEMENTARY TABLES I–VI). A larger proportion of basidiospores fell on the prevailing downwind transect versus the combined backwind transect. These proportions represent a fraction of the total amount of basidiospores where the total is obtained by summing over all three transects.

Combined analyses.—The 95% dispersal distance for individual species ranges from 3 cm for *I. lacera* to 58 cm for *L. rufus* (TABLE II, FIG. 3). For each species this distance falls within the 90% confidence interval produced, with the average of all individuals modeled

separately always slightly higher than when they are modeled together. *Lactarius rufus* has an extremely wide (90%) confidence interval compared with the other species sampled, most likely influenced by its sample size ($n = 2$).

DISCUSSION

The fungal species sampled follow a pattern of dispersal that is based both on their height and basidiospore volume (TABLES II, III). Basidiospores from taller species will more easily clear the boundary layer of still air and disperse farther than those from shorter species (Buller 1909). The volume of the basidiospore determines its terminal velocity in still air (Okubo and Levin 2001). In accordance with Stokes' law the rate of fall of a spherical body is proportional to the square of its radius with larger objects falling faster than smaller ones (Ingold 1971). The dispersal range is inversely related to settling velocity with smaller spores being moved farther from the source (Okubo and Levin 2001).

Inocybe lacera disperses closest to the cap with 95% dispersal distance of 3 cm. It can be inferred that this is due to its height, 2.8 cm (± 1.1 cm), and basidiospore volume in the upper-middle range of the species sampled at $208 \mu\text{m}^3$ ($\pm 85 \mu\text{m}^3$). *Thelephora americana* does not have a height variable to compare with the other species, but its basidiospore volume of $211 \mu\text{m}^3$ ($\pm 45 \mu\text{m}^3$) is a possible cause of it having a 95% dispersal distance (7 cm) similar to *Inocybe lacera* (3 cm). The height for *T. americana* individuals in this study ranged from ground level to roughly 5 or 6 cm, depending on what they were growing on. These comparatively tall heights should have led to farther dispersal distances than those observed. Reasons for this discrepancy are unknown but could be due to the different pileus shape and growth form of this species (Deering et al. 2001). *Laccaria laccata* has the largest basidiospore volume sampled at $279 \mu\text{m}^3$ ($\pm 59 \mu\text{m}^3$) and the second tallest height at 4 cm (± 1.1 cm). These two factors seem to cancel each other for this species, resulting in a 95% dispersal distance of 14 cm. *Suillus tomentosus* is shorter than *Laccaria laccata* but not quite as short as *Inocybe lacera* at 3.3 cm (± 0.9 cm) and has the second smallest basidiospore volume at $84 \mu\text{m}^3$ ($\pm 19 \mu\text{m}^3$). Its mid-range height along with small basidiospore volume contributes to 95% of its basidiospores dispersing 16 cm from the sporocarp. *Suillus brevipes* has the same average height as *Suillus tomentosus* at 3.3 cm (± 0.7 cm) but the smallest basidiospore volume of $65 \mu\text{m}^3$ ($\pm 19 \mu\text{m}^3$). Perhaps due to the slightly smaller basidiospore volume, 95% of basidiospores of *Suillus brevipes* move farther from

TABLE III. AIC model selection analysis of species dispersal models where AIC values were obtained by fitting different combinations of parameters in six models to observed dispersal data from all individuals of the same species

Parameters	Model ^a	Model Δ AIC values ^b					
		<i>Inocybe lacera</i>	<i>Thelephora americana</i>	<i>Laccaria laccata</i>	<i>Suillus tomentosus</i>	<i>Suillus brevipes</i>	<i>Lactarius rufus</i>
Spore vol. + wind + cap	$Y = \frac{abc}{\pi(b+c)} (\cos^2(\theta)e^{-br} + \sin^2(\theta)e^{-cr})e^{+dh+fs}$	0	ND ^c	0	0	0	0
Spore volume + wind	$Y = \frac{abc}{\pi(b+c)} (\cos^2(\theta)e^{-br} + \sin^2(\theta)e^{-cr})e^{+fs}$	81	0	28	8	24	32
Cap height + wind	$Y = \frac{abc}{\pi(b+c)} (\cos^2(\theta)e^{-br} + \sin^2(\theta)e^{-cr})e^{+dh}$	175	ND ^b	89	87	140	18
Spore volume	$Y = \frac{ab}{\pi(2)} e^{-br+fs}$	177	127	148	156	180	50
Cap height	$Y = \frac{ab}{\pi(2)} e^{-br+dh}$	231	ND ^b	182	185	265	35
Wind direction	$Y = \frac{abc}{\pi(b+c)} (\cos^2(\theta)e^{-br} + \sin^2(\theta)e^{-cr})$	256	252	202	212	325	191

^aThe best model was determined for each species as the model with the lowest AIC value (Akaike 1974).

^bAll models include a parameter of exponential decline with radial distance. The model AIC values shown are standardized against the best model where $\Delta_i = \Delta_{\min} = 0$ and all other models show $\Delta_i = \text{AIC}_i - \text{AIC}_{\min}$.

^cCap height was not determined (ND) for *Thelephora americana*, which excludes models including cap height for this species.

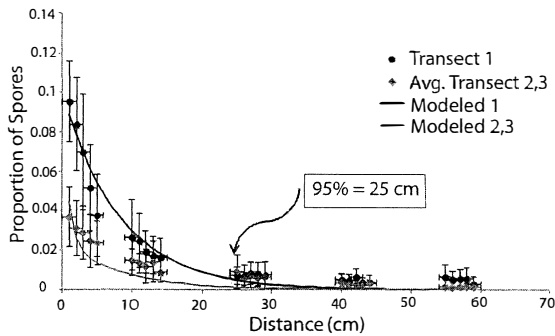


FIG. 2. Actual and modeled downwind (transect 1) and backwind (av. transect 2, 3) dispersal data collected for *Suillus brevipes* sporocarps ($n = 5$). The y axis represents the proportion of basidiospores dispersed and the x axis represents distance from the sporocarp in centimeters with 0 cm being directly beneath the cap. Actual dispersal data was measured only at specific distances on the microscope slides while the model estimates dispersal at all distances. Backwind transects 2 and 3 (i.e. at $\pm 120^\circ$ downwind) were averaged because the model predicts the same dispersal curve for each. Error bars represent one standard deviation of the mean proportion of basidiospores for all sporocarps of *Suillus brevipes* at that distance (cm). The model predicts that 95% of this species' basidiospores will fall within 25 cm of the cap ($r^2 = 0.75$).

the cap than *Suillus tomentosus* basidiospores to a distance of 25 cm. Dispersing the farthest of all species analyzed is *Lactarius rufus*. *Lactarius rufus* is the tallest species with an average height of 5.1 cm (± 0.3 cm) and a mid-range basidiospore volume of $171 \mu\text{m}^3$ ($\pm 49 \mu\text{m}^3$); 95% of its basidiospores disperse 58 cm from the sporocarp. It is possible that dispersal distance of *Lactarius rufus* is affected by the ridged basidiospores. More work is needed on the role of spore ornamentation and dispersal distance.

Sample size was $n = 2$ to $n = 5$. While four and five individuals for *Inocybe lacera*, *Suillus tomentosus*, *Suillus brevipes* and *Thelephora americana* are sufficient to allow for variation between individuals, two individuals for *Laccaria laccata* and *Lactarius rufus* are too low to support strong inferences about dispersal for these species. Low sample size results in the dispersal distance 90% confidence interval for *Lactarius rufus* being extremely large, ranging from -189 to 331 cm (FIG. 3).

Because radial area increases quadratically ($A = \pi r^2$) with increasing linear distance from the sporocarp the number of basidiospores measured are spread over a greater area with increasing distance. This dilution effect is part of the radial decline of spore density captured by the model. In this study the greatest dispersal distance observed (i.e. the distance

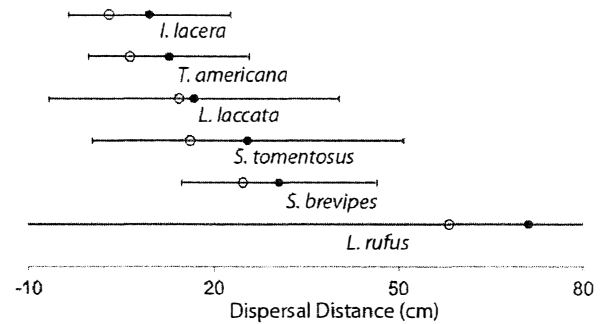


FIG. 3. 90% confidence interval for 95% dispersal distance of the six species studied. Solid circles represent the mean of the individuals' dispersal modeled separately. Open circles represent the modeled 95% dispersal distance with all individuals in a species included. Sample size is 5 for all species studied except *Inocybe lacera* (4), and *Laccaria laccata* and *Lactarius rufus* (2). Error bars for *Lactarius rufus* range from -189 to 331 .

downwind of the sporocarp for which less than 5% of basidiospores were estimated to have traveled) was 58 cm. While 5% may not seem like a large proportion, if a single sporocarp were to produce and successfully release an estimated 1×10^9 basidiospores (Buller 1909), then 5×10^7 could disperse farther than 58 cm downwind. Basidiospores released from an average fruiting body height have the potential to be carried up to 40 m by a wind speed of 1.5 m/s^{-1} (Okubo and Levin 1989). At this site wind speed ranged from 3.2 m/s^{-1} to 8.4 m/s^{-1} during the collection periods (TABLE I), meaning that basidiospores of the species studied have the potential to be carried more than 40 m from the sporocarp. Wind speeds at this site actually can be much higher in the late fall (pers obs), which could result in even greater dispersal distances.

This study does not address the basidiospores that are carried up and away from the fungus, such as those measured from the rust *Gymnosporangium juniper-virginianae* (Ingold 1953). Spores that are carried away into the turbulent mixing layer can be carried by the wind for days before deposition (Pedgley 1986). As reviewed in Okubo and Levin (2001) medium-sized spores ($14 \times 6 \mu\text{m}$ diam, volume = $923 \mu\text{m}^3$) can be carried to a height of 165 m and a horizontal distance of 2865 km, settling within five and a half days. Small spores ($5 \times 3 \mu\text{m}$ diam, volume = $26 \mu\text{m}^3$) can be carried even farther to a height of 650 m and a horizontal distance of 44571 km, settling within 86 d. If this upward movement is significant it could be important for long distance dispersal, although obviously such long distance transport do not guarantee successful establishment.

Many studies have shown that animals are long distance dispersal vectors for basidiospores across the landscape. Basidiospores dispersed through animals are found in abundance in deer feces (Ashkannejhad and Horton 2006) and may benefit from the associated nitrogen pools (Lilleskov and Bruns 2003). Our study demonstrates that, while cap height and basidiospore volume can affect the variation in the distance basidiospores are dispersed by wind, most EMF basidiospores tend to fall within a meter of the cap. Our study focused on horizontal dispersal at the scale of tens of centimeters on relatively calm days. Additional work explicitly considering advection and dispersion in two or three dimensions is required to evaluate the importance of vertical movement of basidiospores and dispersal under medium to high winds for long distance dispersal.

ACKNOWLEDGMENTS

This research partly fulfilled the requirements for a master of science degree at the State University of New York, College of Environmental Science and Forestry. We thank Randy Molina, Jane Smith, Sara Ashkannejhad, Joe Vineis, Nicholas Keuler and Dan Segotta for support and logistical help and Dr June Wang for the use of her microscope and image-capturing equipment. We also thank two anonymous reviewers and Peter Avis for constructive comments that helped improve the quality of this paper. This project was financially supported by Joint Venture Agreement No. PNW 06-JV-11261976-292 with the USDA Forest Service PNW Research Station and NSF award DEB-0949175 to TR Horton, a SUNY-ESF EFB departmental TA fellowship, and a Hugh Wilcox-Josiah Lowe graduate student award to T. Galante.

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