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SEED DISPERSAL CHARACTERISTICS OF *BRASSAVOLA NODOSA* (ORCHIDACEAE)[1]

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We used mathematical models for wind-dispersed seeds and wind-tunnel experiments to predict modal seed dispersal distance of the Neotropical orchid *Brassavola nodosa* under conditions approximating those found in its natural habitat: mangrove islands in Belize, Central America. Key variables in a simple ballistic model for predicting modal dispersal distance (x_m) of an individual seed include: height of release (h); free-stream velocity (U_c); and terminal velocity of the seed (U_t): $x_m = hU_c/U_t$. Modal dispersal distance of dust-like orchid seeds were predicted adequately by this ballistic model at low wind velocities and low release heights, but it underestimated the increasing importance of turbulence at higher wind velocities and greater release heights. We estimated the magnitude and relative importance of one measure of turbulence, vertical mixing velocity (W^*), on x_m in wind tunnel experiments. Our estimates of W^* were within the same order of magnitude as those found for other small dust-like seeds and pollen. In high turbulence conditions, incorporation of vertical mixing velocity effects into the ballistic model of seed dispersal overestimated modal seed dispersal distances.

Key words: aerodynamics; Belize; *Brassavola nodosa*; Orchidaceae; seed dispersal; turbulence.

Dispersal of seeds into suitable habitats is a critical stage of any plant's life history. Because plants are sessile, their seeds must be dispersed by external agents, such as wind, water, or animals (Fenner, 1985). Wing and Tiffney (1987) regarded small, presumably abiotically dispersed seeds to be the primitive dispersal syndrome among angiosperms, although anemochory (wind dispersal) is not restricted taxonomically (Willson, 1983). Plants are subject to strong selective pressures to invade suitable microhabitats, and such selection can lead to increased dispersal distances (e.g., Harper, Lovell, and Moore, 1970; Janzen, 1970; Howe and Smallwood, 1982). Most anemochorous species either have very small seeds or produce seeds with secondary structures such as plumes and samaras that increase dispersal distances from parent plants (Burrows, 1973, 1975a, b; Augspurger, 1986).

Existing mathematical models of seed dispersal predict different dispersal distances of anemochorous seeds. For example, Cremer (1977) predicted "approximate [dispersal] distance" of *Eucalyptus* seeds using a simple ballistic model:

$$x_m = h\frac{U_c}{U_t} \qquad (1)$$

where x_m is the approximate (mean) distance that a seed will disperse given height of release h, terminal velocity U_t, and average wind velocity (between point of release and ground) U_c. This model refers to a single, ideal (spherical) propagule, and variation among such propagules would arise simply from variability in either U_t or lateral wind velocity (Cremer, 1977).

In an attempt to incorporate variation in U_c, Okubo and Levin (1989) assumed that x_m in Eq. 1 referred to *modal* dispersal distance, and extended Eq. 1 to incorporate one measure of atmospheric turbulence—vertical mixing velocity. Okubo and Levin's (1989) model is a "tilted plume model," derived from models of atmospheric particulates (Pasquill and Smith, 1983), that under steady-state conditions predicts modal dispersal distance of unadorned, dust-like seeds or pollen resulting from gravitational settling and concomitant diffusion. Because of its apparent applicability to the dust-like unplumed seeds characteristic of the Orchidaceae, we hypothesized that dispersal properties of anemochorous seeds of the Neotropical epiphytic orchid *Brassavola nodosa* L. would be predicted well by Okubo and Levin's (1989) model of seed dispersal.

We experimentally investigated dispersal properties of *Brassavola nodosa* (henceforth, *Brassavola*), which has tiny, cigar-shaped seeds that lack wings or plumes. In this study, we addressed the following questions through a combination of mathematical modeling, and laboratory and wind-tunnel experiments: (1) based on the model of Okubo and Levin (1989), how would expected modal dispersal distance of *Brassavola* seeds vary with height and wind velocity at point of release? (2) on mangrove islands where *Brassavola* commonly grows, what is the range of wind velocities and plant heights from which

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seeds are released? (3) under experimental conditions, using wind velocities and seed release heights found in the field, what are observed modal dispersal distances of *Brassavola* seeds, and how do experimental results compare with theoretical predictions?

MODELS FOR DISPERSAL

To determine horizontal dispersal distances for natural populations of pollen, seeds, or fruit, many authors have used either an inverse power or a negative exponential equation (e.g., Cremer, 1977; Augspurger, 1986; Greene and Johnson, 1996). Okubo and Levin (1989) argued that although these are useful because of their simplicity and reasonable fit to data, they poorly predict the behavior of different species in habitats different from those for which the models were developed (Greene and Johnson, 1989, Okubo and Levin, 1989; but see Greene and Johnson, 1996). A Gaussian plume model originally developed for modeling dispersal of pollutants (Pasquill and Smith, 1983) is a more appropriate approach for describing dispersal of particulates or small, dust-like seeds. This model begins with the simple ballistic model given above (Eq. 1), with x_m equal to modal dispersal distance. However, the ballistic model includes neither turbulence nor convection (Okubo and Levin, 1989; Niklas, 1992).

Eddies, the swirling wind patterns caused by convection or turbulent flow, can hold seeds suspended in air for long periods of time (Harper, 1977). Such eddies may increase *or decrease* maximal horizontal dispersal distances. Okubo and Levin (1989) incorporated turbulence into the ballistic dispersal model (Eq. 1). For heavy seeds (where $U_t \gg 1$ m/s), turbulence has little effect on terminal velocity, and Eq. 1 is appropriate for determining x_m. For very small, light seeds, $U_t \ll 1$ m/s and vertical airflow mixing velocity (W^*) should strongly affect dispersal patterns (Okubo and Levin, 1989):

$$x_m = \frac{hU_c}{U_t + W^*} \tag{2}$$

where W^* is defined as the rate at which a suspended particle would reach the ground simply by eddy diffusion in the absence of gravity. For light seeds, the ratio W^*/U_t describes the relative effects of turbulence and gravity on seed dispersal (Okubo and Levin, 1989). A dimensionless parameter λ, which includes effects of W^*, represents the spread (variance) of settling particles around their estimated (mean) location (Okubo and Levin, 1989):

$$\lambda = \sqrt{1 + \left(\frac{W^*}{2U_t}\right)^2} + \frac{W^*}{2U_t}. \tag{3}$$

For small values of W^*/U_t (heavy particles),

$$\lambda \approx \frac{W^*}{U_t} \gg 1 \tag{4}$$

while for light seeds, $W^*/2U_t$ is large and

$$\lambda \approx 1 + \frac{W^*}{2U_t} \approx 1 \tag{5}$$

(Okubo and Levin, 1989). Knowing U_c, U_t, x_m, and h, λ can be estimated from Eqs. 1 and 5 as:

$$\lambda \approx \frac{U_c/U_t}{x_m/h} \tag{6}$$

and W^* can be determined empirically using Eq. 3 (Okubo and Levin, 1989).

The model incorporating turbulence (Eq. 6) assumes that the ambient wind velocity remains constant as a seed falls, but this assumption clearly is not realistic under most natural conditions (cf. Niklas, 1992). First, if the wind velocity above the canopy is relatively constant, the wind velocity at points within the canopy will decay as a function of surrounding vegetation (Cionco, 1972):

$$U_c = U_f e^{a[(h-z)/z]} \tag{7}$$

where U_f is the wind velocity above the canopy (free-stream velocity) and z is the canopy height. The empirically determined constant a describes the degree of canopy openness. For open canopies, $a \rightarrow 0$, while for dense canopies, $a \rightarrow 4$ (Cioncio, 1972). Although a has not been determined for most canopy types, both Cioncio (1972) and Niklas (1992) presented values of $a = 0.02$ for a pine forest, $a = 2$ for a corn field, and $a = 4$ for a dense field of grass. Based on Eqs. 1 and 2, modal dispersal distance for seeds of a given size, within a canopy of fixed height (z) and constant free-stream velocity (U_f), should increase as a decreases. For fixed a, increases in either U_f or z also should result in higher modal dispersal distances. Okubo and Levin (1989) showed that as long as the parameters of Eq. 6 vary relatively slowly, substitution of U (the mean wind velocity over the course of the seeds' descent) for U_c in Eq. 6 gave reasonably accurate predictions of x_m. U can be measured in the field, or estimated from Eq. 7.

Second, very small seeds within a dry, dehiscent fruit are likely to be released only when ambient wind velocity reaches a certain threshold, i.e., during localized gusts. Aylor (1982) showed that incorporation of gusts into a model similar to that of Eq. 6 gave better predictions for dispersal of fungal spores within a barley canopy than did a model without gusts. In our experiments, we compared predictions of modal dispersal distances from the model (Eq. 6) with data from the behavior of orchid seeds under laboratory conditions in a laminar-flow wind tunnel, and under turbulent air conditions with higher wind velocities at point of release (gusts). Wind velocities used in the laboratory were determined from measurements of wind velocities at different canopy depths in the natural habitat of *Brassavola*.

STUDY SPECIES AND STUDY SITE

Brassavola nodosa is an epiphytic and lithophytic orchid that ranges from Mexico, throughout Central America, and into Venezuela and Peru (Ames and Correll, 1985). We studied *Brassavola* forest conditions on Peter Douglas Cay (16°42′N, 88°10′W), an ~10-ha mangrove island in the barrier reef lagoon complex of Belize, Central America where two populations of *Brassavola* occur. At Peter Douglas Cay, *Brassavola* grows most commonly as an epiphyte on the red mangrove *Rhizophora mangle* L. (Rhizophoraceae). We observed *Brassavola* in flower and fruit on this island throughout the year. A single mature capsule contains ~300 000 seeds (a complete site

Fig. 1. SEM photograph of *Brassavola* seeds. Scale bar = 100 μm.

description and report on reproductive patterns of *Brassavola* are given by Murren and Ellison [1996]). Prevailing winds throughout Belize are northeasterly tradewinds.

MATERIALS AND METHODS

Seed characteristics—Scanning electron microscopy (SEM) was used to determine size and shape of *Brassavola* seeds (Fig. 1). Mean seed mass was determined by weighing 100-seed lots (±10 μg). Terminal velocity (U_t) was obtained from stroboscopic photographs (Cole-Parmer 87000 stroboscope, Cole-Parmer Instruments, Vernon Hills, IL; Nikon F-3 with a 1:1 macro lens; and Kodak T-Max 32000 black-and-white film) by dividing the distance between repeated images of the falling seed on the negative by the flash frequency (37.5 flashes/s). This process was repeated for seeds coated in fluorescent dust (Radiant Color, Richmond, CA). Because the mass of the dust approximately equaled the mass of the seed to which it was applied, its use nearly doubled the observed terminal velocity (see Results, below).

Field-determined parameters—We examined wind conditions and mangrove canopy structure at Peter Douglas Cay, and used these parameters in our laboratory studies of seed behavior. One population (59 plants) was on the leeward (southwest) side of the cay, and the other (44 plants) was on the windward (northeast) side. Approximately 85% of the canopy above these two orchid populations was *Rhizophora*. At three random locations within each population, we measured mangrove canopy height with a clinometer. Ambient wind velocity was measured at 1.5-m intervals from ~1 m above the mangrove canopy to 1 cm above the ground with a hot-bead anemometer (Cole-Parmer 37000–60). Average free-stream wind velocity was computed from continual observations collected at 10-min intervals by the automated weather station at Carrie Bow Cay, 10 km north of Peter Douglas Cay (Hagerman and Smith, 1993). Degree of canopy openness (a in Eq. 2) was estimated from these data using nonlinear regression (NLIN procedure of SYSTAT version 5.03 [Wilkinson et al., 1992]). We predicted seed dispersal distances from Eqs. 1 and 6. We compared these predicted values with measured dispersal distances of *Brassavola* seeds under wind tunnel and laboratory conditions.

Wind-tunnel experiments—Because of the small size of orchid seeds and the muddy substrate of mangrove swamps, we could not track individual seeds in the field. Therefore, we obtained population seed dispersal curves (seed shadows) in a laminar-flow wind tunnel at the University of Connecticut (Department of Natural Resources), to obtain estimates of dispersal distances with minimal air mixing (turbulence). Groups of seeds coated with fluorescent dust were dispersed onto a 7 × 1.8 m sheet of paper divided into a grid of 10 × 10 cm squares. Seeds were released 0.5 m above ground level at four mean wind velocities (1.25, 1.29, 1.40, and 2.09 m/s). Wind velocities during trials were measured with a hot-bead anemometer. We counted the number of seeds dispersed into each square under ultraviolet illumination.

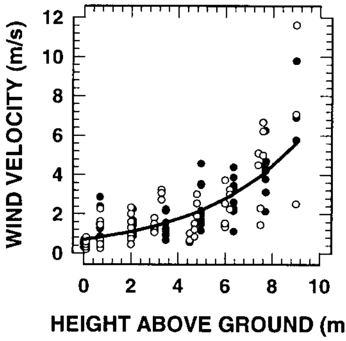

Fig. 2. Results of nonlinear regression used to estimate the parameter a of Eq. 2. Solid symbols are data from Site I, open symbols are data from Site II, and the solid line is the best-fit nonlinear regression line through all the data.

Laboratory experiments—Due to limitations of the construction of the wind tunnel we were unable to vary the height of release or generate measurable turbulence. We therefore repeated this experiment using a larger fan in an open laboratory. We measured dispersal shadows of seeds released at three heights (0.5, 1, and 1.5 m) representing the range of heights at which we found *Brassavola* growing in Belize. In addition, using a fan greatly increased turbulence relative to wind tunnel conditions and these swirling air patterns created by the fan allowed us to assess more directly the influence of turbulence on dispersal patterns. Wind velocity at point of release directly in front of the fan ("gust" velocity) varied from 1 to 4 m/s. We also measured actual wind velocities at 50-cm intervals from the fan parallel to the forward flow of air throughout the wind field. Seeds were dispersed and counted in a similar fashion as in the wind tunnel, although size of the dispersal area in the laboratory was 8 × 1.2 m.

RESULTS

Seed characteristics—Mean dimensions of a *Brassavola* seed were 640 ± 40.6 [SD] × 56 ± 4.8 μm (Fig. 1). Mean seed mass was 1.60 μg, and mean terminal velocity (U_t) was 0.157 m/s for seeds without dust. Addition of fluorescent dust nearly doubled terminal velocity to 0.29 m/s.

Field conditions—Average mangrove canopy height was 8.05 m at both sites on Peter Douglas Cay. Average daily peak free-stream wind velocity (i.e., above the canopy) from September 1991 to January 1993 at nearby Carrie Bow Cay was 4.9 m/s (range 4.15–6.66 m/s). We used nonlinear regression to estimate canopy openness (a) from Eq. 2 by combining this value for U_f together with our field measurements of wind velocities under the mangrove canopy of Peter Douglas Cay (Fig. 2). The estimated value for a did not differ significantly between the two sites (site 1: a = 1.99 ± 0.167, r^2 = 0.90; site 2: a = 2.33 ± 0.794, r^2 = 0.79; both sites pooled: a = 2.14 ± 0.155, r^2 = 0.85). Plants grew 1–2.9 m above ground with most (90%) occurring between 0.2 and 1.2 m (0.9 ± 0.51 m).

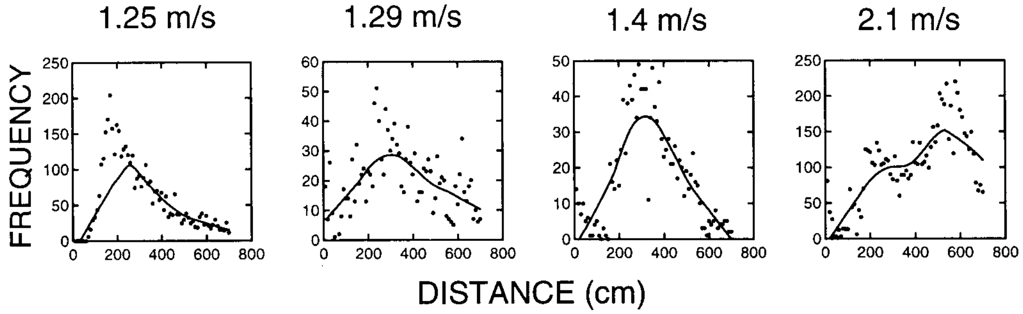

Fig. 3. Dispersal curves for wind-tunnel observations. Wind velocities are 1.25, 1.29, 1.40, and 2.09 m/s. All release heights are 0.5 m. Smoothed curves fitted by loess.

Wind-tunnel dispersal experiments—The four trials in the laminar-flow wind tunnel had average wind velocities of 1.25 ± 0.135, 1.28 ± 0.155, 1.40 ± 0.075, and 2.09 ± 0.25 m/s. Modal dispersal distances were estimated from local regression (loess; Cleveland, 1979) as 2.00, 2.30, 3.30, and 5.90 m respectively (Fig. 3).

Height of release and modal dispersal distance were used to estimate λ and W^* of dusted seeds for each trial under nearly laminar flow conditions. Equations 2, 3, and 5 yielded estimates of $\lambda = 0.71 \pm 0.456$ ($N = 4$) and $W^* = -0.04 \pm 0.055$ (N = 4), while if we assumed that seeds were "heavy" ($\lambda \approx 1$), we would estimate $W^* = 0.11 \pm 0.347$ from Eq. 4.

Laboratory dispersal experiments—Directly in front of the fan, the wind velocity was nearly 8 m/s, but it declined to 1.03 ± 0.443 m/s within 2 m. Average wind direction was $\pi/6$ radians (30°) off from directly parallel to the plane of seed release and perpendicular to the fan blade. Because of variation in dispersal from the straight line perpendicular to the plane of seed release, we constructed a two-dimensional seed shadow by computing the sum of all seeds dispersed along parallel planes at a given distance from the plane of release. This "crosswind integrated deposition" (CWID) shadow was used to estimate x_m in these experiments (see Okubo and Levin [1989] for a mathematical discussion of the validity of using CWID in this model).

Seed dispersal curves in the open laboratory are illustrated in Fig. 4 for all combinations of seed release heights and wind velocities at point of release (gust velocity). The average wind velocities that seeds encountered in the 8-m wind field in these trials were 1.24 m/s (4 m/s gust velocity), 1.11 m/s (3 m/s gust velocity), 1.05 m/s (2 m/s gust velocity), and 0.96 m/s (1 m/s gust velocity). Modal seed dispersal distance based on CWID

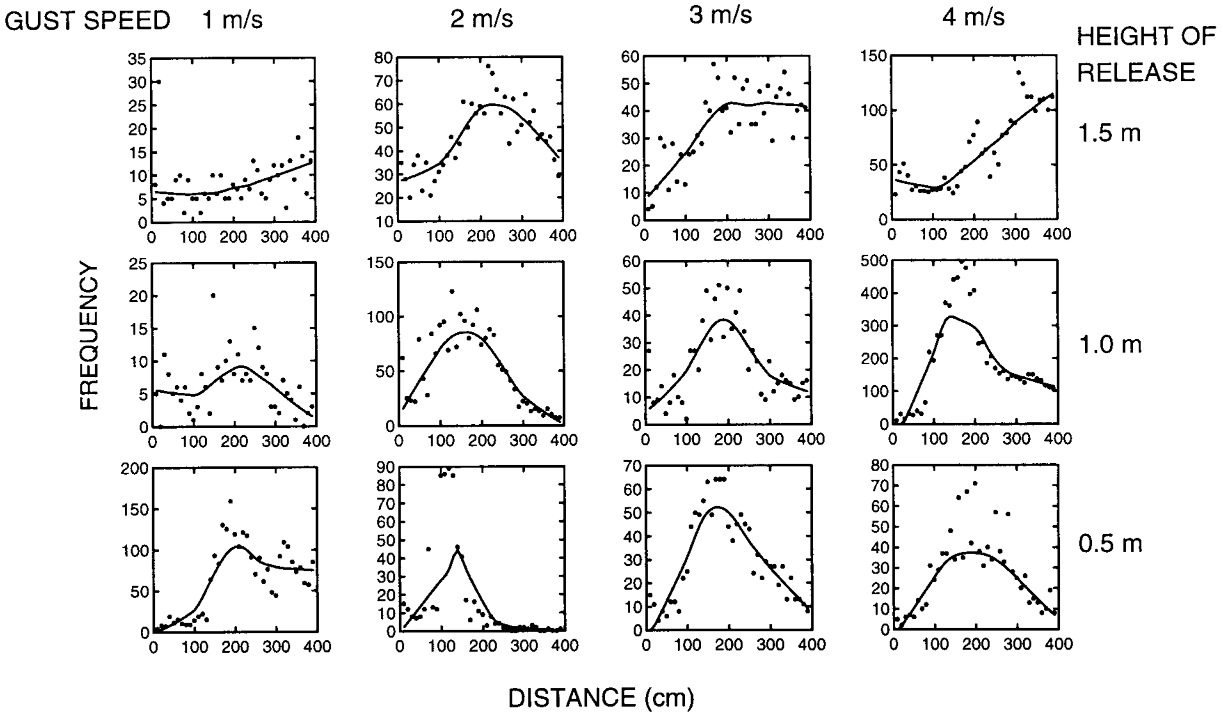

Fig. 4. Dispersal curves in the open laboratory, for varying heights of release and wind velocity at release. Note that the scale of the ordinates varies by up to a factor of 20 among panels. Symbols represent CWID at 10-cm intervals. Curves were fitted by loess.

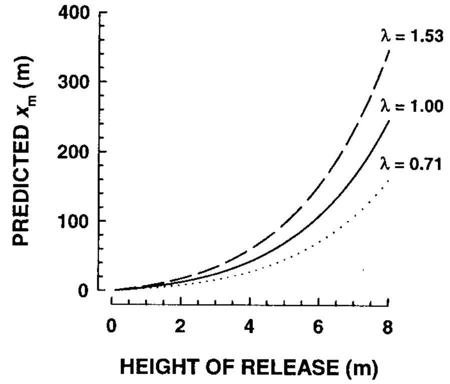

Fig. 5. Predicted x_m for different heights of release where a = 2.14, z = 8.05 m, and U_t = 4.9 (conditions at Peter Douglas Cay). Curves shown are for λ = 1 (Eq. 1), λ = 0.71 (wind tunnel), and λ = 1.53 (laboratory).

perpendicular to the plane of release and the CWID perpendicular to the direction of wind flow (π/6 off from the plane of release) did not differ significantly (Z = 0.14, P = 0.89, Wilcoxon signed-rank test). Therefore, we used the results based on CWID perpendicular to the plane of release for further analysis.

Gust velocity at release did not significantly affect x_m ($F_{3,6}$ = 2.17, P = 0.19, ANOVA), while height of release did ($F_{2,6}$ = 6.13, P = 0.04, ANOVA). Using x_m derived from Fig. 4, we estimated λ = 1.55 ± 0.530 and W* = 0.94 ± 0.867 (Eq. 5) and W*= 0.14 ± 0.166 for dusted seeds. Assuming no change in x_m as a result of the fluorescent dust, but using U_t for undusted seeds gives an estimate of λ = 3.23 ± 1.392 (N = 12) and W^* = 0.51 ± 0.219 (N = 12). Modal seed dispersal distances derived from the simple ballistic model (Eq. 1) and the model with a turbulence term added (Eq. 6) for the conditions observed at Peter Douglas Cay are shown in Fig. 5. Observed x_m in the wind tunnel did not differ significantly from x_m predicted by Eq. 6 (Fig. 6; Z = 1.29, P = 0.20, Wilcoxon signed-rank test), although x_m observed in the laboratory was significantly lower than that predicted (Z = 2.74, P = 0.006, Wilcoxon signed-rank test). The addition of λ (turbulence) significantly increased the predicted x_m relative to that predicted by the ballistic model. As height of release and wind velocity increased, the difference in x_m predicted by the two models also increased.

DISCUSSION

Our estimates of modal dispersal distance of *Brassavola* seeds corresponded well to that of the ballistic model, but less well with the predictions of Okubo and Levin's (1989) model. Our estimates of λ and W^* fell within the same order of magnitude that they reported for other dust-like seeds and pollen, but our estimates of λ increased by a factor of 2–5 with increases in wind velocity at point of release and height of release. These results highlight not only that modal dispersal distance depends on ambient wind velocity and turbulence and height of release, but also that estimates of the magnitude or effect of turbulence based simply on modal dispersal distance and terminal velocity of seeds are strongly dependent on experimental conditions.

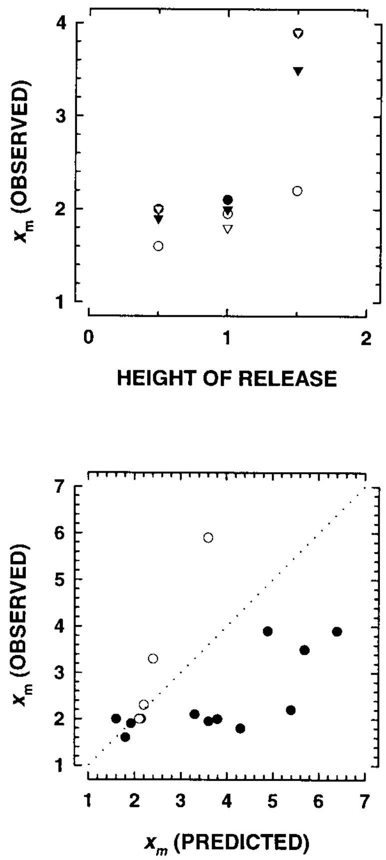

Fig. 6. (Top) Relationship between height of release and x_m in the open laboratory. Symbols represent different wind velocities at point of release. (Filled circle = 1 m/s; open circle = 2 m/s; inverted filled triangle = 3 m/s; open inverted triangle = 4 m/s). (Bottom) Comparison between observed x_m and x_m predicted from Eq. 6 for seeds with fluorescent dust. Open circles are wind-tunnel values and closed circles are laboratory values.

Seeds of the size found in *Brassavola* are particularly interesting because λ approaches 1 in laminar-flow conditions, but increases with increasing turbulence. Okubo and Levin (1989) categorized the response of seeds to vertical mixing (turbulence) based on whether λ ≈ 1 (heavy seeds) or λ ≫ 1 (light seeds). *Brassavola* seeds coated with fluorescent dust are on the edge between "heavy" and "light," and λ for dusted seeds in laminar flow conditions was just below 1. However, in turbulent conditions, dusted *Brassavola* seeds behaved more like "light" seeds: λ = 1.5. Once we accounted for the effects of the fluorescent dust (by using measured terminal velocities of undusted seeds), our estimate of λ increased to 3.3. It appears that the use of fluorescent dust, necessitated by the small, dust-like nature of the seeds, was sufficient to shift the seeds from "light" to "heavy." Nevertheless, based on observed terminal velocity of *Brassavola* seeds and observed conditions of the mangrove forest at Peter Douglas Cay, our predictions of modal dispersal distance paralleled more closely the expectations of this model than have previous studies, most of which used larger seeds with plumes or wings (reviewed by Willson, 1993).

We used our data to explore the ballistic model (Eq.

1) and Okubo and Levin's (1989) model (Eq. 6) of dispersal for populations of small, dust-like seeds. In laminar-flow conditions of a wind tunnel, the effects of turbulence approach zero and release height was constrained to be low (0.5 m). At these low release heights, and with the low turbulence and relatively low wind velocities at point of release in the wind tunnel, the data closely conformed to the ballistic model of seed dispersal (Fig. 6). However, with increased height of release, increased wind velocity at point of release, and increased turbulence in an open laboratory, x_m was greatly reduced relative to that predicted by the ballistic model (Fig. 6). Because wind flow patterns in tropical forests may correspond more closely to turbulent air flow patterns used in the laboratory than in the laminar flow conditions of the wind tunnel, the importance of incorporating effects of turbulence into ballistic models of seed dispersal should not be underestimated.

On tropical islands, one of the most important sources of turbulence is convection, the transfer of heat by moving air. Although convection could lift some orchid seeds high into the atmosphere in swirling eddies and thus increase the maximum possible seed dispersal distance, turbulence under a forest canopy serves to reduce the modal dispersal distance (Okubo and Levin, 1989; Eq. 6 and Figs. 3, 4, above). Although there are apocryphal reports of the recovery of orchid seeds high in the stratosphere, Arditti (1992) noted that once orchid seeds reach high altitudes, ultraviolet radiation rapidly renders them inviable. Furthermore, the variance in seed dispersal distance observed in the wind tunnel and the laboratory was relatively small (Figs. 3, 4) although the proportion of seeds that resulted in rare long-distance dispersal was not considered.

Because orchids are epiphytic, successful seeds will be those that are deposited on aboveground structures (branches, boles, etc.), whereas wind-tunnel experiments predict modal dispersal distance at ground level. For seeds to land on branches or boles, the arc of seed deposition from height of release must be intercepted before the seed reaches the mangrove forest floor (Aylor, 1982), thus shortening expected dispersal distances even further. On the other hand, to understand landscape-level patterns of orchid distribution on the hundreds of mangrove islets in the lagoon of the Belizean barrier reef complex, we need to document and better understand the long "tail" of the dispersal curve and the consequent importance of rare long-distance events in the establishment of new populations. In a subsequent paper, we will develop a dynamic model relating dispersal characteristics of *Brassavola* and size and tracks of irregular tropical cyclones to the distribution of this orchid on Belizean mangrove cays.

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