DISPERAL OF SEEDS BY THE TROPICAL SEA BREEZE

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Abstract. Given the dependence of most wind-pollinated and wind-dispersed species on low relative humidity (RH) for abscission, and the minimization of RH in the early afternoon, there ought to be a marked directional bias in seed dispersal at sites with a strong local diurnal circulation. We filmed the abscission of seeds of five wind-dispersed tropical species near the coast of Mexico (Jalisco). We found that (1) most abscission occurred during the period from 10:00 to 17:00 hours; (2) there was a strong bias for landward dispersal due to the midday sea breeze; (3) the little nocturnal dispersal that occurred was toward the sea (due to the night land breeze); (4) there was no abscission in the absence of wind (i.e., indoors) except for one species; and (5) holding relative humidity constant, the proportion of seeds diurnally abscising is strongly correlated with horizontal wind speed. We predict that a similar bias (this time for upslope dispersal) for xerochastic dispersal will occur in complex terrain. We conclude that in coastal and mountainous terrain, dispersal models (and inverse modeling efforts) must include a directionality term.

Key words: abscission; anisotropy; diurnal local air circulation; island, coast, and montane seed dispersal; Mexican tropical fruit; pollen dispersal; relative humidity and ascission; seed dispersal; wind speed and dispersal.

INTRODUCTION

There has been relatively little study of anisotropy (directional bias) of seeds, spores, or pollen dispersed by the wind. The lack of interest may be due to the dearth of convincing evidence that the effect is sufficiently strong to matter ecologically or genetically. Anisotropy can arise from the interaction of a brief abscission window (characteristic of most wind-pollinated and some wind-dispersed plants) with the prevailing wind direction of a slowly passing mid-latitude cyclone. This sort of bias would be averaged out over several years. Here we concentrate on situations where strong directional bias persists both within and among years.

Consistent and strong anisotropy is of interest for several reasons. In regional-scale biogeography, anisotropy can be more important than proximity among islands (e.g., Munoz et al. 2004). Also, as shown recently by Staelens et al. (2003), inverse modeling to solve for parameter values within a dispersal model can be seriously hampered by the simplifying assumption of isotropy. An additional way in which direction might matter was first broached in a letter from C. Darwin to J. D. Hooker (Burkhardt 1998), where he commented on the very large number of species of wingless Coleoptera on islands he had visited when he was younger, and arrived at an explanation: too many adults would be blown out to sea. Similar assertions have been made for flightless birds and for reduced dispersal capacity in insular plants (although alternative arguments are available: Carlquist 1966, Diamond 1991). We will argue that most diurnally active organisms (including seeds) will tend to be transported inland.

For dispersal by wind we can imagine two main ways in which directional biases might be consistently strong. First, anisotropy could result from relatively constant prevailing winds at the global circulation scale, with this effect not counteracted by other, smaller-scale factors. Especially for long-distance dispersal of pollen, spores, very small seeds (e.g., the Orchidaceae), and pathogens among islands, the westerly or trade-wind belts dominate the spatial patterning (e.g., Close et al. 1978, Munoz et al. 2004).

A second way in which we might obtain strong anisotropy is where the wind direction is correlated with large shifts in relative humidity (RH). For wind-dispersed plants (pollen and seeds), the sparse literature on seed abscission suggests that the bulk of angiosperm and gymnosperm species are xerochastic (separation layer development is dependent upon drying) and thus abscission occurs primarily when (1) RH is low (Greene and Johnson 1992, Jackson and Lyford 1999); and (2) wind speeds are greater (i.e., a motive force—drag or branch vibration—is required to effect the final separation of the seed from the maternal parent) (Aylor et al. 1981 [for spores], Greene 2005, Schippers and Jongejans 2005). (Indeed, the probability of abscission is propor-
tional to drag, which is, in turn, proportional to the square of the wind speed; Greene 2005.)

At the synoptic scale, winds derived from air masses situated over extensive deserts (e.g., the Sirocco in the Sahara or Sharav/Hamsin in the eastern Mediterranean) will tend to be much drier than air masses developed over other locations. Thus, as shown by Nathan et al. (1999), there is far more abscission from dry southeastern winds in Israel than would be expected from an examination of vane readings. The Santa Ana wind or any other Foehn-type wind represents a descending, adiabatically warmed mass, and since in this process the saturation mixing ratio (amount of water vapor per unit volume) increases, the air can readily extract water from plant tissues, favoring rapid drying of separation zones. Harris (1969) showed that in coastal British Columbia, where north–south mountain ranges lie perpendicular to prevailing winds developed over an ocean, most seed abscission in Picea and Tsuga occurred during the few days when drying air descended from the mountains.

The other way in which RH could exert a consistent anisotropy is via interaction with a diurnal local circulation, for example along sea coasts and the margins of very large lakes. RH typically decreases during the day, reaching a minimum in the early afternoon, because warmer air can hold more water vapor than cooler air (Fig. 1). Land surfaces near coasts heat up during the day (and lose heat at night) far more rapidly than the adjacent water body. In consequence, a local circulation develops with a surface sea breeze (air moving from the sea toward the land) initiating in the morning and intensifying to an early afternoon peak (Simpson, 1994; McGregor and Nieuwolt, 1998; Fig. 1). Following sunset, the land cools rapidly and a land breeze, typically much weaker than the preceding sea breeze, dominates during the evening, the surface air now moving toward the water.

The sea breeze attenuates with distance inland, and is barely detectable at 50 km from the coast (McGregor and Nieuwolt 1998). While this local circulation is especially strong in the tropics and subtropics, it can be largely overridden by synoptic-scale circulation events, and especially strong in the tropics, for wind, temperature, and humidity during the day, reaching a minimum in the early afternoon, because warmer air can hold more water vapor than cooler air (Fig. 1). Land surfaces near coasts heat up during the day (and lose heat at night) far more rapidly than the adjacent water body. In consequence, a local circulation develops with a surface sea breeze (air moving from the sea toward the land) initiating in the morning and intensifying to an early afternoon peak (Simpson, 1994; McGregor and Nieuwolt, 1998; Fig. 1). Following sunset, the land cools rapidly and a land breeze, typically much weaker than the preceding sea breeze, dominates during the evening, the surface air now moving toward the water.

In 2004 we appended mature fruits of five tropical species (Table 1; Fig. 2) from a wooden crossbar and recorded the direction traveled, relative humidity (RH), and time of day for seed abscission (see Plate 1). We also determined the relationship between wind speed and the probability of abscission at a short averaging time using a camcorder and anemometer. This abscission experiment was conducted during the dry (leafless) winter season in a small clearing, 20 × 40 m, amid 20-m-tall trees, 200 m from the coast at Careyes (Jalisco, Mexico; 19°26′37.2″ N, 105°01′32.1″ W).

All of the species (Cosbea aesculifolia (H.B.K.) Britt. & Baker, Pseudobombax ellipticum (H.B.K.) Dugand., Cochlospermum vitifolium (Willd.) Sprq., Matelea quirosii (Standl.) Woods., and Swietenia humilis Zucc.) had dehiscent fruits with seed numbers averaging 40 (S. humilis) to ~80 (M. quirosii) seeds (examples in Fig. 2). All but the winged seeds of S. humilis have drag-promoting fibers. The diaspores are large: the smallest (C. vitifolium) had a diameter of about 2.5 cm from fiber tip to tip. The fruits were attached to the horizontal bar at 1.45 m height only after they showed marked pericarp dehiscence. We deliberately chose this very low height in a small clearing as we wanted to limit the distance that seeds might travel so we could easily gather data on abscission events at night; that is, we assumed we could find every seed lying on the ground within that clearing the next morning. For each fruit, the pedicel was attached to the bar with 2-mm-diameter wire; the fruit

![Fig. 1](https://example.com/fig1.png)

**Fig. 1.** The temporal pattern, typical of a coastal station in the tropics, for wind, temperature, and humidity during the hours 07:00 to 21:00, at the Manzanillo airport recording station (70 km south of our site in southwestern Mexico and 2 km from the coast) for the 24 days of our 2004 abscission experiment. Here we show RH (a measure of how much moisture the air can hold before it is saturated), temperature, wind speed (at 10-m height above the ground), and specific humidity (ratio of the absolute mass of water vapor to the mass of the air).

**Methods**

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was able to sway with the wind somewhat, and each was sufficiently far from others so that inter-fruit contact could not occur in a strong wind. We used 6–12 fruits per species (Table 1). When few seeds remained, a fruit was removed. The camcorder (mini-DV) was placed about 0.5 m lower than, and 1.5 m from, the bar. Filming was done from 08:00 to 18:00 hours each day from 18 March to 15 April, a primarily cloudless period, with two gaps: 24–25 March and 1–3 April. There was no rain during the experiment.

To determine direction traveled and time of day for abscission, we systematically searched for the diaspores in the sparse grass in the clearing each hour. Likewise, in the morning we searched for nocturnally abscised seeds. It is very unlikely we overlooked any of these conspicuous diaspores.

### Table 1. Percentage of seeds abscising, by direction.

<table>
<thead>
<tr>
<th>Species</th>
<th>Wind-source direction†</th>
<th>Total no. seeds (fruits)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>West</td>
<td>East</td>
</tr>
<tr>
<td><strong>2004</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Swietenia humilis</em></td>
<td>73.4</td>
<td>10.7</td>
</tr>
<tr>
<td><em>Pseudobombax ellipticum</em></td>
<td>57.2</td>
<td>13.0</td>
</tr>
<tr>
<td><em>Cochlospermum vitifolium</em></td>
<td>57.8</td>
<td>21.5</td>
</tr>
<tr>
<td><em>Matelea quirosii</em></td>
<td>82.1</td>
<td>7.6</td>
</tr>
<tr>
<td><em>Ceiba aesculifolia</em></td>
<td>74.9</td>
<td>16.7</td>
</tr>
<tr>
<td><strong>2003</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>C. aesculifolia</em> (isolated tree)</td>
<td>60.3</td>
<td>11.6</td>
</tr>
</tbody>
</table>

Note: The first five rows are from the 2004 experiment; the final row is for seeds recovered in 2003 from 5–150 m away from a *Ceiba aesculifolia* tree well-isolated from all other fruiting conspecifics.

† At our study site, winds blowing toward the land would be, essentially, from the west, with lesser amounts from the north and south.

![Fig. 2](image_url). Illustrations of fruits and seeds (drawings by V. Crisfield). (Clockwise from upper left): (a) Dehiscing fruit of *Cochlospermum vitifolium* showing the expanded diaspores after drying of the fibers (*Pseudobombax ellipticum* and *Ceiba aesculifolia* [not shown] have similar seeds and fruits except that they are larger and the pericarp will completely absise), (b) The opening of the woody pericarp of *Swietenia humilis* with the winged seeds, appressed to the placenta, pointed downward toward the pedicel. (d) The winged seed of *S. humilis*. (c) The opening fruit of *Matelea quirosii* along with an example of a seed.
RH was measured with a sling psychrometer (Ambient Weather, Phoenix, Arizona, USA) in the shade while wind speed near the fruits was measured with a cup anemometer (Campbell Scientific, Edmonton, Alberta, Canada) on an hourly basis. There were, however, two periods totaling five days (24–25 March and 1–3 April) when no filming took place; the fruits were brought indoors and hung from a length of wire.

As a measure of the likelihood of abscission we used the ratio of the proportion of seeds abscising in a RH class divided by the proportion of the dispersal season occupied by that RH class. We will call this ratio the abscission index. We used the RH classes 30–40%, 40–50%, etc, but lumped 80–100% as a single class because, at this time of year, RH >90% was quite rare.

The abscission index should be proportional to the (unknown) probability of abscission so long as there were enough fruits available to provide a representative sample of the RH and wind-direction range. This assumption is reasonable for three of the species (seeds available for abscission for >20 of the 25 days) but is weaker for M. quirosii and P. ellipticum (6 days in March and 3 days in April, respectively).

We did not film seed abscission or collect weather data at night at the clearing; instead we relied on the weather data of Dr. R. Ahedo at the Chamela Biological Station, 6 km north of the clearing and 2 km from the coast. Unfortunately, the sensors at the Station stopped recording in early April 2004. For that month we had to use data from the recording station at Manzanillo airport, 2 km from the ocean and ~75 km south of the Chamela Station. (Given that we are using mean hourly values over extended periods, the correlation among the three sites is strong; e.g., $r^2 = 0.89$ for March 2002 daily hourly temperature at Manzanillo and Careyes.)

For each species, we regressed the abscission index on RH, expecting a negative slope. One problem was that for the night data we could know the percentage of time spent in any RH class, but for the seeds we could only know the total number collected on the ground in the clearing the next morning. Our solution was to take the mean of the nocturnal RH values, and, since all these
RH means are >80%, add to this category the small number of diurnal RH values that had RH >80%. We need not worry unduly about this as few seeds abscised at night, and very few abscised diurnally on the rare occasions with RH >80%.

We selected four 4-h periods (22, 24, 26 March and 15 April) to study the effect of wind speed on the abscission of the five species. These intervals were chosen because each (1) had a large number of abscission events by at least one of the species; (2) exhibited less than a 5% change in RH (measured in shade) from start to end; and (3) showed little or no cloud cover (so we need not worry about major changes in RH around the fruit surfaces). Using a 10-s averaging time, we divided the ~1440 minutes of each period into a maximum of 11 horizontal wind-speeds classes ranging up to (midpoint) 3.1 m/s (we saw no 10-s speed greater than ~3.2 m/s.) Any speed interval without at least one abscission event was ignored for the log–log regression of $p$ (the proportion of available seeds abscising) on wind speed.

To compare our experimental results with actual dispersal from a plant, we examined seed dispersal from an individual tree of *Ceiba aesculifolia* in a continuous 10–20-m-tall forest 4 km from the coast and about 10 km north of our clearing. These data were collected in 2003 during a two-week period that marked the start (15 January) and end (27 January) of seed abscission from the 42 fruits suspended on the tree. There were no other fruiting conspecific trees within 400 m of this canopy tree in 2003. From its base, we searched the entire area for seeds out to a distance of 250 m using a grid and field tapes, and recorded the distance and direction of all seeds. The hemispherical ball of tangled white fibers (the “kapok”) attached to each seed had an average diameter of 5 cm, and so the black seeds (diameter ~1 cm) were easy to find. We ignored any seeds within 5 m of the trunk; given the crown diameter we could not be sure of the direction traveled. The maximum distance a seed was retrieved was 115 m.

**RESULTS**

The seeds of almost every fruit were exposed to at least one full 24-h cycle of relative humidity (RH), wind speed, and wind direction. Averaging across species in the clearing experiment, the mean time span between 10% and 90% cumulative release of seeds from fruits was about three days (ranging from five hours [a *Pseudobombax ellipticum* fruit] to 12 days [a *Cochlospermum vitifolium* fruit]). For the lone *Ceiba aesculifolia* tree at the Chamela station, the 42 fruits exposed to the much higher wind speeds in the upper canopy were emptied within a 12-day span; the average time for each fruit was not known.

Abscission was significantly (chi-square, $P < 0.05$) concentrated during the middle of the day (10:00–16:30 hours), these 6.5 hours accounting for 93% of all the dispersal during 24 hours (Fig. 3). This period of greatest abscission roughly corresponded to the interval when the sun was above the adjacent tree crowns and therefore directly shining on the fruits: based on the filming, the direct insolation interval averaged from 09:45 to 16:40 hours at this time of year on cloudless days. The footage indicated that direct insolation could fully dry the damp, matted exposed fibers of *C. aesculifolia* or *P. ellipticum* as woody pericarp pieces fell away in as little as 30 minutes, while in cloudy weather it could take as much as 36 hours. The night (defined as the interval from 19:00 hours to 08:00 hours the next day) accounted for <4% of all abscission (Fig. 3). Comparison of video footage (one side of the fruits only of course) from the final evening tape with the first tape from the next morning showed that this result was
due to a paucity of abscission rather than to a high nocturnal predation rate on the ground.

Coarsely, this temporal abscission pattern corresponded to changes in RH. On average, ambient RH (measured in the shade at the edge of the clearing) was 84% at night, 71% at 10:00 hours, declining to a minimum of 64% at 14:00 hours. Nonetheless, there was no significant correlation between the abscission index (see Methods, above) and RH for any of the five species alone ($P > 0.05; N = 4–6$ RH classes; Fig. 4). A significant correlation could only be achieved by lumping all species together ($r^2 = 0.46; P = 0.0002; N = 25$ RH classes; Fig. 4).

The bias toward midday abscission led to a strong eastward (landward) component in dispersal (Table 1) with 68% of the seeds (all species lumped) in the experiment dispersing toward the eastern quadrant. By contrast, the vane data showed that the wind was from the western quadrant only 38% of the time (and mainly during the day, of course). For all individual species, the bias toward the east was highly significant (chi-square; $P \ll 0.05$). Likewise, for the isolated canopy tree of $C. aesculifolia$ in 2003, we found that 60% of the seeds dispersed toward the east (again, a highly significant difference). By contrast, at night 54% of what little dispersal occurred was due to the land breeze (i.e., the seeds moved toward the west), and this corresponded to the vane data where 52% of the nocturnal winds were moving toward the west.

The role of the wind as a motive force was demonstrated when fruits of all species were placed indoors (two intervals totaling five days). Only $Matelea quirosii$ (25% of its seeds) had any abscission in the absence of wind. Further, within the clearing during the day, there was a very strong relationship between horizontal wind speed and the proportion of available seeds abscising for all five species (Table 2). The slope (exponent of the power-law argument) was not significantly different from the expectation of 2.0 except for $M. quirosii$ whose slope was far lower.

**DISCUSSION**

Aside from Greene and Johnson (1992) and Greene (2005), we have little empirical documentation of the

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**Table 2.** Power-law regression results for proportion of available seeds abscising vs. wind speed (m/s) for 4-h periods, together with the date and number of seeds abscised for each 4-h period.

<table>
<thead>
<tr>
<th>Species</th>
<th>Intercept (95% CI)</th>
<th>Exponent (95% CI)</th>
<th>$r^2$†</th>
<th>$N^\dagger$</th>
<th>No. seeds abscised</th>
<th>Date</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Swietenia humilis</em></td>
<td>0.0005 (0.0002–0.0012)</td>
<td>2.75 (1.49–3.99)</td>
<td>0.73</td>
<td>10</td>
<td>59</td>
<td>22 March</td>
</tr>
<tr>
<td><em>Pseudobombax ellipticum</em></td>
<td>0.0005 (0.0003–0.0009)</td>
<td>2.25 (1.69–2.80)</td>
<td>0.89</td>
<td>11</td>
<td>140</td>
<td>15 April</td>
</tr>
<tr>
<td><em>Cochlospermum vitifolium.</em></td>
<td>0.00006 (0.00002–0.00014)</td>
<td>2.75 (1.62–3.88)</td>
<td>0.75</td>
<td>11</td>
<td>67</td>
<td>26 March</td>
</tr>
<tr>
<td><em>Matelea quirosii</em></td>
<td>0.0008 (0.0004–0.0014)</td>
<td>1.02 (0.47–1.56)</td>
<td>0.69</td>
<td>9</td>
<td>167</td>
<td>28 March</td>
</tr>
<tr>
<td><em>Ceiba aesculifolia</em></td>
<td>0.0006 (0.0003–0.0010)</td>
<td>2.03 (1.25–2.81)</td>
<td>0.82</td>
<td>8</td>
<td>115</td>
<td>22 March</td>
</tr>
</tbody>
</table>

*Notes:* The 95% confidence interval (CI) for log–log intercept (rendered here as the exponential of the regression intercept) and exponent are given in parentheses. Each 4-h period is approximately 10:00–14:00 hours for all but *P. ellipticum* (11:00–15:00 hours).

† The proportion of the variance explained by the regression (in all cases, $P < 0.001$).

‡ The number of wind-speed classes.
abscission behavior of anemochorous (wind-dispersed) seeds outdoors at averaging times less than about 24 hours. The results here make clear that dispersal of xerochastic seeds is a *diurnal* process. Essentially, no abscission occurred at night, dawn, or dusk. More specifically, there was very little abscission unless the sun was directly shining on a fruit. For the seeds with fibers (all but *Swietenia humilis*), full expansion of initially damp fibers could occur in less than an hour in full sun but take more than a day in cloudy weather. We followed convention and measured relative humidity (RH) in the shade, but clearly the boundary layer of opening fruits is where the measurement could be more usefully made, and within that 1-mm-thick layer the RH will decrease sharply (due to a sudden elevation of temperature) as the fruit passes from shadow to direct insolation.

Given the dependence of seed abscission on low RH, it follows that any local, reliable diurnal circulation, such as a sea breeze–land breeze regime, should cause a strong dispersal anisotropy; as reported here almost 70% of all seeds were dispersed toward the eastern quadrant by the sea breeze. Our expectation of a pronounced landward bias could only be incorrect if the nocturnal surface flow (the land breeze in this case) tended to be (1) a much stronger wind or (2) a much drier wind due to very low specific humidity. With regard to the magnitude of the wind, generally speeds at night are only one third as strong as during midday (McGregor and Nieuwolt 1998; Fig. 1). Specific humidity declines at night along coasts (e.g., Fig. 1), but this effect on the relative humidity is more than compensated for by the decline in temperature—i.e., the net effect is that RH is much higher at night.

Wind speed was by far the most important agent at the scale of a few hours at mid-day when RH necessarily could change little. Further, there was no abscission in the indoor experiment (except for *Matelea quirosii*) without wind. The diurnal behavior of these xerochastic anemochorous seeds therefore was governed primarily by the direct effect of horizontal wind speed, which, all else equal, is maximized an hour or two after noon (Greene and Johnson 1992, Nathan et al. 2000).

Nonetheless, one hesitates to say that wind is the main actor and RH is limited to merely “setting the stage” by dehiscing covering pericarps or drying diaspore fibers; a sufficiently fast drying time means that many seeds will simply never get the opportunity to be abscised by a land breeze. Disentangling the relative importance of RH and wind speed in field situations is challenging, given their strong inverse relationship. Further, they may interact in subtle ways. For example, drying expands the initially damp, drag-promoting fibers for a species like *Ceiba*, thus increasing the drag force (Greene and Quesada 2005). More obviously, increasing the wind speed will greatly hasten evaporative loss and thus the drying of the fibers. We suggest an experiment in which, simultaneously for a set of conspecific fruits attached to a bar, some are shaded (a parasol above), and some have reduced wind speed (a mesh placed windward). Further, fruits with pericarps removed could be brought outside at night and placed in front of a fan; and fruits, never exposed to the sun, could be placed in front of an indoor fan.

*M. quirosii* is a special case. It was the only species we examined capable of abscising without wind as the motive force. (By contrast, many fungi can abscise spores in the absence of wind; cf. Aylor 1990.) Further, it was the only species in which dependence of the probability of abscission on wind speed had an exponent significantly different from 2.0. Not coincidentally, *M. quirosii*, unlike *Ceiba aesculifolia*, *Cochlospermum vitifolium*, and *Pseudobombax ellipticum*, has fibers that do not curl. Indoors, we observed the fibers of each seed, initially appressed to the placenta as a damp sheath, slowly drying after pericarp dehiscence and then expanding outward *away from one another* and therefore pushing away from the placenta. The net effect of this expansion was that the seed was pulled from the placental wall. Thus, as we found with the indoor experiment, this was the only species that could abscise without any wind providing a motive force. We predict that the same tendency for lessened dispersal will occur among the closely related *Asclepius* (milkweed) or any other Asclepiadaceae.

Aside from *M. quirosii*, the results presented here (Table 2) for the dependence of the abscission probability on horizontal wind speed are similar to the mid-latitude herb *Taraxacum officinale* (dandelion; Greene 2005) and tree *Acer saccharinum* (silver maple: Greene and Johnson 1992). One suspects that a simple dependence of abscission on drag can be accepted as a general argument for most species.

Turning from coastlines, we can assume that the same directional bias demonstrated here will operate in mountainous terrain. The local circulation system within a steep-sided valley creates upslope winds during the middle of the day when, for example, the scales of ovulate cones of gymnosperms such as *Picea* or *Pinus* would be flexed open in response to low RH. Thus, wind-dispersed tree species in well-dissected terrain should migrate more easily upslope than downslope.

We should recall that a minority of angiosperms (e.g., *Hebe*, in New Zealand) and many cryptogams are hygrochastic (i.e., abscission will be dependent on tissue hydration), and so the directional bias would be the opposite of what was described here. Such species would disperse seeds or spores primarily toward the sea (or downslope in mountainous terrain) at night.

As a final consequence for plant dispersal on continents, we postulate that seed abscission for all xerochastic wind-dispersed plants will be concentrated in the early afternoon when atmospheric instability is at its maximum. Therefore, long-distance dispersal, dramatically promoted by updrafts (Soons et al. 2004), will be much greater than we might otherwise have
concluded from meteorological models of dispersal (cf. Jackson and Lyford [1999] for pollen; Aylor et al. [1981] for spores). This will be true whether the source of the vertical turbulence is shear (Soons et al. 2004) or differential surface heating (Tackenberg 2003). Further, it has recently been shown by Skarpaas et al. (2006), at least for seeds with fibers, that diaspores in a wind tunnel are preferentially abscised when horizontal winds are more turbulent (this variation in speed is also enhanced during the middle of the day).

How general will these results be? The sea breeze is too weak to be ecologically significant beyond about 10 km inland on the coasts of mainlands and large islands (McGregor and Nieuwolt 1998), and a reliable local circulation will not be well-developed on islands (e.g., atolls) with a diameter much less than ~15 km (Tijm et al. 1999). Meanwhile, in non-mountainous terrain in continental interiors, the dominance of afternoon dispersal will typically not be associated with a strong directional bias. It is likely therefore that pronounced anisotropy will be of concern most commonly in studies of seed and pollen dispersal in mountains simply because these occupy more of the earth’s land surface than do coastlines. In any case, we conclude that future studies of pollen and seed dispersal need to address directional bias more seriously.

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