Particle filtration through a humid tropical forest canopy

Filtração de partículas através do dossel de uma floresta tropical úmida

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Abstract: Understanding the dinamics of filtration of pollen and spores by plant canopies is crucial to the in the modelling of their dispersal, yet few studies have quantified filtration. Here, we examine the decline in the density of flour particles descending through a 40 m-tall tropical canopy on a windless day at Caxiuanã National Forest, Pará, Brazil. Using these data and estimates of canopy leaf density, we also tested one of the few existing models for the effect of impaction. The Bache model, which incorporates particle and vegetation structure, probability of particle transmission and the probability of impaction, explained approximately 93% of the variation in flour granules captured on passive samplers placed throughout the canopy. The canopy filtered 99.65% of the flour released, but a significant amount of small particles were captured at the forest floor. These findings suggest that the rarity of anemophily seen in the tropics may be more a result of high species richness than high canopy density.

Keywords: Pollen. Particle filtration. Impaction. Wind pollination. Model.

Resumo: Filtragem de pólen e esporos pelos dosséis de plantas é um passo crucial na modelagem da sua dispersão e, mesmo assim, poucos estudos a quantificam. Examinamos a diminuição da densidade de partículas de farinha ao descerem através de um dossel tropical de 40 m de altura em um dia sem vento na Floresta Nacional de Caxiuanã, Pará, Brasil. Usando esses dados e estimativas da densidade de folhas no dossel, também testamos um dos poucos modelos existentes para o efeito do impacto. O modelo de Bache, que incorpora a estrutura da partícula e da vegetação, probabilidade da transmissão da partícula e probabilidade de impacto, explicou 87% da variação dos grânulos de farinha capturados em coletores passivos colocados por todo o dossel. A copa filtrou 99,65% da farinha liberada, mas uma quantidade significativa de grânulos menores ainda foi capturada antes de sua chegada ao chão da floresta. Esses resultados sugerem que a escassez de anemofilia vista nos trópicos pode ser mais um resultado de alta diversidade de espécies de intensa densidade de copa.

Palavras-chave: Pólen. Filtragem de partículas. Impacto. Polinização anemófila. Modelo.

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INTRODUCTION

The physical processes affecting the movement of pollen by wind in forests are important as they can directly or indirectly affect the reproductive potential, and over time the richness, of wind-pollinated species by mediating gene-flow (Friedman & Barrett, 2008, 2009). A number of potential reasons are cited for the relative rarity of anemophily in humid tropical forests, including lack of seasonality, high species richness, frequent rainfall (which removes pollen from the air), large distances between available mates, and higher activity of animal pollinators (Whitehead, 1969; Bawa & Crisp, 1980; Regal, 1982; Lewis, 1986; Meléndez-Ramírez *et al*., 2004). However, a common factor thought to impede the movement of pollen is the density of canopies in tropical forests. These dense canopies are thought to increase the probability of the impaction of pollen grains on vegetal elements instead of a conspecific ovule (Di-Giovanni & Kevan, 1991; Jackson & Lyford, 1999).

The loss of particulates as they pass through a permeable barrier is called filtration (Tauber, 1967). It is impossible to adequately model pollen or spore dispersal or the probability of a grain reaching a stigma or micropyle without accounting for losses due to filtration. Filtration is also of interest in the study of the movement of aerosols (*e.g.* aerially-applied pesticides) though vegetation (Aylor, 1982). However, there is a limited amount of empirical data available on particle filtration through a forest canopy and the concentration of particles with distance and the rate of filtration are not consistent between studies (Belot & Gauthier, 1975; Lorenz & Murphy Jr., 1989; Wiman & Ågren, 1985 and references therein; Lovett & Lindberg, 1992; Ruijgrok *et al*., 1997). The primary goal of this study was to quantify the number of particles that can pass vertically through a humid tropical forest using an experimental release of particles from above the canopy. A secondary objective was to use the data collected to test the Bache (1979a) model of filtration, hereafter referred to as the Bache model.

PARTICLE FILTRATION THEORY

Granted that air must flow around obstacles, there are four ways in which airborne particles can be deposited on a leaf, shoot, or non-plant element such as spider web. These four mechanisms are (a) inertial impaction where particles, having sufficient inertia due to their size, come in contact with an obstacle's surface, rather than moving around it with the airstream; (b) interception where larger particles passing close to an obstacle may be intercepted; (c) diffusion where small particles, are moved very small distances by collisions with air molecules, and in some cases the movement is sufficient to cause them to deviate from the airstream and come into contact with an obstacle; and (d) electrostatic attraction where oppositely charged particles (of small or large size) are attracted to a charged object (Figure 1) (Verreault *et al*., 2008).

Impaction on foliage and other objects in forests is a major factor reducing the amount of pollen in the atmosphere and the distance that pollen is able to disperse (Aylor *et al*., 1981). The probability of impaction increases with particle size and wind speed, and decreases with

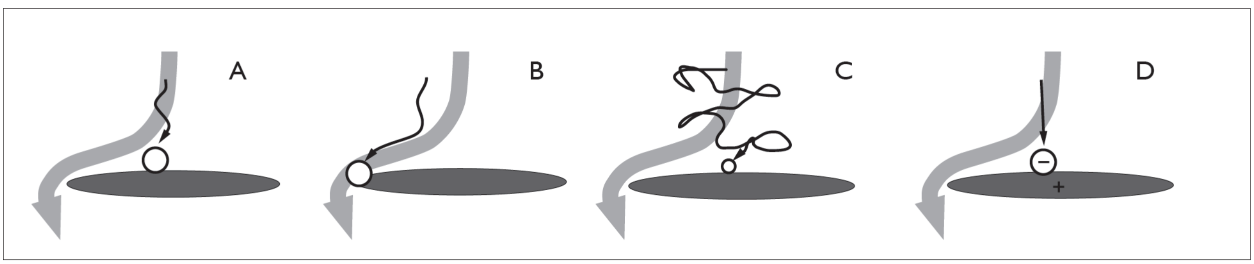

Figure 1. Mechanisms of particle-filtration, by which the path (black) of the pollen particle (white dot) can leave the airstream (grayish) to come in contact with the surface of a hypothetical leaf (dark gray). A) Inertial impaction; B) interception; C) diffusion; D) electrostatic attraction.

the size of the intercepting surface. The latter is because larger obstacles have a larger boundary layer which tends to divert particulate matter around their surfaces with the airstream (Jackson & Lyford, 1999). Larger grains are more prone to impaction, because their inertia tends to carry them through the surface boundary layer, whereas smaller grains follow the air flow around objects more easily (Jackson & Lyford, 1999).

MODELING PARTICLE TRANSPORT AND FILTRATION

Only a few studies have attempted to model filtration of particles throughout a forest canopy (Rosinski & Nagamoto, 1965; Chamberlain, 1975; Chamberlain & Little, 1981; Bache, 1979a, 1979b; Slinn, 1982; Ruijgrok *et al*., 1997; McLachlan & Horstmann, 1998). The most applicable model for the purpose of this study was the Bache model, which related trapping efficiency of the foliage to the vertical distribution of material within a canopy. In particular, the model focuses on the removal of particulate matter by impaction on foliage due to gravitational sedimentation and lateral dispersion by horizontal wind. These two filtering mechanisms are combined to define a probability that particles will be captured along the pre-obstacle trajectory of the particle.

Using turbulent-diffusion equations to model the particle's motion throughout the canopy, Bache (1979a) quantified the probability of particle absorption by a canopy element per unit of depth as:

$$\beta = 1 - T^{1/L} \qquad (1)$$

where L is the change in canopy depth, and T is the probability of particle transmission:

$$T = (1-P_x)^{\frac{1}{t}}(1-P_z) \qquad (2)$$

P_x and P_z describe the probability of capture per meter of depth in the horizontal and vertical directions:

$$P_x = \rho f_x E \qquad (3)$$

$$P_z = \rho f_z \qquad (4)$$

f_x and f_z are directional structure coefficients and ρ denotes foliage density (foliage area per unit volume). E is the impaction efficiency and can be expressed as a function of Stoke's number (Equation 5), a dimensionless value, used to determine the relative importance of inertia (Bache, 1979b; Slinn, 1982).

$$S = \left(\frac{\rho_p d_p^2 u}{9 \nu D}\right) \qquad (5)$$

where ρ_p is particle density, d_p is particle diameter, u is the fluid flow velocity, ν is the kinematic viscosity of air (at 30 °C this is 1.568 x 10^{-5} kg/m/sec) and D is the obstacle diameter. For $S < 0.1$, Bache (1979b) showed that $E \approx S^{1.7}$ provided a good fit to the empirical data collected by Belot & Gauthier (1975). However, impaction efficiency must be modified for larger particles and higher wind speeds, thus for $S > 0.1$, $E = S^2/(S+0.6)^2$ (Bache, 1979b).

Thus, the total probability of particle transmission per distance travelled is $T^{1/L}$, where $L = \sqrt{1+t^{-2}}$ and $t = u/v_s$. The terminal, or sedimentation velocity (v_s) of a single spherical particle (v_s) can be determined by Stoke's law (Vogel, 1981):

$$v_s = \frac{2r^2 g(\rho_o - \rho)}{9\mu} \qquad (6)$$

where r is the radius of the particle, ρ_o is the particle density and ρ is the density of the fluid (for air =1.165 kg/m^3), and μ is the dynamic viscosity of the fluid (for air at 30 °C this is 1.983 x 10^{-5} kg/m/sec).

MATERIALS AND METHODS

LOCATION

The experiment was conducted in the Caxiuanã National Forest Ferreira Penna field station, in the northern Brazilian state of Pará (1° 43' 10" S, 51° 27' 31" W), approximately 350 km west of the city of Belém. The climate in this region is tropical humid with an mean annual temperature of 26 °C, an average relative humidity of around 88% and a mean annual rainfall of between 2,000-2,500 mm. There is a pronounced dry season between June and November where the average rainfall is 55 mm; the monthly average during the rainy season (January-June) is

252 mm (Pinto *et al*., 2009). The area is dominated by a large (33,000 ha) undisturbed terra firme high forest but the Caxiuanã National Forest also includes periodically inundated floodplain forest; permanently inundated Igapó forests; and savanna enclaves (Lisboa, 2002). The field station at Caxiuanã allowed access above the canopy with a 54-metre tower constructed of aluminum stairs, platforms, and cross-beams. The tower was constructed in such a way that it did not affect the density of the surrounding canopy (*i.e.* trees had not been removed or extensively pruned). Metal guy-wires anchoring the tower to the ground and surrounding trees, were used for attachment of equipment for the experiment.

EXPERIMENTAL DESIGN AND PARAMETERIZATION

Sampling was done on the early morning of September 21, 2011; conditions were clear, sunny, and windless, with a temperature of 30 °C and relative humidity of 76%. The experiment was performed during the dry season as flooding impedes access to the canopy tower during the rainy season, and one month prior to the peak of the dry season (October); thus, there was no significant loss of leaves. The dominant tree species bordering the experimental site were found to be *Rinorea guianensis*, *Vouacapoua americana*, *Pouteria decorticans*, *Eschweilera coriacea*, *Tetragastris panamensis* and *Manilkara bidentata* (similar to Costa *et al*., 2010). Ignoring shoots, we obtained the obstacle (leaf) diameter by averaging measurements from a set 10 of leaves from each of the dominant species located along the tower – 60 leaves in total. The mean leaf length was 20 cm; mean diameter was 7cm.

Foliage density was estimated by taking photographs of the canopy cover directly above the level where each megastigma was located. Image analysis software (ImageJ©) was used to estimate the canopy cover. Each photograph was converted to a binary black and white image, allowing the software to easily distinguish pixels representing the canopy (black) from those representing the sky (white) and the percentage of canopy cover was calculated using the number of black (canopy) pixels over the total number of pixels.

The morphology of a flour particle is similar to the characteristic spheroidal shape of an anemophilous pollen grain (Figure 2). Wheat flour particles vary in size from 1-100 μm (Reitz *et al*., 2008). Like anemophilous pollen, it is dry and not prone to clumping (Timerman *et al*., 2014). The model was parameterized separately for large *versus* small particles. Arbitrarily, small particles were considered to be between 0-50 μm and large were between 50-100 μm. The median of each of these two ranges was used as the particle diameter for modeling purposes; 25 μm and 75 μm, respectively. The particle density of wheat flour is 593 kg/m^3 (ISIS Fluid Control Ltd., 2008).

To estimate the amount of particles reaching various levels of the forest canopy, we installed four 'megastigmas' (Kevan *et al*., 2006) directly beneath the drop point. The megastigmas were placed in a line at ten metre intervals, with the first megastigma at the top of the canopy at a height of 40 meters. Megastigmas are passive samplers used for collecting pollen, each consisting of 40 adhesive slides onto which airborne particles are impacted (Kevan *et al*., 2006). Each adhesive surface faced upward and is angled at approximately 40° to the horizontal plane. The total number of small and large particles on the collecting surfaces of the megastigmas were counted under a microscope and converted to grains/m^2.

We released 1 kg of wheat flour from the top of the tower (54 m); based on the typical density of wheat

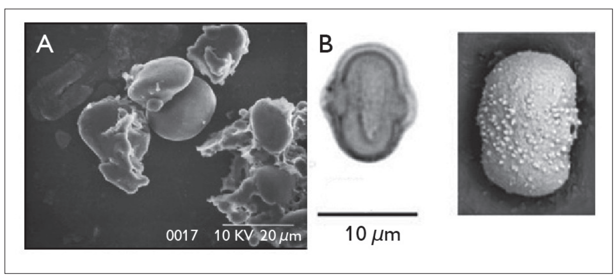

Figure 2. A) Scanning electron micrograph (SEM) of flour particles from a hard red winter wheat cultivar (Reitz *et al*., 2008); B) SEM of *Cecropia* pollen (Barth, 2005).

flour and particle size this corresponds to 3.22×10^9 flour particles. To control the rate of release, the flour was sifted through a cotton bag which, when shaken, slowly released the flour particles into the air. We released all the flour over approximately 30 minutes, and waited for one hour before collecting the samples.

The actual number of particles released (source strength) was 3.22×10^9, but this not a good estimate of the number of particles able to be captured by the megastigmas. This is because of the lateral dispersion of particles due to air currents in the 14 meter distance between the release point and the first megastigma, and because the sampling area was restricted by the number of megastigmas available. To normalize the source strength the number of particles caught on this megastigma at 40 metres ($x = 0$) was considered to represent the source strength for our modeling purposes.

There was no horizontal or vertical wind flowing within the canopy during the brief descent interval. Thus, the flow velocity (u) within the canopy was assumed to be zero. For modeling purposes, this eliminates the horizontal component of the transmission probability (P_x in equation 2) and forces the reduction in particle number with vertical distance descended to be due to filtration alone, rather than lateral dispersion.

RESULTS AND DISCUSSION

The estimation of source strength was 2.42×10^9 small particles per m^2 and 2.70×10^8 large particles per m^2; this estimate is representative of the number of particles entering the canopy available for capture by megastigmas. This was used as the origin point for the observed and predicted curves. The total amount of particles captured at the upper canopy level (20-40 m) was 1.37×10^8 per m^2. However, large flour particles were subject to more drastic filtration than small flour particles (Table 1 and Figure 3). The number of large grains remaining at each level was at least an order of magnitude less than the number of small grains, with a two order of magnitude difference at the ground level. Below the 20 m level, in the stratum where leaves are much less common, the large particles exhibited a steeper decline in number than that of the smaller particles (Table 1). This suggests that filtration by the canopy does not entirely preclude anemophily in humid tropical forests. The amount of simulated pollen reaching the forest floor was, however, relatively small at approximately 0.02% of the source strength (for large grains) and 0.33% of the source strength (for small grains), with a larger proportion of small grains reaching the forest floor.

The Bache model gave a good prediction of the observed data for both small and large flour particles but fit slightly better for the small particles than large particles. The model over-predicted at all distances but followed the overall shape of the dispersal curve quite well (Figure 4).

Table 1. Observed particle concentration at the location of each megastigma, descending through the forest canopy. Concentration is listed in particles m^{-2} and as a percentage of the initial estimation of particles released (source strength).

Height (m)	Foliage density (%)	Large particles/m^2	% of source strength	Small particles/m^2	% of source strength
40	0	2.70E + 08	100	2.42E + 09	100
30	59	1.26E + 07	4.69	1.15E + 08	4.75
20	77	1.80E + 06	0.66	7.81E + 06	0.32
10	80	2.80E + 05	0.11	8.50E + 06	0.35
0	81	8.00E + 04	0.03	7.92E + 06	0.33

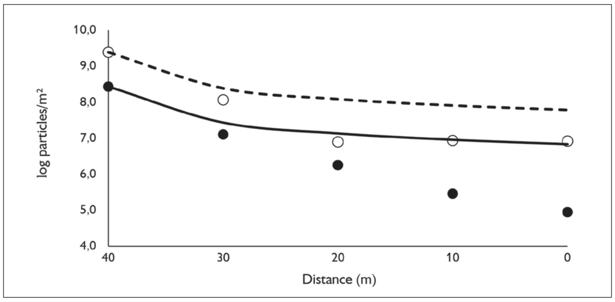

Figure 3. Observed small (○) and large (●) particles/m^2 with predicted small (dashed line) and large (solid line) particles/m^2 from the canopy top to ground. The origin represents the canopy top. Predictions based on the Bache (1979a) model for particle transport within plant canopies.

The model and predicted a flattening of the dispersal curve with distance, which is seen in the observed data for small particles, but less so for large particles. Regressing the observed concentration against the predicted concentration at each level yielded an R^2 of 0.95 for small particles and an R^2 of 0.92 for large particles (Figures 4 and 5). The slope of the regression lines for both small and large particle were not significantly different than 1 and 0 respectively ($p > 0.05$, Table 2). However, since the model over-predicts the rate of particle transmission for both sizes of particles, the regression line intercepts were significantly different from 1 at the 95% confidence level ($p < 0.05$, Table 2).

Our findings demonstrate that a relatively high proportion of pollen released above the canopy is still available within the upper-canopy (approximately 30 m high). This implies that pollen could move between male and female flowers in the upper-canopy, although the horizontal distances of pollen-dispersal in tropical environments remains an open question. The 99.65% loss of particles by about 30 m could in theory be compensated for by the copious amounts of pollen known to be produced by anemophiles. In some coniferous species pollen production is on the order of 10^6 pollen grains per tree per day (Katul *et al*., 2006), with some angiosperms (such as *Ambrosia*) having pollen to ovule ratios of greater than 10^{15} (Ackerman, 2000). The density of foliage in a coniferous forest can also be similar to that of a tropical forest, but species richness is much lower. In the humid tropical forest, the low density of conspecific trees per area may be a more limiting factor to the successful deposition of a pollen grain onto a conspecific ovule.

Although the horizontal wind was negligible in this study and sedimentation velocity (v_s) was the dominant particle filtration mechanism, the Bache model can be used to determine the expected loss of particles due to filtration by horizontal wind (u). Given that a motive force is required for pollen release in anemophiles, it is interesting to use the Bache model to ascertain this expected loss.

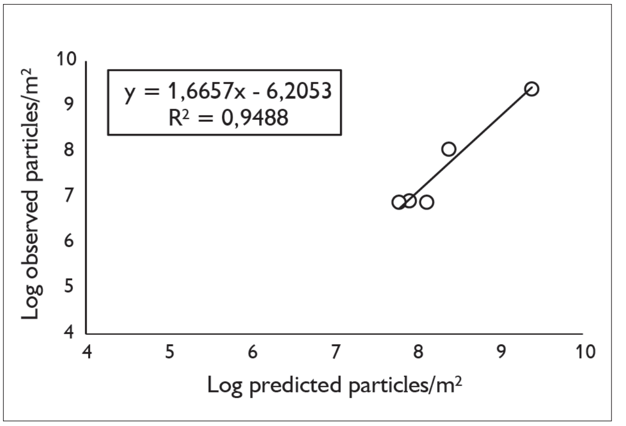

Figure 4. Linear regression of predicted *versus* observed small particle concentrations (○) descending throughout the canopy. Predicted values based on the Bache (1979a) model.

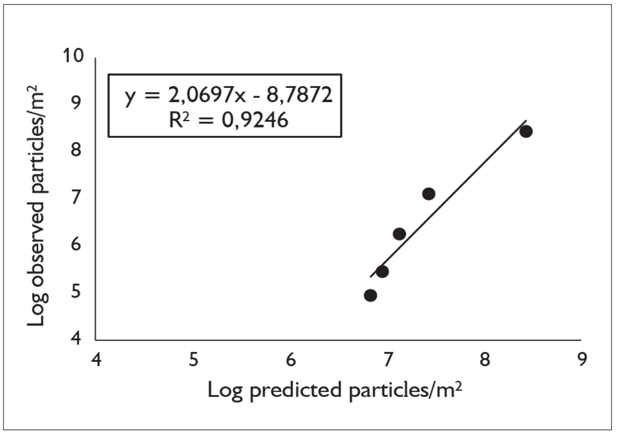

Figure 5. Linear regression of predicted *versus* observed large particle concentrations (●) descending throughout the canopy. Predicted values based on the Bache (1979a) model.

Table 2. Statistical testing of small and large particles the Bache model. R^2, slope (β) and y-intercept (α) of the associated best-fit line of the model predictions *versus* observed concentration. The 95% confidence intervals and the significance ($p = 0.05$) of the slope and y-intercept of the regression are also listed.

	R^2	β	α	Confidence intervals (95%)		$p(\beta)$	$p(\alpha)$
				(β)	(α)		
Small particles	0.949	1.666	-6.205	0.707	5.888	0.220	0.045
Large particles	0.925	2.070	-8.787	1.086	8.006	0.220	0.039

Assuming that flowers are concentrated in the upper half of the canopy and that the mean wind speed in this upper stratum would be about 1 m sec^{-1} (Greene & Johnson, 1996), and ignoring vertical turbulence, the Bache model predicts that 98.52% of particles would be filtered by 20 meters. Because of the high richness and diversity of species in the tropics, the nearest conspecific tree may often exceed this distance, whereas insect pollinators are known to have foraging ranges of on the order of hundreds, sometimes thousands, of meters (Janzen, 1971; Dramstad, 1996; Beekman & Ratnieks, 2000).

Empirical data on ambient pollen concentrations are still quite rare and one advantage of the Bache model is that the parameters can be estimated in the absence of data on pollen dispersal. The model parameters are dependent on grain morphology, canopy coverage, and characteristics of wind and can therefore be used for different types of pollen and environments. The Bache model incorporates some of the other factors fundamental to anemophilous systems, but there are many factors which cannot be included in a model based on properties of the canopy alone. These factors include the shape and size of pollen grains as the structure of wind-borne pollen often optimizes its ability to travel on wind. Wind patterns, especially strong gusts and abrupt changes in wind-direction can have dramatic effects on pollen dispersal distances. Turbulence from leaves and surrounding trees also affect the dispersal patterns and updrafts can carry pollen upwards quite rapidly, and over long distances. The occurrence of re-entrainment can also affect the movement and distribution of pollen grains; viable pollen could theoretically be carried by rain, or stick to leaf surfaces temporarily, but be dislodged by wind or rain and carried to lower levels after several days or hours. Updrafts can also be important; the existence of supra-canopy dispersal of pollen by wind has been demonstrated by observational studies in higher-latitude forests in which large amounts of pollen from upper-canopy species (but also moderate amounts of pollen from lower-canopy or understory species) have been captured in pollen-traps set on a lake in Australia (Kershaw & Hyland, 1975; Kershaw & Strickland, 1990; Di-Giovanni & Kevan, 1991).

As mentioned above, another key finding was that there was an association between the size of simulated pollen grains and their ability to avoid deposition. Our finding that small grains were more likely to penetrate the canopy than large grains is consistent with the principles of particle attraction theory and with the morphological characteristics of anemophilous pollen grains, which tend to be much smaller than those of entomophilious plants. Smaller particles are less affected by impaction and more likely to be guided around leaves or branches by the boundary layer created by air flow around these obstacles.

CONCLUSIONS

Both our experiment and the Bache theoretical model suggest that the rarity of anemophily in tropical forest environments may be due to other factors such as species richness rather than high foliage density. Anemophily is much more common in the higher latitudes as species richness is lower and the number of conspecific individuals per area is much higher. Comparatively, the pollen flux for any one species in a tropical forest environment would be much lower per unit area. Although filtration by impaction on leaves does greatly affect the attenuation of pollen grains through the forest canopy, these findings suggest that the copious amount of pollen known to be produced by anemophiles may be able to compensate for a high canopy density.

Consideration of anemophilous pollen dispersal in the tropics has a number of important implications. It can be used to draw analogies to dispersal of airborne seeds in addition to pollen, which can estimate the effects of fragmentation on forests, and particularly how fragmentation might affect reproduction of plants in isolated patches and natural regeneration of patches from which vegetation has been removed. At a more abstract level, it brings into question some fundamental assumptions about the evolution of anemophily as an evolutionary strategy (Friedman & Barrett, 2009), and the nature of latitudinal patterns in the importance of biotic interactions (*e.g.* Schemske *et al*., 2009). It is reasonable to ask if wind-pollination could, in fact, be advantageous for plants under conditions where there is intense competition for access to a limited numbers of pollinators (*e.g.* Vamosi *et al*., 2006), and pollen-stealing is frequent (Bullock, 1994). Although it is biomechanically feasible for pollen transport to occur in humid tropical forests, a future study should relate aerial pollen concentration to the density of individuals.

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REFERENCES

ACKERMAN, J. D., 2000. Abiotic pollen and pollination: ecological, functional, and evolutionary perspectives. **Plant Systematics and Evolution** 222(1-4): 167-185.

AYLOR, D. E., 1982. Modeling spore dispersal in a barley crop. **Agricultural Meteorology** 26(3): 215-219.

AYLOR, D. E., H. A. MCCARTNEY & A. BAINBRIDGE, 1981. Deposition of particles liberated in gusts of wind. **Journal of Applied Meteorology** 20(10): 1212-1221.

BACHE, D. H., 1979a. Particle transport within plant canopies – I. A framework for analysis. **Atmospheric Environment** 13(9): 1257-1262.

BACHE, D. H., 1979b. Particulate transport within plant canopies – II. Prediction of deposition velocities. **Atmospheric Environment** 13: 1681-1687.

BARTH, O. M., 2005. Análise polínica de mel: avaliação de dados e seu significado. **Mensagem Doce** 81. Available at: <www.apacame.org.br>. Acessed on: 20 January 2012.

BAWA, K. S. & J. E. CRISP, 1980. Wind-pollination in the understorey of a rain forest in Costa Rica. **Journal of Ecology** 68: 871-876.

BEEKMAN, M. & F. L. W. RATNIEKS, 2000. Long-range foraging by the honey-bee, *Apis mellifera* L. **Functional Ecology** 14(4): 490-496.

BELOT, Y. & D. GAUTHIER, 1975. Transport of micronic particles from the atmosphere to foliar surfaces. In: D. A. DE VRIES & N. H. AFGAN (Eds.): **Heat and mass transfer in the biosphere**: 1: 583-591. Scripta, Washington.

BULLOCK, S. H., 1994. Wind pollination of neotropical dioecious trees. **Biotropica** 26(2): 172-179.

CHAMBERLAIN, A. C., 1975. The movement of particles in plant communities. In: J. L. MONTEITH (Ed.): **Vegetation and the atmosphere**: 1: 155-203. Academic Press, London.

CHAMBERLAIN, A. C. & P. LITTLE, 1981. Transport and capture of particles by vegetation. In: J. GRACE, E. D. FORD & P. G. JARVIS (Eds.): **Plants and their atmospheric environment**: 147-173. Blackwell Scientific Publications, Oxford.

COSTA, A. C. L., D. GALBRAITH, S. ALMEIDA, B. T. T. PORTELA, M. COSTA, J. A. SILVA JUNIOR, A. P. BRAGA, P. H. L. GONÇALVES, A. A. R. OLIVEIRA, R. FISHER, O. L. PHILLIPS, D. B. METCALFE, P. LEVY & P. MEIR, 2010. Effect of 7 yr of experimental drought on vegetation dynamics and biomass storage of an eastern Amazonian rainforest. **New Phytologist** 187(3): 579-591.

DI-GIOVANNI, F. & P. G. KEVAN, 1991. Factors affecting pollen dynamics and its importance to pollen contamination: a review. **Canadian Journal of Forest Research** 21(8): 1155-1170.

DRAMSTAD, W. E., 1996. Do bumblebees (Hymenoptera: Apidae) really forage close to their nests? **Journal of Insect Behavior** 9(2): 163-182.

FRIEDMAN, J. & S. C. H. BARRETT, 2008. A phylogenetic analysis of the evolution of wind pollination in the angiosperms. **International Journal of Plant Sciences** 169(1): 49-58.

FRIEDMAN, J. & S. C. H. BARRETT, 2009. Wind of change: new insights on the ecology and evolution of pollination and mating in wind-pollinated plants. **Annals of Botany** 103(9): 1515-1527.

GREENE, D. F. & E. A. JOHNSON, 1996. Wind dispersal of seeds from a forest into a clearing. **Ecology** 77(2): 595-609.

ISIS FLUID CONTROL LTD., 2008. **Technical Data**: density of materials. ISIS, Oxfordshire. Available at: <http://www.isis-fluid.co.uk/technical-data.asp>. Accessed on: 19 August 2014.

JACKSON, S. T. & M. E. LYFORD, 1999. Pollen dispersal models in Quaternary plant ecology: assumptions, parameters, and prescriptions. **The Botanical Review** 65(1): 39-75.

JANZEN, D. H., 1971. Euglossine bees as long distance pollinators of tropical plants. **Science** 171(3967): 203-205.

KATUL, G., C. G. WILLIAMS, M. SIQUEIRA, D. POGGI, A. PORPORATO, H. MCCARTHY & R. OREN, 2006. Dispersal of transgenic conifer pollen. In: C. G. WILLIAMS (Ed.): **Landscapes, genomics and transgenic conifers**: 121-146. Springer (Managing Forest Ecosystems, 9), Houten.

KERSHAW, A. P. & B. P. M. HYLAND, 1975. Pollen transfer and periodicity in a rain-forest situation. **Review of Palaeobotany and Palynology** 19(2): 129-138.

KERSHAW, A. P. & K. M. STRICKLAND, 1990. A 10 year pollen trapping record from rainforest in northeastern Queensland, Australia. **Review of Palaeobotany and Palynology** 64(1-4): 281-288.

KEVAN, P. G., F. DI-GIOVANNI, R. H. HO, H. TAKI, K. A. FERGUSON & A. K. PAWLOWSKI, 2006. A simple method for collecting airborne pollen. **Journal of Biological Education** 40(4): 181-183.

LEWIS, W. H., 1986. Airborne pollen of the Neotropics: potential roles in pollination and pollinosis. **Grana** 25(1): 75-83.

LISBOA, P. L. B., 2002. **Natureza, homem e manejo de recursos naturais na região de Caxiuanã, Melgaço, Pará**: 1-237. Museu Paraense Emílio Goeldi, Belém.

LORENZ, R. & C. E. MURPHY JR., 1989. Dry deposition of particles to a pine plantation. **Boundary-Layer Meteorology** 46(4): 355-366.

LOVETT, G. M. & S. E. LINDBERG, 1992. Concentration and deposition of particles and vapors in a vertical profile through a forest canopy. **Atmospheric Environment. Part A. General Topics** 26(8): 1469-1476.

MCLACHLAN, M. S. & M. HORSTMANN, 1998. Forests as filters of airborne organic pollutants: a model. **Environmental Science & Technology** 32(3): 413-420.

MELÉNDEZ-RAMÍREZ, V., V. PARRA-TABLA, P. G. KEVAN, I. RAMÍREZ-MORILLO, H. HARRIES, M. FERNÁNDEZ-BARRERA & D. ZIZUMBO-VILLAREAL, 2004. Mixed mating strategies and pollination by insects and wind in coconut palm (*Cocos nucifera* L. (Arecaceae)): importance in production and selection. **Agricultural and Forest Entomology** 6(2): 155-163.

PINTO, C. S., U. E. C. CONFALONIERI & B. M. MASCARENHAS, 2009. Ecology of *Haemagogus* sp. and *Sabethes* sp. (Diptera: Culicidae) in relation to the microclimates of the Caxiuanã National Forest, Pará, Brazil. **Memórias do Instituto Oswaldo Cruz** 104(4): 592-598.

REGAL, P. J., 1982. Pollination by wind and animals: ecology of geographic patterns. **Annual Review of Ecology and Systematics** 13: 497-524.

REITZ, L. P., C. W. ELLETT, D. D. KASARDA, M. A. UEBERSAX & O. D. ANDERSON, 2008. Wheat. In: **AccessScience**. Available at: <www.accessscience.com/content/wheat/744900>. Accessed on: 20 January 2012.

ROSINSKI, J. & C. T. NAGAMOTO, 1965. Particle deposition on and reentrainment from coniferous trees. **Kolloid-Zeitschrift und Zeitschrift für Polymere** 204(1-2): 111-119.

RUIJGROK, W., H. TIEBEN & P. EISINGA, 1997. The dry deposition of particles to a forest canopy: a comparison of model and experimental results. **Atmospheric Environment** 31(3): 399-415.

SCHEMSKE, D. W., G. G. MITTELBACH, H. V. CORNELL, J. M. SOBEL & K. ROY, 2009. Is there a latitudinal gradient in the importance of biotic interactions? **Annual Review of Ecological and Evolutionary Systematics** 40: 245-269.

SLINN, W. G. N., 1982. Predictions for particle deposition to vegetative canopies. **Atmospheric Environment** 16(7): 1785-1794.

TAUBER, H., 1967. Investigations of the mode of pollen transfer in forested areas. **Review of Palaeobotany and Palynology** 3(1-4): 277-286.

TIMERMAN, D., D. F. GREENE, J. D. ACKERMAN, P. G. KEVAN & E. NARDONE, 2014. Pollen aggregation in relation to pollination vector. **International Journal of Plant Sciences** 175(6): 681-687.

VAMOSI, J. C., T. M. KNIGHT, J. A. STEETS, S. J. MAZER, M. BURD & T.-L. ASHMAN, 2006. Pollination decays in biodiversity hotspots. **Proceedings of the National Academy of Sciences of the United States of America** 103(4): 956-961.

VERREAULT, D., S. MOINEAU & C. DUCHAINE, 2008. Methods for sampling of airborne viruses. **Microbiology and Molecular Biology Reviews** 72(3): 413-444.

VOGEL, S., 1981. **Life in moving fluids**: the physical biology of flow: 1-352. Willard Grant, Boston.

WHITEHEAD, D. R., 1969. Wind pollination in the angiosperms: evolutionary and environmental considerations. **Evolution** 23(1): 28-35.

WIMAN, B. L. B. & G. I. ÅGREN, 1985. Aerosol depletion and deposition in forests: a model analysis. **Atmospheric Environment** 19(2): 335-347.