

derived features of the pectoral girdle of *Jeholornis* such as a strut-like coracoid and the well-developed carpal trochlea of the carpo-metacarpus, suggest the capability of powerful flight.

One of the most significant features of *Jeholornis* is the preservation of dozens of ovules in the stomach (Fig. 2c). Although hundreds of excellently preserved Mesozoic birds such as *Confuciusornis* have been discovered, our knowledge about their diet has been at best speculative. *Jeholornis* represents direct evidence for seed-eating adaptations in Mesozoic birds. The ovules, referable to the generic name *Carpolithus*<sup>24</sup>, cannot be positively included into any of the chief plant groups (J. Hilton and Q. Leng, personal communication). It is difficult to determine whether, in life, *Jeholornis* ate cones on a tree, ovules from intact cones, or ovules shed from their cones. The intact nature of the ovules, however, may indicate that the bird ate them whole, to be digested in the gizzard, rather than breaking them up to eat them in small pieces (J. Hilton, personal communication). The large number of seemingly undigested ovules in the specimen probably indicates a large crop. Furthermore, the robust mandibles with fused mandibular symphysis, reduced teeth and well-developed hyoid bones seem to lend further support for the seed-eating habit of *Jeholornis*.

*Jeholornis* certainly possessed an arboreal capability, as evidenced by its reversed hallux, long and strongly curved pedal unguals, and toe proportions (Fig. 1a). However, as in other basal birds such as *Archaeopteryx* and *Confuciusornis*, there is no evidence to discount the possibility that *Jeholornis* spent some time on the ground<sup>26,27</sup>. Therefore, without further evidence, it is difficult to conclude whether *Jeholornis* fed on ovules from cones on trees, or on the ground. This discovery, together with many others in recent years, suggests that by the Early Cretaceous, early birds had not only diverged significantly in morphology, size and ecology<sup>11,28</sup>, but had also differentiated with respect to feeding adaptation. □

Received 15 March; accepted 21 June 2002; doi:10.1038/nature00930.

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Supplementary Information accompanies the paper on Nature's website (<http://www.nature.com/nature>).

**Acknowledgements**

We thank X. Xu and X. Wang for discussions and help in the field, and L. Witmer for review. J. Hilton and Q. Leng helped with the analysis of the ovules, and Y. Li prepared the specimens. This work was supported by the Special Funds for Major State Basic Research Projects of China, the National Natural Science Foundation of China, the Hundred Talents Project of CAS, and the National Science Fund for Distinguished Young Scholars of China to Z.Z.

**Competing interests statement**

The authors declare that they have no competing financial interests.

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**Mechanisms of long-distance dispersal of seeds by wind**

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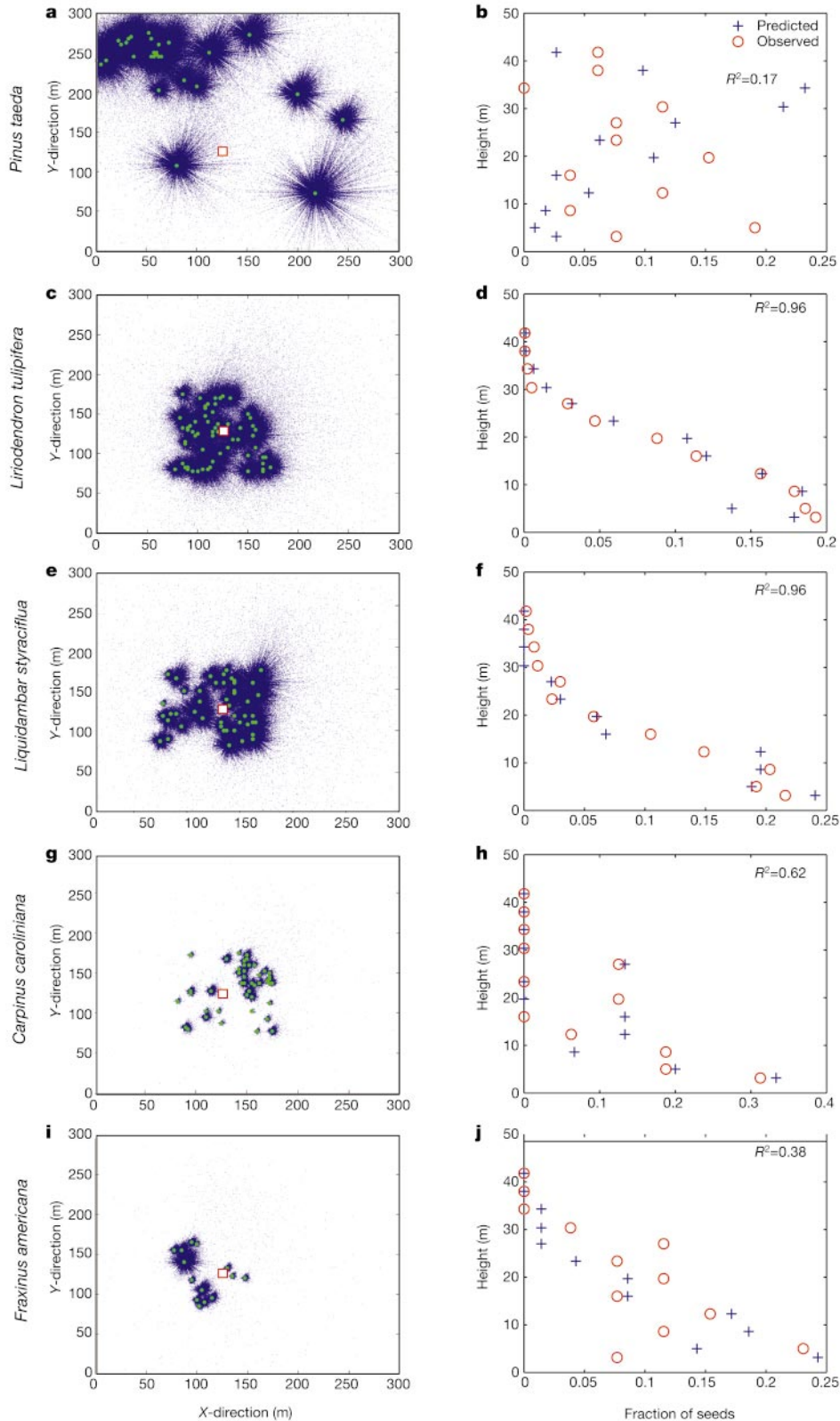
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**Long-distance dispersal (LDD) is central to species expansion following climate change, re-colonization of disturbed areas and control of pests<sup>1–8</sup>. The current paradigm is that the frequency and spatial extent of LDD events are extremely difficult to predict<sup>9–12</sup>. Here we show that mechanistic models coupling seed release and aerodynamics with turbulent transport processes provide accurate probabilistic descriptions of LDD of seeds by wind. The proposed model reliably predicts the vertical distribution of dispersed seeds of five tree species observed along a 45-m high tower in an eastern US deciduous forest. Simulations show that uplifting above the forest canopy is necessary and sufficient for LDD, hence, they provide the means to define LDD quantitatively rather than arbitrarily. Seed uplifting probability thus sets an upper bound on the probability of long-distance colonization. Uplifted yellow poplar seeds are on average lighter than seeds at the forest floor, but also include the heaviest seeds. Because uplifting probabilities are appreciable (as much as 1–5%), and tree seed crops are commonly massive, some LDD events will establish individuals that can critically affect plant dynamics on large scales.**



**Figure 1** Seed dispersal simulations of five wind-dispersed tree species around the Duke Forest tower, for 35 days during the autumn of 2000. **a, c, e, g, i**, The difference in spatial distribution among species—together with differences in dispersal factors (Table 1)—generate distinct seed shadow (left column; green circles represent adult trees and the red square indicates the tower). **b, d, f, h, j**, Vertical profiles of predicted proportions of seeds at different heights along the tower generally match the observed profiles (right column). The fits are high for the two species for which the observed profiles are estimated from large

samples (Table 1); for the other species, the coefficient of determination ( $R^2$ ) was lower. Nonetheless, the low  $R^2$  is associated with weak vertical gradients in seed proportions (compare **b** and **d**) which appear random (or well mixed), in particular in **b**, where both observed and predicted distribution describe a random distribution (Runs up-and-down randomness test,  $P > 0.1$ ). In such cases, the model correctly predicts a random vertical distribution, albeit at a low  $R^2$ . We emphasize that  $R^2$  is not an appropriate model diagnostic here as  $R^2$  is inherently low between two approximately random distributions.

**Table 1 Canopy and seed aerodynamic attributes for dispersal simulations**

Tree species	Seed terminal velocity ( $\text{m s}^{-1}$ ; mean $\pm$ s.d.)	Tree height (m; mean $\pm$ s.d.)	Seed release height (fraction of tree height; mean)	Seed counts in traps	Estimated uplifting probability (%)	
					From trap data	From simulations
<i>Pinus taeda</i>	0.70 $\pm$ 0.13	31.49 $\pm$ 3.61	0.72	36	11.11	4.80
<i>Liriodendron tulipifera</i>	1.48 $\pm$ 0.52	26.13 $\pm$ 7.82	0.66	3,294	0.36	1.80
<i>Liquidambar styraciflua</i>	1.05 $\pm$ 0.24	25.55 $\pm$ 7.04	0.63	1,609	1.42	0.98
<i>Carpinus caroliniana</i>	0.98 $\pm$ 0.21	11.17 $\pm$ 2.78	0.74	17	0	0.05
<i>Fraxinus americana</i>	1.41 $\pm$ 0.26	18.72 $\pm$ 5.91	0.70	33	0	0.02

The two main biological parameters are terminal velocity of seeds and height of seed release (see Methods for empirical estimation). The height of seed release is the product of the height of reproductive trees and the fraction from tree height at which seeds are released. Predicted seed uplifting probabilities, based on simulations of  $10^5$  to  $10^8$  seeds for each species, are compared with direct estimates based on seed-trap data collected in the autumn of 2000 along a 45-m high tower in Duke Forest. The total number of seeds counted in all traps during this period is also given.

Many common and economically important tree species, especially those of temperate and boreal forests, have morphological adaptations that facilitate dispersal by wind<sup>13,14</sup>. It has long been suggested that wind updrafts provide the key mechanism for LDD of seeds<sup>13,15,16</sup>. However, while uplifting of parachute or fluffy seeds is commonly observed, seeds of many wind-dispersed tree species are relatively heavy, and fall in still air with terminal velocities typically greater than the usual vertical wind velocity. Uplifting events, in which upward vertical wind velocity exceeds seed terminal velocity, are rare and difficult to quantify. Consequently, despite successful predictions of the short-distance dispersal of most seeds by both phenomenological<sup>5,17,18</sup> and mechanistic<sup>19,20</sup> models, attempts to predict rare events of LDD have repeatedly failed<sup>9–12</sup>. Phenomenological models are fitted to the observed data, which are limited by inherent difficulties in obtaining data on LDD<sup>6–8</sup>, and extrapolation beyond the observed range is questionable. The failure of previous mechanistic models probably emanates from their use of time-averaged wind statistics (for example, hourly and longer), thereby averaging over the critically strong turbulent updrafts with timescales of the order of seconds. Here, we propose a new generation of mechanistic dispersal models based on the intermittent yet coherent nature of canopy turbulent airflow within vegetation. We show that for species representing a broad spectrum of seed and tree morphologies, such models can reliably predict important statistical attributes of rare LDD events.

We applied a coupled eulerian–lagrangian approach<sup>21,22</sup> to describe the turbulent statistics within and above the canopy (see Methods). All parameters were independently estimated from

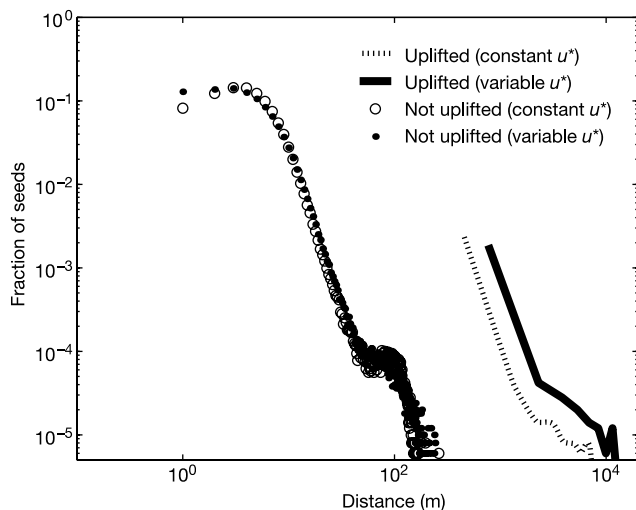
laboratory and field experiments. The model was tested against further wind and seed data collected along a 45-m walk-up tower in a 33-m tall, 80-yr-old deciduous stand in Duke Forest, North Carolina (35° 58' N, 79° 08' W; see Methods). Velocity statistics estimated by the moment closure model agreed well with the high frequency wind data measured at three heights along the tower. This agreement is consistent with earlier comparisons<sup>23</sup>.

We then tested the coupled eulerian–lagrangian model against seed data collected in 102 traps placed at 12 levels along the tower. The model simulated the three-dimensional dispersal of seeds given: (1) location of source trees around the tower, (2) seed terminal velocity and (3) distribution of seed release height (Table 1, Fig. 1; and see Methods for simulation details). Observed proportions of seeds at different heights along the tower closely match the model's predictions (Fig. 1).

During a period of 35 days in the autumn of 2000, we collected 4,989 seeds of five wind-dispersed tree species in the traps along the tower. Thirty-nine seeds belonging to three species were collected above the top of the canopy (Table 1). Direct calculation of seed uplifting probability from the observed proportion of seeds above the top-canopy height at a single tower is problematic. This proportion depends on the specific spatial arrangement of the trees around the tower. At our site, the observed proportion would underestimate true uplifting probability for species clumped close to the tower, such as yellow poplar (*Liriodendron tulipifera*) (Fig. 1c), since some seeds caught in vertical updrafts may terminate their flight in traps before escaping the canopy. For species far from the tower, such as loblolly pine (*Pinus taeda*) (Fig. 1a), the observed proportion would overestimate the true uplifting probability, since only seeds travelling relatively long distances are trapped at the tower, and these are more likely to have been uplifted.

The above sampling problem could be resolved by placing seed-traps along many side-by-side towers. Because such a set-up is intractable in tall forests, we estimate uplifting probabilities using the verified dispersal model. Given that the model reliably describes the vertical structure of both wind statistics and trapped seeds, its predictions of uplifting probabilities can be used to provide a spatially integrated estimate of the number of seeds of each species arriving at each height on the tower. Comparisons between these two estimates (Table 1) reveal that the model corrected direct estimates in the expected direction; that is, it increased the underestimated probability for yellow poplar, and reduced the overestimated probability for loblolly pine.

We next used the verified model to estimate dispersal kernels of wind-dispersed tree species, assuming that a model that predicts the frequency of LDD could also provide reasonable estimates for travel distances. However, seeds travelling long distances are likely to encounter variable wind conditions during flight, which may be different from those at the site of release. We therefore ran two sets of simulations, one with a planar, homogeneous wind, the other with variable wind (see Methods for simulation details). In both cases, we found that dispersal kernels were bimodal: seeds that were uplifted travelled much further than those that did not escape the forest canopy (Fig. 2). Most seeds are not uplifted and are predicted to travel only up to several hundred metres, with a modal distance of



**Figure 2** Bimodal dispersal kernel for yellow poplar (*Liriodendron tulipifera*) seeds released from 18 m in a 33-m-high forest, with a secondary peak at the tail generated exclusively by seed uplifting. The same pattern emerges assuming either constant or variable friction velocity ( $u^*$ ), of 0.8 and  $0.8 \pm 0.4 \text{ m s}^{-1}$ , respectively. Each dispersal kernel is computed from simulations of 500,000 dispersal events.



roughly the canopy height. In stark contrast, the few seeds that are uplifted are predicted to travel at least several hundred metres, and perhaps tens of kilometres. These findings hold for both spatially constant and variable wind conditions. We conclude that the seed uplifting probability, or equivalently the frequency of LDD, is predictable from the statistical distributions of seed release height, seed terminal velocity, and turbulent flow at the time of release. A consequence of such a clearly bimodal dispersal kernel (Fig. 2) is that quantitative rather than arbitrary distinction between short- and long-distance dispersal is possible for wind-dispersed tree species<sup>6,8</sup>.

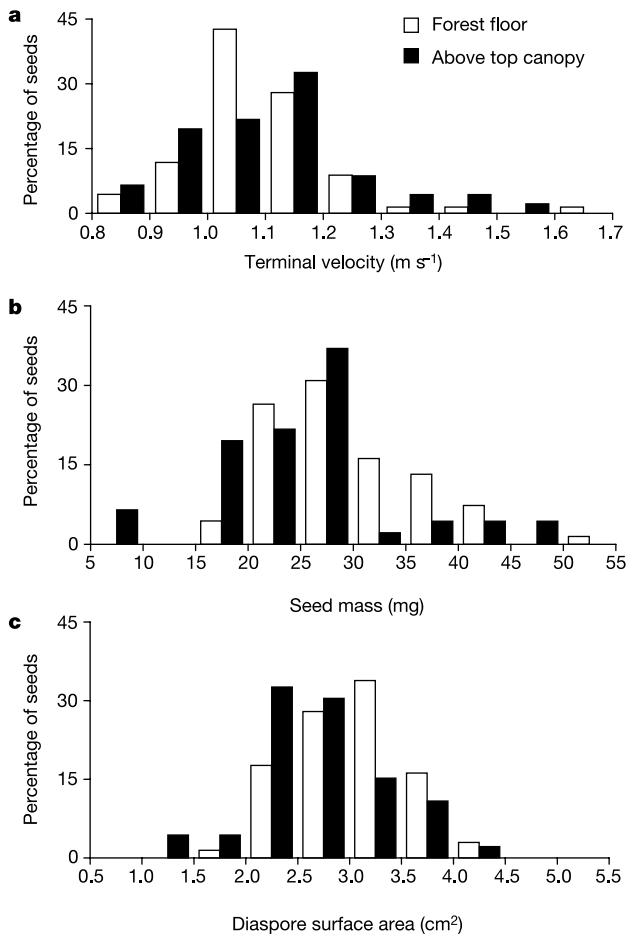
While standard phenomenological models assume a gradual monotonic decline of the frequency of dispersal events with distance<sup>5,17,18</sup>, our mechanistic model predicts a bimodal distribution of short- and long-distance dispersal<sup>23</sup> (Fig. 2). Such bimodal distributions mirror the two flow regimes: (1) short-distance, controlled by within-canopy flow and characterized by small mean windspeed, damped turbulence, and energetic eddies of approximately one-third of the mean canopy height<sup>24</sup>, and (2)

long-distance, controlled by atmospheric surface-layer turbulence having mean windspeed and characteristic eddy sizes that rapidly increase with increasing height above ground.

Seeds uplifted and dispersed long distances are meaningful for plant dynamics only if establishment follows dispersal. Thus, developing a predictive ability for LDD—as shown here—is necessary but not sufficient in developing predictive ability for long-distance plant colonization. Information on two other major processes—fecundity and post-dispersal survival—is needed. Fecundity in wind-dispersed trees is usually high, for example, on the order of  $10^4$  seeds per tree per year for yellow poplar<sup>25</sup>, but varies considerably among species, sites, individuals and over time<sup>18</sup>. Mortality occurs mostly during seed and seedling stages<sup>7</sup>, and seed-to-sapling survival probability also varies considerably among species and sites. For example, in two sites close to ours, survival has been estimated as 6% for loblolly pine, and 0% in one site and 0.06% in another for yellow poplar<sup>26</sup>. The survival of seeds travelling long distances is poorly quantified, because LDD events are rare and difficult to track; quantifying this survival probability is a major current challenge<sup>27</sup>. Seeds dispersing very far may have higher survival probabilities than seeds dispersing near, because they escape the high mortality caused by density-dependent processes such as competition, predation and disease. Furthermore, depending on the pattern of spatial autocorrelation in the environment, they may be deposited at sites that are more (or less) suitable for establishment than sites near the source location<sup>7</sup>.

Post-dispersal survival depends not only on the environment but also on seed traits. Lighter seeds are expected to fall more slowly, hence are more likely to be uplifted and dispersed further, but they also make less competitive seedlings. We tested such differences by comparing the mass and terminal velocity of yellow poplar seeds collected at traps above the canopy and, during the same period, at the forest floor (adequate samples were available only for this species). We found no difference in terminal velocity (Fig. 3a;  $P > 0.5$ ), in accordance with an independent test we carried out in Princeton, New Jersey<sup>28</sup>. However, seeds collected above the canopy were significantly lighter than those collected at the forest floor (Fig. 3b;  $P = 0.004$ ). This apparent discrepancy is explained by the fact that the relatively light yellow poplar seeds that are uplifted have relatively small surface area (Fig. 3c;  $P = 0.003$ ), hence, their terminal velocity is conserved. Despite the statistical difference between their means, the two sample distributions overlap extensively and samples appear to come from the same population (Fig. 3). This suggests that relatively heavy yellow poplar seeds also get uplifted, so the overall effect of the difference in mean seed mass between uplifted and non-uplifted seeds on establishment is not expected to be strong.

There is still a high degree of uncertainty in predicting long-distance colonization. Probabilities of LDD, as quantified here, can be as large as 1–5%, hence making long-distance colonization more frequent than previously believed. Nevertheless, we found that for some species, uplifted seeds are on average lighter than non-uplifted seeds, suggesting they are less likely to germinate and survive seedling competition, making long-distance colonization more difficult. Multiplying the arrival and survival probabilities by the typical high fecundity of wind-dispersed trees ( $\sim 10^4$  seeds per tree per year) should yield enough long-distance colonization events to significantly impact plant dynamics on large scales. □



**Figure 3** Frequency histograms of morphological traits of seeds collected at traps above the forest canopy top versus seeds collected on the forest floor during the autumn of 2001. There is no difference in terminal velocity (**a**) (mean  $\pm$  s.e.:  $1.12 \pm 0.02 \text{ m s}^{-1}$ ,  $n = 46$  and  $1.10 \pm 0.02 \text{ m s}^{-1}$ ,  $n = 68$ , respectively;  $t$ -test,  $P > 0.5$ ), but seeds collected above canopy top are significantly lighter (**b**) ( $25.4 \pm 1.3$  and  $29.5 \pm 0.8 \text{ mg}$ , respectively;  $t$ -test,  $P = 0.004$ ), and have smaller surface area (**c**) ( $2.20 \pm 0.09$  and  $2.53 \pm 0.07 \text{ cm}^2$ , respectively;  $t$ -test,  $P = 0.003$ ). The Wald–Wolfowitz runs test reveals that for each of the three traits the observations of the two samples are randomly scattered throughout the ranking ( $P > 0.1$ ). Therefore, despite the differences among means, the two samples appear to come from the same population.

Methods

Setting

The study site is an 80–100-year-old oak–hickory forest composed of mixed hardwood species with *Quercus alba*, *Q. michauxii*, *Q. velutina*, *Carya tomentosa*, *C. ovata*, *Liriodendron tulipifera*, and *Liquidambar styraciflua* as canopy dominant (and *Pinus taeda* as a minor component), and mostly *Ostrya virginiana*, *Carpinus caroliniana* and *Cornus florida* in the understorey. The oldest individuals exceed 180 years. Tree density is  $311 \text{ ha}^{-1}$ , basal area is  $26.3 \text{ m}^2 \text{ ha}^{-1}$ , maximum leaf area index (projected foliage area per ground area) is 5.6, and maximum tree height is 33 m.

We placed 102 seed traps at 12 levels along a 45-m high tower, with the three upper levels above the tallest trees (33 m). Traps were checked at weekly or biweekly intervals.

We surveyed all trees in a radius of 50 m around the tower. Trees were identified to species, mapped on a 2.5-m grid, and measured for DBH (diameter at breast height, 1.3 m). For a sample of at least 15 trees of each species, we measured tree height and regressed its logarithm against basal area. All regression slopes were significantly greater than zero ( $P < 0.001$  in all cases) and basal area explained 61–85% of variance in tree height. We estimated height from the basal area using the regression function for trees whose heights were not measured.

We sampled the time series of the velocity components at 10 Hz using three triaxial sonic anemometers positioned at 40, 33 and 18 m above the forest floor. Plant area density (PAD) was measured with a LAI-2000 canopy analyser every 2 m, and leaf area density was inferred from PAD. A drag coefficient of 0.15 was chosen to match measured mean windspeed inside the canopy at these three levels.

**Model simulations**

We apply a coupled eulerian–lagrangian approach<sup>22,23</sup> to simulate seed dispersal from trees around the tower. We calculated statistics of wind velocities (vertical, longitudinal and lateral) inside the canopy using an eulerian second-order closure model forced by the 30-min measured friction velocity ( $u^*$ ) at 40 m. Closure models, and the mixing layer analogy that describes key length and timescales of organized eddy motion for canopy flows, have been reviewed by Finnigan<sup>29</sup>. The lagrangian velocity used to model seed trajectories is constructed at 10 Hz in a manner that: (1) conserves coherency of intermittent eddies and (2) when averaged at a given canopy layer recovers 30-min statistics computed by the eulerian model.

We ran spatially explicit simulations of seed dispersal from all reproductive adults in a radius of 50 m around the tower. Because *P. taeda* was rare near the tower, we extended the mapping radius to 150 m for this species. Based on local observations, we define adult trees as those having DBH  $\geq$  15 cm for all species but *C. caroliniana*, for which we set a threshold of 7 cm.

The number of seeds released from each tree was linear with basal area<sup>18</sup>. For each simulated dispersal event, release height and seed terminal velocity were randomly selected from a normal distribution (Table 1). For each species, we estimated the vertical distribution of seed release by counting seeds or inflorescences along tree height for at least five trees. On the basis of these observations, we calculated the mean release height (Table 1) and assumed a normal distribution with a standard deviation of 0.2 of local tree height. The mean and variance of terminal velocity were estimated from video photos of falling seeds (collected at the study site), for at least 100 seeds per species. We incorporated temporal variation in wind conditions by running the model for all 1,271 half-hour averages of  $u^*$  and wind direction recorded by the upper anemometer during the simulated period.

In Fig. 2 we examine whether the bimodal patterns observed in the dispersal kernels, given spatially constant wind conditions, remain persistent when spatial variation in winds is introduced. In the first set of simulations, we assume that  $u^*$  above the canopy is constant in the plane parallel to the forest floor. Its value is related to the time-averaged shear stress above the canopy ( $\tau_t = \rho u^{*2}$ , where  $\rho$  is the air density), typically produced by meso-scale pressure gradients. In the second set,  $\tau_t$  varies randomly in space, while keeping the same mean as in the first set (and hence the same  $u^*$ ). Because the mean horizontal windspeed and vertical velocity standard deviation at any height within (or above) the canopy scale linearly with  $u^*$ , probability density functions generated from uncorrelated random normal variations of  $u^*$  in space or time converge to the ensemble average by the ergodic theorem<sup>30</sup>. For simplicity, the  $u^*$  variations in Fig. 2 were produced in time with a mean identical to the constant  $u^*$  scenario. However, they can be interpreted as variations of  $u^*$  in space when the number of seeds released is large (as is the case here).

Received 24 December 2001; accepted 29 April 2002; doi:10.1038/nature00844.

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**Acknowledgements**

We thank M. Siqueira, C.-T. Lai, C.-I. Hsieh, I. Ibanez, S. LaDeau, B. Poulter, D. Ellsworth, J. Chave and O. Nathan for their help with data collection, and M. Cain for his comments. This study is supported by the National Science Foundation and the US Department of Energy through their Integrative Biology and Neuroscience, Terrestrial Carbon Processes, and National Institute for Global Environmental Change (South-East Regional Center) programmes.

**Competing interests statement**

The authors declare that they have no competing financial interests.

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**A neural correlate of response bias in monkey caudate nucleus**

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Primates are equipped with neural circuits in the prefrontal cortex<sup>1–6</sup>, the parietal cortex<sup>7</sup> and the basal ganglia<sup>6,8–11</sup> that predict the availability of reward during the performance of behavioural tasks. It is not known, however, how reward value is incorporated in the control of action. Here we identify neurons in the monkey caudate nucleus that create a spatially selective response bias depending on the expected gain. In behavioural tasks, the monkey had to make a visually guided eye movement in every trial, but was rewarded for a correct response in only half of the trials. Reward availability was predictable on the basis of the spatial position of the visual target. We found that caudate neurons change their discharge rate systematically, even before the appearance of the visual target, and usually fire more when the contralateral position is associated with reward. Strong anticipatory activity of neurons with a contralateral preference is associated with decreased latency for eye movements in the contralateral direction. We conclude that this neuronal mechan-