

Long-distance dispersal of tree seeds by wind

HENRY S. HORN,* RAN NATHAN[†] AND SARAH R. KAPLAN

*Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey
08544-1003, United States of America*

Some mechanisms that promote long-distance dispersal of tree seeds by wind are explored. Winged seeds must be lifted above the canopy by updrafts to have a chance of further dispersal in high velocity horizontal winds aloft or in landscape-scale convection cells. Shear-induced turbulent eddies of a scale up to one-third of canopy height provide a lifting mechanism. Preliminary data suggest that all seeds of a given species may be viable candidates for uplift and long-distance dispersal, despite the evidence that slow-falling seeds are dispersed farther under any given wind conditions. Turbulence is argued more often and more extensively to advance long-distance dispersal than to retard it. Seeds may take advantage of 'Bernoulli sailing' to move with faster than average winds. Elasticity of branches and trees may play a role in regulating the release of seeds into unusually favorable winds. Dispersal is at least biphasic, and the study of long-distance dispersal calls for mixed models and mixed methods of gathering data.

Key words: Bernoulli; model; samara, turbulence; updraft.

INTRODUCTION

Most wind-blown seeds fall near the parental tree, but long-distance dispersers are disproportionately important at both evolutionary and ecological scales of time and space (Nathan & Muller-Landau 2000; Nathan 2001). Long-distance dispersal helps to maintain metapopulations and gene flow in fragmented and changing habitats like those that humans produce habitually (Cain *et al.* 2000). Dispersal interacts with competition and predation, as well as with other aspects of plant community dynamics (Green 1983; Horn 1991; Shigesada *et al.* 1995; Muller-Landau, Levin & Keymer, unpubl. data, 2001). Long-distance dispersal determines rates of invasions, epidemics, range expansions, and responses to climate change (Clark 1998; Clark, Fastie, Hurtt *et al.* 1998, Clark

et al. 1999; Higgins & Richardson 1999; Neubert & Caswell 2000).

Long-distance dispersal is indeed rare (Cain *et al.* 2000; Nathan & Muller-Landau 2000), but in the present paper we shall argue that it may not be as rare as some might think. Many of the aerodynamic mechanisms that promote long-distance dispersal in light, fluffy or plumed seeds (Burrows 1973; Sheldon & Burrows 1973; Burrows 1975, 1986) may apply to heavier winged seeds at somewhat different scales. In particular, high winds are necessarily turbulent, and turbulence has effects that both retard and advance wind-blown seeds, with a balance that needs further exploration (Sheldon & Burrows 1973; Greene & Johnson 1989a; Okubo & Levin 1989).

We review some recent literature, emphasizing how variations in wind velocity may promote long-distance dispersal of winged seeds. A major theoretical and empirical result is that dispersal is biphasic. However, it appears that entry of seeds of a given species into the long-distance phase depends more on the characteristics of the winds encountered than on intrinsic differences between seeds (Augsburger & Franson 1987; Greene & Johnson 1990, 1992a; Nathan *et al.* 2001). We discuss some consequences of these results for

*Author to whom correspondence should be addressed. Email: hshorn@princeton.edu.

[†]Present address: Department of Life Sciences, Ben-Gurion University, Beer Sheva 84105, Israel. Email: rnathan@bgumail.bgu.ac.il

Accepted 16 October 2001.

theoretical models and for future studies of the long-distance wind dispersal of tree seeds.

BACKGROUND

Other things being equal, the distance of dispersal over level ground increases with horizontal wind velocity and height of a seed's launch, and decreases with the rate at which a seed would fall in still air. Indeed, dispersal distance is 'simply' the integral, from time of launch, of the seed's instantaneous horizontal velocity (to a first approximation wind velocity) over the time it takes to fall to the ground; that is, the time that its net instantaneous vertical velocity (to a first approximation velocity of free fall in still air minus updrafts plus downdrafts) takes to integrate to its height of initial release. It is the 'simply' part that is not at all simple.

Accordingly, seeds of canopy trees are farther dispersed if they fall slowly, are presented higher on the tree, and are preferentially launched in winds of higher velocity (Greene & Johnson 1989a, 1989b, 1992b; Nathan *et al.* 1999). Winds of higher velocity are necessarily turbulent, which adds variance to both horizontal wind velocity and to the rate of a seed's fall, as downdrafts add to its sinking velocity and updrafts retard it, or even lift it.

Although light, fluffy or plumed seeds are likely to travel farther than heavy winged seeds (Burrows 1975; Matlack 1987; Tackenberg 2001; *inter alia*), within a species most seeds of a given morphology are viable candidates for long-distance dispersal (Augspurger & Franson 1987; Greene & Johnson 1992a; Nathan *et al.* 2001). This is because the temporal, vertical and horizontal variations of wind velocity are typically greater than the variation within species in the rate of a seed's descent in still air.

Figure 1 shows how average moderate horizontal wind varies in velocity with height in and above a forest (e.g. Grace 1977; Brutsaert 1982; Nathan *et al.* In press). Going down from the top of the canopy, the average velocity decreases rapidly and approximately exponentially with depth. Going above the canopy, the average velocity increases gradually and approximately logarithmically with height. The gradient of velocity is greatest near the

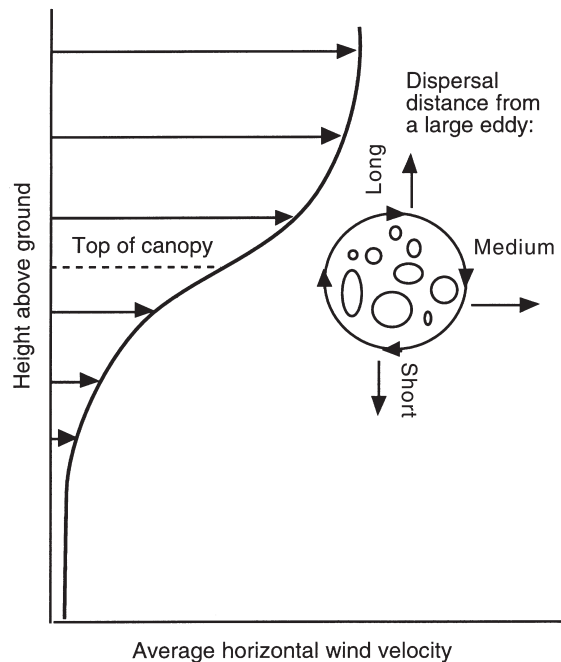


Fig. 1. Schematic diagram of average wind velocity profile in and above a forest (adapted from Nathan *et al.* In press). This figure represents time-averaged characteristics that are never present at any one instant. Velocity decreases approximately exponentially going down from the top of the canopy and increases approximately logarithmically going up above the canopy. The gradient of velocities is most steep at the top of the canopy. The large eddy is also schematic rather than real. Small ellipses inside are reminders of smaller-scale eddies and of irregular features that inhabit and characterize larger eddies. See text for interpretations relative to long-distance dispersal.

top of the canopy, which is where, we shall argue, uplift of seeds is crucial to long-distance dispersal. Shear-induced turbulent eddies near the top of the canopy provide a mechanism for such uplift. It is important to note that, to a first approximation, the instantaneous wind profile never matches its average. The average is an exceedingly complex integral of systematic and turbulent eddies at many temporal and spatial scales.

Nevertheless, one can still argue from the average profile that seeds will, on average, suffer qualitatively different fates if they fall below the canopy compared with if they rise above it. A typical seed falling below the canopy experiences ever-decreasing wind velocities and so falls far short of the distance it would travel in the initial wind at release. A seed rising above the canopy

experiences faster winds with increasing height and, at least until it re-enters the canopy, it can travel farther than it could in a constant wind of the velocity at release.

Accordingly, wind dispersal of forest tree seeds is at least biphasic, quantitatively if not also qualitatively. Those that fall within the canopy are doomed to dispersal not far beyond a distance corresponding to a few tree heights from the parent. Those that encounter updrafts faster than their intrinsic rate of descent rise above the canopy and become candidates for long-distance dispersal. Furthermore, only by rising above the canopy do seeds have a chance to become entrained in convective updrafts at the landscape scale (Avisar, Walko, Thomas *et al.* 2001; Tackenberg 2001) and, thus, potentially to travel across prodigious distances.

METHODS

The primary method used in the present study consisted of old-fashioned natural history. We watched the flight of seeds in nature, and we released and watched additional seeds in varied wind conditions in the laboratory and the field. We supplemented our observations of real seeds with experiments using artificial seeds made of paper (McCutchen 1977; Walker 1981; Augspurger & Franson 1987; Yasuda & Azuma 1997).

Ripe seeds were sampled from a tuliptree (*Liriodendron tulipifera*) prior to natural release, using a mobile 'cherry-picker' aerial lift (<http://timecon.com>). We also sampled seeds that had fallen to the ground, and that had been uplifted to the roof of a nearby building.

We measured trajectories and velocities of descent in the laboratory, taking stroboscopic photographs of seeds against a dark background (cf. Green 1980; Azuma & Yasuda 1989; Yasuda & Azuma 1997), with continuous lighting and a charge-coupled device camera (EDC-1000; Electrim Corporation, <http://electrim.com>) connected to a computer, and synchronized with a seed-dropping shelf actuated by a solenoid. We constructed a wind jet (cf. Hensen & Müller 1997), powered by a 50 cm window fan blowing through diffusers made of plastic 'egg-crate' fluorescent light baffles (cf. AIAA Savannah Section

Mini Wind Tunnel; <http://home.earthlink.net/~savaiaa/wt.html>). It generates winds of 2–4 m s⁻¹ over a cross-wind area of 25 cm × 25 cm.

INSIGHTS, RESULTS AND DISCUSSION

Observations

The fluffy seeds of willow (*Salix*), cottonwoods, poplar and aspen (*Populus*) have a rate of descent in still air of approximately 0.1 m s⁻¹ or 0.2 m s⁻¹ (Tackenberg 2001), and are often seen floating on mild breezes, blowing up to prodigious heights, and sailing off out of sight. Anyone who has cleaned roof gutters on a windy spring day in the temperate zone has found the winged disks of elm (*Ulmus*) and the samaras of maple (*Acer*), and watched them fly up and over the house. Comparable updrafting eddies occur near the canopy of a forest (Fig. 1). The size of these eddies can be as large as one-third of the canopy height, although they contain many smaller scales of turbulence (Katul & Chang 1999). The intrinsic rate of descent of many winged seeds falls in the range 0.5–1.5 m s⁻¹ (Green 1980; Augspurger 1986; Matlack 1987; Azuma & Yasuda 1989; Greene & Johnson 1995; Tackenberg 2001). Accordingly, if updrafts exceed these velocities for several seconds, the eddies can drive winged seeds up out of the canopy and into winds of higher average horizontal velocity, and perhaps into convective updrafts at the landscape scale (Avisar, Walko, Thomas *et al.* 2001; Tackenberg 2001; Nathan, Kataul, Avisar, Thomas, Oren, Horn, Pacala & Levin, unpubl. data, 2001). Consequently, those seeds that exit the top of the eddy are candidates for long-distance dispersal. Those that exit the bottom are doomed to short-distance dispersal, and those that exit leeward may travel an intermediate distance (Fig. 1). Eddies at smaller scales and turbulence within large eddies should generally increase residence time within the larger eddy without greatly affecting the relative probabilities of short, medium or long-distance dispersal. However, if the eddy itself is travelling systematically downwind, longer residence in the eddy means farther transport.

Another mechanism that could potentially promote uplifting is the elastic oscillation of the

tree itself. A tree of a given height and stiffness has a natural frequency of vibration, with a period of oscillation in the range of several seconds (McMahon 1975; McMahon & Kronauer 1976). The energy of sudden downdrafts can be stored by elastic deformation of a tree and then released as it returns to its static position with a time constant in the range of a few seconds. Correlated movement among neighbors could produce updrafts sufficient to lift winged seeds. We have observed such updrafts qualitatively, and they deserve quantitative exploration.

Greene and Johnson (1992b) have described a mechanism whereby silver maple (*Acer saccharinum*) may bias the release of its seeds toward the most favorable wind conditions for far dispersal. The abscission layer develops more rapidly when humidity is low. The lowest humidity in a typical diurnal cycle is in the early afternoon, when winds are typically highest, and when thermal convection cells often develop. Greene and Johnson (1992b) also showed that upward-directed winds were more effective at launching seeds than horizontal winds of equal velocity, suggesting that the natural release of seeds might be biased toward updrafts. Nathan *et al.* (1999) have similarly argued that seeds of the serotinous pine (*Pinus halepensis*) are released preferentially during dry weather, thus synchronizing with weather events that are favorable for long-distance dispersal.

We have observed an additional mechanism that may bias release of seeds toward high and turbulent winds. Again, it involves elastic properties of branches (McMahon & Kronauer 1976). The seeds of tuliptree (*L. tulipifera*) develop in a tight cluster, with the central seeds abscising first to nestle within a cup formed by the outer seeds. The seeds are only launched in winds high enough to jostle twigs and branches. Seeds of white ash (*Fraxinus americana*) are in a loose cluster that collapses into a streamlined airfoil in moderate winds, so that tightly held seeds are only pulled away in high winds that shake the twig or branch violently. In both tuliptree and white ash, seeds are released from early autumn through the winter, exclusively in high winds early and in moderate winds later. This suggests that the mechanism of adjustment is the development of the abscission layer, although at a much slower rate than in silver maple as described by Greene and Johnson (1992b).

Field experiments

Given the importance of the intrinsic rate of descent for potential uplift, one might expect that only the slowest falling seeds are candidates for uplift and long-distance dispersal. To test this, during October and November 2000 we collected tuliptree (*L. tulipifera*) seeds from the roof of three apartment buildings in Princeton (NJ, USA), 25–40 m above the ground. The nearest tuliptrees were 23 m or 24 m tall, and a distance of 35 m or more to the west, the direction from which prevailing winds blow. We compared the velocities of descent in still air in the laboratory for these seeds and for comparable samples collected on the ground beneath nearby trees and also from the trees themselves. Figure 2 shows that all three samples had the same range of terminal velocities, and the same coefficient of variation (i.e. 0.1; cf. Green 1980; Greene & Johnson 1992a). Apparently it is not special seeds that are lifted during average wind conditions, but rather all seeds are lifted during unusually windy conditions.

This result was provisionally confirmed during May and June 2001 for red maple (*Acer rubrum*) collected from a roof (25 m high) and from the ground beneath the nearest red maple, a tree 16 m tall and a distance of 15 m to the west of the building. Rather than measuring exact velocities of descent, seeds from the rooftop and the ground were dropped simultaneously in paired 'races' over 2.5 m (the method of Greene & Johnson 1990). In 25 tests there were 12 roof winners, 10 ground winners, and two ties.

This is more a plausibility argument than a definitive test of what happens in a forest because an apartment building is an obstruction that necessarily causes stronger updrafts than a semipermeable forest of the same height. Nevertheless, seeds that fall at velocities ranging 0.9–1.6 m s⁻¹ were uplifted. The species tested have two different mechanisms of generation of lift; the red maple as a standard airfoil (Norberg 1973), whereas the tuliptree spins about its central axis (McCutchen 1977). The mechanisms have different lift:drag ratios (Azuma & Yasuda 1989), and have been argued to have different stabilities in flight in turbulent wind (McCutchen 1977; Green 1980; Burrows 1986), but we found them to have similar performances, as have Greene and Johnson (1990).

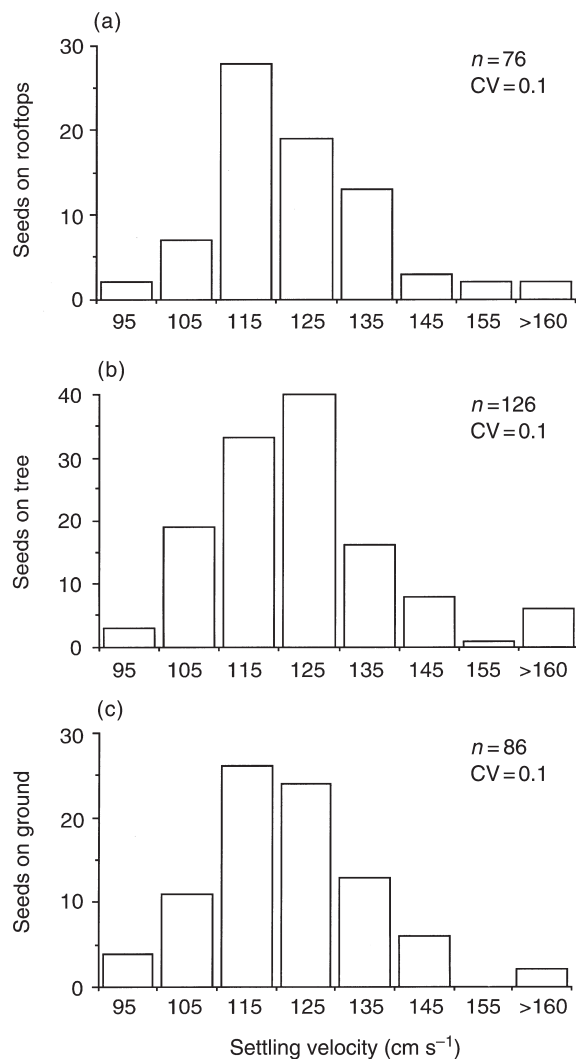


Fig. 2. Settling velocities in still air for seeds of tulip-tree (*Liriodendron tulipifera*). (a) Those found on the rooftops of three apartment buildings, 26 m, 26 m and 40 m above the ground. (b) Those sampled from a 25 m tall tree at heights from 20 m to 25 m. (c) Those sampled from below nearby trees. Seeds from the tops of the buildings must have been uplifted, and there is no evidence that they differ in their terminal velocities from the seeds on the tree or those falling to the ground.

The results of the present study fits with those results of Augspurger and Franson (1987), Greene and Johnson (1992a) and Nathan *et al.* (2001), who argue that variation in wind velocities (typically with a coefficient of variation >0.6) outweigh the variation in rates of descent within a species (typically with a coefficient of variation of the order 0.1–0.2). Accordingly, we suggest that all seeds within a wind-dispersed species may be viable can-

didates for long-distance dispersal. However, we are working on a more definitive test under natural circumstances, using a 45 m tall tower in a 33 m tall hardwood forest at the Duke Forest in North Carolina (USA) (Nathan, Horn, Levin *et al.* 2001).

Theory

To date, the results argue that a realistic mechanistic model of wind dispersal must take explicit account of wind variability (Augspurger 1986; Greene & Johnson 1989a; Andersen 1991; Nathan *et al.* 2001; Nathan *et al.* In press). A particularly promising analytical model is that of Okubo and Levin (1989; also explored by Andersen 1991). They start with the 'tilted Gaussian plume' model proposed by engineers interested in the ranging of wind-borne pollutants from a point source. In the engineers' model, turbulence tends to add to the intrinsic settling velocity of particles, decreasing the mode of their dispersal distance. Okubo and Levin add explicit deposition to make an 'advection–diffusion deposition model', which further decreases the modal dispersal distance. This tendency for turbulence to decrease dispersal fits with qualitative arguments made by Burrows (1975, 1983). Okubo and Levin are not able to calculate an exact mean or variance for their complete model, but they do calculate a parameter related to the 'spread' of the distribution of dispersal distances, and this parameter increases with turbulence.

Hence, in the model proposed by Okubo and Levin (1989), turbulence decreases modal dispersal but increases the variance of dispersal. How these effects combine to affect mean dispersal or, more importantly, long-distance dispersal is currently unclear but worthy of study. We can argue, referring to Fig. 1, that turbulence will produce a net increase in long-distance dispersal, despite the decrease in modal dispersal. Because the average horizontal wind velocity increases with height within and above the canopy, turbulence at all scales will promote biphasic dispersal. Those seeds that are retarded in their descent, or even lifted, by updrafts will have their range augmented more than the loss in range of those that suffer an equal downdraft. Such an argument has been made by Greene and Johnson (1989b), although it is made for temporal variations in average wind

velocity rather than for a vertical gradient and, indeed, variance increases the mean dispersal in Greene and Johnson's model, despite decreasing the mode.

Further work with the model of Okubo and Levin (1989) may help to explain why, both in practice and in other models, extremes of dispersal are poorly predicted by modal dispersal (Greene & Johnson 1989a; Andersen 1991; Portnoy & Willson 1993; Greene & Johnson 1995; Kot *et al.* 1996; Clark 1998; Jongejans & Schippers 1999; Bullock & Clarke 2000).

An additional, speculative mechanism may dramatically increase the range of dispersal in high and turbulent winds. Such winds have many small-scale gradients in velocity such that seeds may experience higher velocities on one side rather than the other, producing a Bernoulli pressure, which tends to drive the seed toward the higher velocity. The pressure is proportional to the difference in the squares of the velocities on either side (Vogel 1994). A rough calculation using wing loadings from Green (1980) suggests that a velocity gradient as small as 5 cm s^{-1} to 10 cm s^{-1} within 2 cm would be sufficient to draw a winged seed of tulip-tree or red maple toward the faster wind. The presence and persistence of such gradients in natural winds remains to be demonstrated, but a similar mechanism has been proposed by Hensen and Müller (1997), which extends the range of plumed seeds in unsteady winds. In laboratory experiments with a wind jet, Hensen and Müller found that dispersal distance increased approximately quadratically with wind speeds in excess of 2 m s^{-1} .

If confirmed, this 'Bernoulli sailing' could entrain seeds in larger eddies so that they traveled with faster than average winds, magnifying all of the effects discussed earlier. It is important to note that we are not suggesting a systematic pressure-induced uplift. The vertical gradient in time-averaged horizontal velocity portrayed in Fig. 1 is unlikely to be stable over a long enough time and short enough distance to produce a consistent uplift.

The final mechanism of critical importance to long-distance dispersal is the capture of seeds in convection cells of the scale of hundreds of meters to kilometers. This has long been recognized as important for fluffy and plumed seeds (e.g.

Burrows 1973). Tackenberg (2001) has recently presented and provisionally tested a mechanistic stochastic model of wind dispersal that explicitly incorporates topography and thermally induced turbulence and convection. He has tested it successfully by releasing seeds of grassland species in an open but complex landscape, and characterizing their dispersal up to 150 m. Tackenberg observes that strong horizontal winds will disrupt light, thermally induced updrafts, and so reduce the dispersal distance of his plants in an open landscape. Conversely, the uplifts within a forest that we postulate in the present report may be driven by eddies induced by the shear of strong wind (Higgins, Nathan & Cain, unpubl. data, 2001). Both mechanisms come together in violent storms, in which strong thermal updrafts induce strong horizontal winds, which in turn induce strong turbulent eddies. We hope eventually to incorporate such meso-scale meteorology into models for the dispersal of winged seeds in a forested landscape (Avisar, Walko, Thomas *et al.* 2001). In any case, escape from the canopy is a prerequisite to take advantage of landscape-scale turbulent and convective cells.

CONCLUSIONS AND FUTURE WORK

The mechanisms that we have presented all conspire to make long-distance dispersal of winged tree seeds both more common and farther than simple models suggest. This echoes an argument made by Sheldon and Burrows (1973), back in the days when some investigators questioned the efficacy of long-distance wind dispersal for the plumed seeds of Compositae!

In particular, turbulence and variations in wind velocities may more often and more extensively advance extreme dispersal rather than retard it, despite the fact that, on average, they decrease the modal distance of dispersal. A speculative 'Bernoulli sailing' in unsteady winds may carry seeds with faster than average winds. Forest seeds must get above the canopy to have a chance of long-distance dispersal, and wind-generated eddies on the scale of one-third of canopy height provide a mechanism to take them there. Higher average wind velocities aloft mean that uplifted

seeds are advanced more than downthrust seeds are retarded. This effect deserves more explicit exploration, using models like those of Okubo and Levin (1989) to discover the conditions under which turbulence advances rather than prevents long-distance dispersal.

The elastic properties of trees deserve further study in relation to wind dispersal (McMahon & Kronauer 1976). Trees may respond to wind in ways that produce sustained updrafts in their immediate surroundings. Trees may regulate their attachment to seeds to ensure release into high or optimally oriented wind speeds (Greene & Johnson 1992b; Nathan *et al.* 1999). The release of seeds into local gusts of wind by elastic responses of branches is a promising mechanism that is underexplored in comparison to its demonstrated importance in herbs and grasses (Burrows 1986). Trees can bias the release of their seeds to particular wind conditions, and so it is important to know what those conditions are, and how they differ from species to species. This is crucial so that mechanistic models can use appropriate parameters of wind behavior. It also underscores the need to survey seeds that are naturally released to correct extrapolations from laboratory and artificial release experiments (Greene & Calogeropoulos, In press).

Preliminary data in an artificial setting suggest that most seeds within a wind-dispersed species can be uplifted and are therefore candidates for long-distance dispersal. We are currently gathering the same kind of data in a natural setting (Nathan, Horn, Levin *et al.* 2001).

Greene and Calogeropoulos (In press) have recently reviewed both the data and theory related to the seed dispersal of terrestrial plants, and concluded that different approaches may be needed for studies of near-parental dispersal compared with long-distance dispersal. Dispersal of forest tree seeds by wind is distinctly biphasic. Seeds that fall within the canopy have no chance of long-distance dispersal; seeds that rise above the canopy do. Different mechanisms are involved in transport above compared with within the forest. Accordingly, we recommend more work on mixed models of transport such as those of Higgins, Nathan and Cain (unpubl. data, 2001), Nathan *et al.* (In press), Bullock & Clarke (2000), Higgins and Richardson (1999), Clark (1998), Turchin (1998), Clark,

Fastie, Hurtt *et al.* (1998), Clark *et al.* (1999), and Shigesada *et al.* (1995). There will always be a conflict between statistical power to fit a single model to copious data near the mode of a dispersal curve, and biological interest in the sparse data at the extremely long distances (Portnoy & Wilson 1993; Turchin 1998; Higgins & Richardson 1999), especially when inverse methods (e.g. Ribbens *et al.* 1994; Clark 1998) are used to estimate parameters from field data for models. Mixed models at least allow these conflicting interests to be separated, and they also provide an opportunity to estimate separately the partitioning of seeds between viable candidates for long-distance dispersal and those doomed to falling locally. Higgins, Nathan & Cain (unpubl. data, 2001) argue persuasively for the use of mixed models wherever dispersal can take place by different modalities, as we argue it does for seeds that fall within the canopy compared with those that rise.

We are currently testing a micrometeorological model for its accuracy in predicting the probability that seeds will rise above the canopy (Nathan, Horn, Levin *et al.* 2001). So far, we have successfully predicted the relative probabilities of uplift of five species with terminal velocities of descent ranging from 0.7 m s^{-1} to 1.5 m s^{-1} (Nathan, Kataul, Avissar, Thomas, Oren, Horn, Pacala & Levin, unpubl. data, 2001). Our hope is to couple accurately with models currently being developed to explore wind dispersal of tree seeds in yet another phase, at the landscape scale of kilometers (Avissar, Walko, Thomas *et al.* 2001; cf. Tackenberg 2001).

ACKNOWLEDGEMENTS

We are grateful for extensive discussions with Prof. S. A. Levin, Prof. S. W. Pacala, Prof. G. G. Katul, Prof. R. Avissar, and Dr H. C. Muller-Landau. Prof. D. F. Greene gave extensive and constructive criticism of the manuscript; Ms K. S. Yamasato gathered some preliminary data to help calibrate our machinery; and Mr R. Phillips of the Princeton University Buildings and Grounds Department helped us to collect seeds directly from high in a tree. The work was supported by National Science Foundation Grant IBN-9981620.

REFERENCES

- ANDERSEN M. (1991) Mechanistic models for the seed shadows of wind-dispersed plants. *American Naturalist* 137: 476–497.
- AUGSPURGER C. K. (1986) Morphology and dispersal potential of wind-dispersed diaspores of neotropical trees. *American Journal of Botany* 73: 353–363.
- AUGSPURGER C. K. & FRANSON S. E. (1987) Wind dispersal of artificial fruits varying in mass, area, and morphology. *Ecology* 68: 27–42.
- AVISSAR R., WALKO R. E., THOMAS S., ROY S. B., KATUL G., NATHAN R., HORN H. & LEVIN S. (2001) A Large-Eddy/Lagrangian Dispersion model to study long-distance dispersal of tree seeds [abstract]. In: *Symposium Abstracts of the 86th Annual Meeting of the Ecological Society of America*. pp. 6. Ecological Society of America, Washington, D.C.
- AZUMA A. & YASUDA K. (1989) Flight performance of rotary seeds. *Journal of Theoretical Biology* 138: 23–53.
- BRUTSAERT W. (1982) *Evaporation into the Atmosphere: Theory, History, and Applications*. D. Reidel Publishing Co., Dordrecht, The Netherlands.
- BULLOCK J. M. & CLARKE R. T. (2000) Long distance seed dispersal by wind: Measuring and modelling the tail of the curve. *Oecologia* 124: 506–521.
- BURROWS F. M. (1973) Calculation of the primary trajectories of plumed seeds in steady winds with variable convection. *New Phytologist* 72: 647–664.
- BURROWS F. M. (1975) Wind-borne seed and fruit movement. *New Phytologist* 75: 405–418.
- BURROWS F. M. (1983) Calculation of the primary trajectories of seeds and other particles in strong winds. *Proceedings of the Royal Society of London* A389: 15–66.
- BURROWS F. M. (1986) The aerial motion of seeds, fruits, spores and pollen. In: *Seed Dispersal*. (ed. D. R. Murray) pp. 1–47. Academic Press, New York.
- CAIN M. L., MILLIGAN B. G. & STRAND A. E. (2000) Long-distance seed dispersal in plant populations. *American Journal of Botany* 87: 1217–1227.
- CLARK J. S. (1998) Why trees migrate so fast: Confronting theory with dispersal biology and the paleorecord. *American Naturalist* 152: 204–224.
- CLARK J. S., FASTIE C., HURTT G., JACKSON S. T., JOHNSON C., KING G. A., LEWIS M., LYNCH J., PACALA S., PRENTICE C., SCHUPP E. W., WEBB III T. & WYCKOFF P. (1998) Reid's paradox of rapid plant migration. *Bioscience* 48: 13–24.
- CLARK J. S., SILMAN M., KERN R., MACKLIN E. & HILLERISLAMBERS J. (1999) Seed dispersal near and far: Patterns across temperate and tropical forests. *Ecology* 80: 1475–1494.
- GRACE J. (1977) *Plant Response to Wind*. Academic Press, New York.
- GREEN D. S. (1980) The terminal velocity and dispersal of spinning samaras. *American Journal of Botany* 67: 1218–1224.
- GREEN D. S. (1983) The efficacy of dispersal in relation to safe site density. *Oecologia* 56: 356–358.
- GREENE D. S. & CALOGEROPOULOS C. (In press) Measuring and modelling seed dispersal of terrestrial plants. In: *Dispersal Ecology*. (eds J. Bullock, R. Kenward & R. Hails), Blackwell Science, Oxford.
- GREENE D. F. & JOHNSON E. A. (1989a) A model of wind dispersal of winged or plumed seeds. *Ecology* 70: 339–347.
- GREENE D. F. & JOHNSON E. A. (1989b) Particulate diffusion models and the dispersal of seeds by the wind. *Trends in Ecology and Evolution* 4: 191–192.
- GREENE D. F. & JOHNSON E. A. (1990) The dispersal of winged fruits and seeds differing in autorotative behaviour. *Canadian Journal of Botany* 68: 2693–2697.
- GREENE D. F. & JOHNSON E. A. (1992a) Can variation in samara mass and terminal velocity on an individual plant affect the distribution of dispersal distances? *American Naturalist* 139: 825–838.
- GREENE D. F. & JOHNSON E. A. (1992b) Fruit abscission in *Acer saccharinum* with reference to seed dispersal. *Canadian Journal of Botany* 70: 2277–2283.
- GREENE D. F. & JOHNSON E. A. (1995) Long-distance wind dispersal of tree seeds. *Canadian Journal of Botany* 73: 1036–1045.
- HENSEN I. & MÜLLER C. (1997) Experimental and structural investigations of anemochorous dispersal. *Plant Ecology* 133: 169–180.
- HIGGINS S. I. & RICHARDSON D. M. (1999) Predicting plant migration rates in a changing world: The role of long-distance dispersal. *American Naturalist* 153: 464–475.
- HORN H. S. (1991) Some causes of variety in patterns of forest succession. In: *Forest Succession: Concepts and Applications*. (eds D. C. West, H. H. Shugart & D. B. Botkin) pp. 24–35. Springer-Verlag, New York.

- JONGEJANS E. & SCHIPPERS P. (1999) Modeling seed dispersal by wind in herbaceous species. *Oikos* 87: 362–372.
- KATUL G. G. & CHANG W.-H. (1999a) Principle length scales in second-order closure models for canopy turbulence. *Journal of Applied Meteorology* 38: 1631–1643.
- KOT M., LEWIS M. A. & VAN DEN DREISSCHE P. (1996) Dispersal data and the spread of invading organisms. *Ecology* 77: 2027–2042.
- MATLACK G. R. (1987) Diaspore size, shape and fall behavior in wind-dispersed plant species. *American Journal of Botany* 74: 1150–1160.
- MCCUTCHEN C. W. (1977) The spinning rotation of ash and tulip tree samaras. *Science* 197: 691–692.
- MCMAHON T. A. (1975) The mechanical design of trees. *Scientific American* 233: 92–102.
- MCMAHON T. A. & KRONAUER R. E. (1976) Tree structures: Deducing the principle of mechanical design. *Journal of Theoretical Biology* 59: 443–466.
- NATHAN R. (2001) The challenges of studying dispersal. *Trends in Ecology and Evolution* 16: 481–483.
- NATHAN R., HORN H. S., CHAVE J. & LEVIN S. (In press) Mechanistic models for tree seed dispersal by wind in dense forests and open landscapes. In: *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation* (eds D. J. Levey, W. R. Silva & M. Galetti) pp. 69–82. CAB International Press, Oxfordshire, UK.
- NATHAN R., HORN H. S., LEVIN S. A., PACALA S. W., KATUL G. G., AVISSAR R., WALKO R. L. & THOMAS S. M. (2001) Long-distance dispersal of tree seeds by wind: The role of vertical wind updrafts [abstract]. *Symposium Abstracts of the 86th Annual Meeting of the Ecological Society of America*, pp. 28–29. Ecological Society of America, Washington D.C.
- NATHAN R. & MULLER-LANDAU H. C. (2000) Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology and Evolution* 15: 278–285.
- NATHAN R., SAFRIEL U. N. & NOY-MEIR I. (2001) Field validation and sensitivity analysis of a mechanistic model for tree seed dispersal by wind. *Ecology* 82: 374–388.
- NATHAN R., SAFRIEL U. N., NOY-MEIR I. & SCHILLER G. (1999) Seed release without fire in *Pinus halepensis*, a Mediterranean serotinous wind-dispersed tree. *Journal of Ecology* 87: 659–669.
- NEUBERT M. G. & CASWELL H. (2000) Demography and dispersal: Calculation and sensitivity analysis of invasion speed for structured populations. *Ecology* 81: 1613–1628.
- NORBERG R. A. (1973) Autorotation, self-stability, and structure of single-winged fruits and seeds (samaras) with comparative remarks on animal flight. *Biological Reviews* 48: 561–596.
- OKUBO A. & LEVIN S. A. (1989) A theoretical framework for data analysis of wind dispersal of seeds and pollen. *Ecology* 70: 329–338.
- PORTNOY S. & WILLSON M. F. (1993) Seed dispersal curves: Behavior of the tail of the distribution. *Evolutionary Ecology* 7: 25–44.
- RIBBENS E., SILANDER JR J. A. & PACALA S. W. (1994) Seedling recruitment in forests: Calibrating models to predict patterns of tree seedling dispersion. *Ecology* 75: 1794–1806.
- SHELDON J. C. & BURROWS F. M. (1973) The dispersal effectiveness of the achene-pappus units of selected Compositae in steady winds with convection. *New Phytologist* 72: 665–675.
- SHIGESADA N., KAWASAKI K. & TAKEDA Y. (1995) Modeling stratified diffusion in biological invasions. *American Naturalist* 146: 229–251.
- TACKENBERG O. (2001) *Methode zur Bewertung gradueller Unterscheide des Ausbreitungspotentials von Pflanzenarten* [dissertation]. (Dr. rer. nat.), Fachbereich Biologie, Philipps-Universität, Marburg. Available from URL: <http://archiv.ub.uni-marburg.de/diss/z2001/0107>
- TURCHIN P. (1998) *Quantitative Analysis of Movement: Measuring and Modelling Population Redistribution in Animals and Plants*. Sinauer Associates, Sunderland, MA.
- VOGEL S. (1994). *Life in Moving Fluids*, 2nd edn. Princeton University Press, Princeton, NJ.
- WALKER J. (1981) The aerodynamics of the samara: Winged seed of the maple, the ash and other trees. *Scientific American* 245: 226–238.
- YASUDA K. & AZUMA A. (1997) The autorotation boundary in the flight of samaras. *Journal of Theoretical Biology* 185: 313–320.