DETERMINANTS OF LONG-DISTANCE SEED DISPERSAL BY WIND IN GRASSLANDS

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Abstract. Long-distance seed dispersal is an important topic in ecology, but notoriously difficult to quantify. Previous modeling approaches have failed to simulate long-distance dispersal, and it has remained unclear which mechanisms determine long-distance dispersal and what their relative importance is. We simulated wind dispersal of grassland plant seeds with four mechanistic models of increasing complexity and realism to assess which processes and which attributes of plants and their environment determine dispersal distances. We compared simulation results of the models to each other and to data from field dispersal experiments. The more complex and realistic models predicted short-distance dispersal more accurately and were the only models able to simulate long-distance dispersal. The model comparisons showed that autocorrelated turbulent fluctuations in vertical wind velocity are the key mechanism for long-distance dispersal. Seed dispersal distances are longest under high wind velocity conditions, when mechanically produced turbulent air movements are large. Under very low wind velocity conditions seeds are dispersed farther when there is more surface heating, but never as far as during strong wind events. Model sensitivity analyses showed that mean horizontal wind velocity, seed release height, and vegetation height are crucial determinants of dispersal potential and dispersal distances. Between plant species (but not within a species), seed terminal velocity is an additional important determinant of long-distance dispersal. These results imply that seed release height is the most important plant-controlled dispersal parameter for grassland plants, and that the structure of the local vegetation greatly affects dispersal distances. Thus, management plans for grasslands should take into account that changes in vegetation structure, e.g., due to eutrophication, can reduce the seed dispersal ability of wind-dispersed plant species.

Key words: atmospheric stability; dispersal experiments; grassland; long-distance seed dispersal; mechanistic dispersal models; seed release height; terminal velocity; turbulence; uplifting; wind dispersal.

INTRODUCTION

The dispersal of plant seeds in space has many implications for population, community, and ecosystem biology and has been the topic of many recent studies. The ecological importance of long-distance dispersal (LDD) has been especially stressed (Cain et al. 1998, 2000, Clark 1998, Clark et al. 1999, 2001, Nathan and Muller-Landau 2000, Nathan 2001), although LDD is notoriously difficult to quantify (Bullock and Clarke 2000, Cain et al. 2000, Nathan et al. 2003). The main mechanism of LDD that has been studied is wind dispersal (e.g., Greene and Johnson 1995, Horn et al. 2001, Nathan et al. 2002*b*). Wind dispersal is one of the most common LDD mechanisms (Van der Pijl 1982, Bouman et al. 2000), and appears to be less complex than the other LDD mechanisms, such as dispersal by large animals.

Important insight in the wind dispersal process has been gained from experimental studies (e.g., Augspurger and Franson 1987, McEvoy and Cox 1987, Greene and Johnson 1993, Bullock and Clarke 2000) and various mechanistic modeling approaches (e.g., Okubo and Levin 1989, Andersen 1991, Greene and Johnson 1996, Nathan et al. 2002*b*, Tackenberg 2003). These studies, however, also provided different and sometimes conflicting answers as to which processes and which plant and environmental attributes determine seed dispersal distances, and in particular LDD. Many studies focused on seed terminal velocity as a major determinant because it is a seed attribute (e.g., Matlack 1987, Andersen 1992, 1993, Greene and Johnson 1993). A recent model study confirmed that seed terminal velocity is important in determining LDD (Tackenberg et al. 2003). However, others state that wind velocity is much more important in determining LDD than any plant attribute (Augspurger and Franson 1987, Greene and Johnson 1992, Horn et al. 2001, Nathan et al. 2001). This has lead to recent model developments

in which great effort was made to simulate horizontal and vertical wind velocities in a realistic way. Tackenberg (2003) suggested that a mean upward vertical wind velocity under unstable atmospheric conditions (i.e., when high surface heating and low horizontal wind velocity cause air parcels to move upward locally) is the most important wind characteristic responsible for seed uplifting events, and that seed uplifting is the key mechanism for LDD in grasslands. Studies on forests have put forward the effects of gusts and other rapid fluctuations in the wind field that occur under near-neutral atmospheric conditions (i.e., when high horizontal wind velocities create large turbulent wind movements) as the most important processes for seed uplifting, and hence LDD (Horn et al. 2001, Nathan et al. 2002b).

The relative importance of different processes and different attributes of plants and their environment, and especially the role of vertical wind movements, in determining LDD are now central research themes in dispersal ecology. We address these themes for grassland ecosystems, in which the statistics of wind flow are relatively simple to parameterize. We used a combination of model simulations and field experiments to determine which wind flow-related processes and which plant-controlled and environmental-controlled parameters determine seed dispersal distances, and in particular long distances. Our approach differs from previous studies because we used a hierarchical framework of mechanistic models of increasing complexity and realism to assess the relative importance of specific processes. We used field data to test whether the addition of specific processes to the simulation of dispersal improved the realism of the simulations. We also carried out model sensitivity analyses to assess which parameters are most important in determining seed dispersal distances. We conclude this study by discussing the implications of our findings for the dispersal ability of plants in grassland ecosystems.

METHODS

The simulation models

To model seed dispersal, we considered the trajectories of single seeds in Cartesian coordinates ($x_1 = x$, $x_2 = y$, $x_3 = z$). The general form of a seed dispersal trajectory is given by

$$x_i(t + \Delta t) = x_i(t) + \int_t^{t+\Delta t} (u_i - v_t \delta_{i3})\, dt \qquad i = 1, 2, 3$$

(1)

where u_i is the instantaneous wind velocity in direction x_i, Δt is the discrete simulation time interval, v_t is the seed terminal velocity, and δ_{i3} is 1 for $i = 3$ and 0 otherwise. The velocity of the seed is assumed to adjust to the wind velocity instantaneously.

It is necessary to compute the instantaneous velocity u_i across the entire seed trajectory to estimate seed dispersal. Different mechanistic modeling approaches vary in the level of realism and complexity in which they compute u_i. We compared four different mechanistic seed dispersal trajectory models of increasing realism. The first model is used as a basic reference model, because of its simplicity and minimal data requirements. The other three models form a series of model development and extend the basic model with (1) random fluctuations in vertical wind velocity, (2) (auto-) correlated mechanically produced wind turbulence, or (3) (auto-) correlated mechanically produced and buoyantly produced wind turbulence. Along with the increasing realism, the level of complexity of the models also increases. Comparison of the results of the models allows assessment of the optimal model for simulating seed dispersal, and especially LDD.

1. *The simple deterministic model.*—The simplest mechanistic model, which serves as our basic model, describes the trajectory of a seed as determined by the air resistance and gravitational forces. It assumes that the seed dispersal distance (D) depends only on the falling time of a seed from its release height (H_0) to its interception height and on the horizontal wind velocities it experiences during this time. The mean (i.e., time-averaged) horizontal wind velocity ($\bar{U}$) increases with height above the ground surface (Monteith 1973, Stull 1988):

$$\overline{U}(z) = \frac{u_*}{k} \ln\left(\frac{z - d}{z_0}\right)$$

(2)

where u_* is the friction velocity, z is the height from the ground surface, d is the zero-plane displacement height, z_0 is the momentum roughness length, and $k = 0.4$ is the Von Karman constant. The overbar indicates time averaging, typically over periods of 15–60 minutes. The seed interception height is set at ($z_0 + d$), the height at which $\bar{U}$ is reduced to zero. Estimates of d and z_0 can be obtained from the mean vegetation height (h) for dense canopies, using $d = 0.63 \times h$ and $z_0 = 0.13 \times h$ (Monteith 1973). Based on these assumptions, an analytical function for D can be derived (cf. Nathan et al. 2001) as follows:

$$D = \frac{u_*}{k \times v_t}\left[(H_0 - d)\ln\left(\frac{H_0 - d}{e \times z_0}\right) + z_0\right].$$

(3)

Advantages of this model are its simplicity, fast analytical computation, and the deterministic relation between model input and output (Fig. 1a). Therefore, this model was used as a baseline model in several dispersal studies (Sharpe and Fields 1982, McCartney 1990, Nathan et al. 2001, 2002a). However, it is a disadvantage that upward vertical air movement is not included in this model (Fig. 2a). Upward vertical air movement may cause seed uplifting, which is generally assumed to be a key process determining LDD (Horn et al. 2001, Nathan et al. 2002b, Tackenberg 2003). Although it is possible to add upward vertical air movement to this
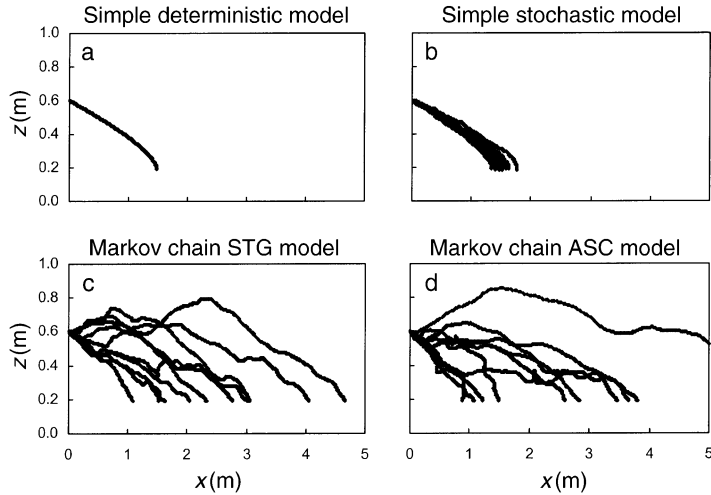
FIG. 1. Ten random dispersal trajectories of a single plumed seed dispersing from a long flowering stalk in a shortgrass grassland for an average wind velocity. Dispersal trajectories simulated by the two Markov chain models (Synthetic Turbulence Generation [STG] and Atmospheric Stability Correction [ASC]) show more variation and longer dispersal distances than trajectories simulated by the two simple models. Simulated time series are all based on the same parameter set: $\bar{U}_{5.2m} = 3.0$ m/s, $h = 0.25$ m, LAI = 3.5, $H_0 = 0.60$ m, $v_t = 0.30$ m/s; and for the ASC model, $T = 20°C$ and $Q_H = 250$ W/m².

simple model, this must be constrained to be at a lower absolute velocity than v_t (Nathan et al. 2001), and hence, seed uplifting cannot be simulated. The following three models incorporate vertical air movements with increasing realism and complexity.

2. *The simple stochastic model.*—The simplest way to incorporate vertical air movement without constraints is to assume that seeds are subject to random and uncorrelated fluctuations in vertical wind velocity (w') while moving horizontally with $\bar{U}$. To assess how
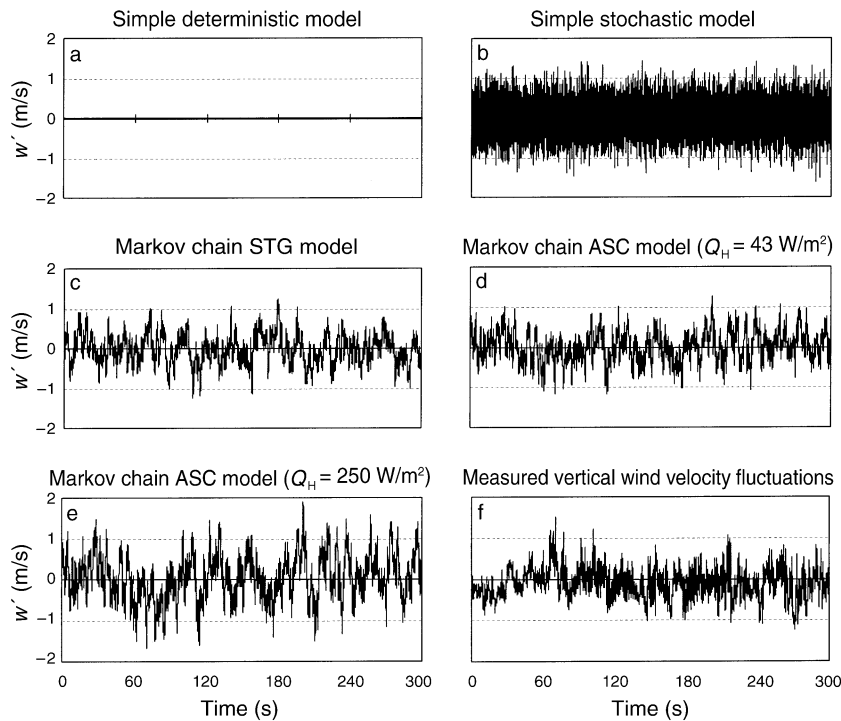

FIG. 2. Randomly selected time series of simulated fluctuations in vertical wind velocity (w') are much more realistic in the two Markov chain models (STG and ASC) than in the two simple models. (a) The simple deterministic model, no simulation of vertical wind velocity; (b) the simple stochastic model, with simulation of random fluctuations in vertical wind velocity; (c) the Markov chain STG model, with simulation of mechanically produced autocorrelated fluctuations in vertical wind velocity; (d) the Markov chain ASC model, with simulation of mechanically and buoyantly produced autocorrelated fluctuations in vertical wind velocity; (e) the Markov chain ASC model with increased sensible heat flux ($Q_H = 250$ W/m²); and (f) a measured time series of fluctuations in vertical wind velocity from a long-term micrometeorological study in a grassland (measured with a triaxial sonic anemometer, sampling rate 56 Hz, height 5 m, data from ⟨http://www.env.duke.edu/faculty/katul/sample_data.html⟩). Simulated time series are based on the measured data set (with $\bar{U}_{5m} = 3.3$ m/s, $T = 32°C$, $Q_H = 43$ W/m²), except for Q_H in (e).

random vertical velocity fluctuations affect seed dispersal distances, the previous model is extended by adding a vertical velocity component given by

$$\overline{W} = 0$$

$$w' = W - \overline{W} = \sigma_w \times \varepsilon(t)$$

$$\sigma_w = (\overline{w'^2})^{1/2} \qquad (4)$$

where $\bar{W}$ is the mean (i.e., time-averaged) vertical wind velocity, W is the instantaneous vertical wind velocity, σ_w is the standard deviation of the fluctuations in vertical wind velocity (w'), and $\varepsilon(t)$ is a Gaussian white-noise random variable with zero mean and unit variance. For near-neutral atmospheric conditions, $\sigma_w = 1.25 \times u_*$ (Panofsky and Dutton 1984, Kaimal and Finnigan 1994, Katul et al. 1995). The Gaussian $\varepsilon(t)$ ensures that the probability density function of w' follows the statistical distribution of turbulent velocity fluctuations under near-neutral atmospheric conditions, which is near-Gaussian (Chu et al. 1996).

This model requires numerical calculation. The vertical wind velocity W is computed from $\bar{W}$ and a randomly assigned w' for each calculation time step Δt. For each Δt, the vertical displacement, computed from W and v_t, and new vertical position of the seed are determined. The rest of the model is a numerically calculated version of the simple deterministic model; the calculations stop when the seed reaches the interception height ($z_0 + d$). Due to the fluctuations in vertical velocity, this model produces stochastic dispersal trajectories (Fig. 1b). However, the temporally uncorrelated vertical velocity fluctuations are not very realistic (Fig. 2b, f).

We are not aware of any studies that have used this exact same modeling approach to simulate seed dispersal. Greene and Johnson (1996) used random vertical wind velocity fluctuations following a realistic Gaussian distribution (zero mean, fixed σ_w) to calculate the variance of seed drop times. They then used the seed drop times in a model similar to a stochastic version of the simple deterministic model to simulate the post-dispersal density distribution of a large number of seeds. In their model, stochastic variation in vertical wind velocity was incorporated in the dispersal distribution of seeds, instead of in the trajectory of each single seed. For our study, we selected the trajectory-based approach to facilitate comparison between models.

3. *The Markov chain model for Synthetic Turbulence Generation (STG model).*—In reality, fluctuations in wind velocity are spatially and temporally correlated (Fig. 2f). Several authors have elaborated the simple deterministic model to include autocorrelated fluctuations in vertical wind velocity. Greene and Johnson (1995) used autocorrelated vertical wind velocity fluctuations to calculate the variance in drop time of tree seeds in a model otherwise closely similar to their previously discussed model (Greene and Johnson 1996, see previous section, *Methods*, *The simple stochastic model*). Andersen (1991) and Jongejans and Schippers (1999) used a version of the simple stochastic model in which w' was autocorrelated. Their approach was mechanistic but highly simplified, and ignored the conservation of turbulent kinetic energy, effects of the vegetation structure, and the correlation between fluctuations in vertical and horizontal wind velocities. Therefore, we selected the mechanistic dispersal model of Nathan et al. (2002b) to simulate turbulence (i.e., the fluctuations in both vertical and horizontal wind velocity) in a realistic manner, and adjusted this model for grassland ecosystems. In this model, the instantaneous wind velocities W and U are random variables that possess the basic statistical properties of canopy and surface layer turbulence, namely spatial and temporal coherence of eddies. This was shown to be crucial in predicting realistic LDD of tree seeds in forests (Nathan et al. 2002b). Spatial and temporal correlations in wind velocity are incorporated based on their statistical properties and in a manner designed to retain the same simple input parameters as used in the previous models. Only one additional input parameter is required: the vegetation leaf area index (LAI), a vegetation structure characteristic that influences turbulence.

The model is a Lagrangian stochastic dispersion model, which assumes that the change in position and velocity of a seed are described by a Markov chain process. Basic concepts, details, and references to the use of this approach in atmospheric sciences are given by Rodean (1996). Using the Markov process assumption, the change in u_i can be expressed by

$$du_i = a(x_i, u_i, t)dt + b(x_i, u_i, t)d\Omega \qquad (5)$$

where u_i is the instantaneous wind velocity in direction x_i, a is the drift coefficient, b is the stochastic acceleration coefficient, and $d\Omega$ is a Gaussian random variable with zero mean and variance dt, with dt dependent on the time-scale of turbulent air movements ($dt = 0.05 \times T_L$; Appendix A). The estimation of a and b is described in Appendix A. We refer to Nathan et al. (2002b) for a more detailed description of the model, and to Appendix B for an overview of the model equations adjusted for grasslands.

The major advantage of this model over the previous models is the (auto-) correlation of fluctuations in wind velocity, which greatly increases model realism (Fig. 2c, f) and results in coherent stochastic seed dispersal trajectories (Fig. 1c). However, the Markov process assumption and the incorporation of a coherent time scale, which ensure this (auto-) correlation, also greatly increase model complexity.

A less complex approach to simulate realistic autocorrelated fluctuations in vertical wind velocity was taken by Tackenberg (2003). He simulated vertical wind velocity by drawing from a database of time series of W as measured at one study site at 0.6 m height

(Tackenberg 2001). His method results in highly realistic simulations of vertical wind velocity for that specific site and height. However, the simulations cannot be extrapolated to other sites, other heights above the ground surface, or other conditions than those under which W was specifically measured. Given that Tackenberg used measured time series with non-zero $\bar{W}$, it is especially important that his measured series are not extrapolated to other sites. In the general case $\bar{W} = 0$. $\bar{W} = 0$ is a necessary condition for a planar-homogeneous boundary layer flow and the validity of the logarithmic wind-profile (Eq. 2), which Tackenberg also applied in his model. A non-zero $\bar{W}$ implies that $\bar{U}$ must vary in both x and z via the continuity equation for incompressible flows, not just z as assumed by the logarithmic wind profile. As consistent spatial variation in $\bar{U}$ is not incorporated in Tackenberg's model, data series with non-zero $\bar{W}$ can never be applied to other sites than the site at which W was measured. For this reason, we selected the mechanistic and general, though more complex, STG model for our model study.

4. *The Markov chain model with Atmospheric Stability Correction (ASC model).*—The STG model simulates mechanically produced turbulence caused by frictional drag of wind flowing over and within the vegetation. This form of turbulence dominates under near-neutral atmospheric boundary layer conditions. Another important source of fluctuations in vertical and horizontal wind velocity is buoyantly produced turbulence. Buoyantly produced turbulence dominates under unstable boundary layer conditions, when solar heating of the ground causes parcels of warm air to rise. As a final step in increasing model realism, we accounted for atmospheric stability and simulate both mechanically and buoyantly produced turbulence, and any combination thereof. For this purpose, we developed a new simulation model by extending the STG model to calculate atmospheric stability corrections to all first- and second-order model statistics, turbulent kinetic energy, and the mean turbulent kinetic energy dissipation rate using the standard surface layer formulations described by Hsieh and Katul (1997). For a specified sensible heat flux (Q_H) and $\bar{U}$ at a reference height z_{ref}, the value of u_* is now computed by numerically solving

$$\overline{U}_{zref} = \frac{u_*}{k}\left[\ln\left(\frac{z_{ref} - d}{z_0}\right) - \Psi_m\left(\frac{z}{L}\right)\right] \quad (6)$$

where

$$L = -\frac{u_*^3}{k \times g \dfrac{Q_H}{\rho \times C_{pd} \times T_a}}. \quad (7)$$

L is the Obukhov length, g is the gravitational acceleration, ρ is the mean air density, C_{pd} is the specific heat capacity of dry air under constant pressure, T_a is the air temperature, and Ψ_m is the stability correction

function for mean momentum (Katul et al. 1995, Hsieh and Katul 1997). L is an indicator of the relative importance of buoyantly produced vs. mechanically produced turbulence (Stull 1988): When $\bar{U}$ is low (and hence u_* is low) and Q_H is high, buoyantly produced turbulence is dominant, whereas mechanically produced turbulence is dominant at high $\bar{U}$ (and hence high u_*) and low Q_H. The values of Q_H and $\bar{U}$ determine whether the model computes turbulent wind fluctuations typical of more unstable or more neutral atmospheric conditions.

In the ASC model, turbulent fluctuations adjust to the atmospheric stability conditions, resulting in larger fluctuations under more unstable boundary layer conditions (compare Fig. 2d, for a summer day with relatively low surface heating, to Fig. 2e, for a summer day with high surface heating). This is the most realistic and flexible model of the series used in this study, simulating a wide range of possible seed trajectories (Fig. 1d). However, it is also the most complex model, and it is important to assess the value of the added realism and complexity.

Field data

We compared the different models using seed dispersal data from field experiments. These experiments were carried out in several grassland ecosystems in The Netherlands, ranging from mown *Lolium perenne* production grasslands to species-rich *Molinia caerulea* grassland reserves. All sites were located in flat and open terrain to insure planar homogeneity in the wind flow. Seeds were released on six days with different weather conditions (but no rain). In total, 330 seeds were released individually from specific release heights and observed successfully during their entire dispersal trajectory. The horizontal dispersal distance of each seed was measured as the straight line connecting release point to landing point. Vegetation height (excluding protruding flowering stalks) was measured at each experimental site. LAI and leaf area density profiles of the selected grassland types were estimated from literature (Fliervoet and Werger 1984, Werger et al. 1986). During the flight of each seed, air temperature and horizontal wind velocity were measured close to the seed release point using a transportable mini-meteorological station (Eijkelkamp Agrisearch Equipment, Giesbeek, The Netherlands; thermometer at 2.7 m height; cup-anemometers at three heights (0.7, 2.7, and 5.2 m); data logged every 10 s).

The experimentally released seeds were collected from several populations of four wind-dispersed grassland forbs. Seeds of two species, *Cirsium dissectum* (L.) Hill and *Hypochaeris radicata* L. (both Asteraceae), are equipped with plumes that facilitate LDD by wind (Bouman et al. 2000). Seeds of the other two species, *Centaurea jacea* L. (Asteraceae) and *Succisa pratensis* Moench (Dipsacaceae), are also classified as wind dispersed, but their plumeless seeds are dispersed

by wind over much shorter distances. The smooth-surfaced seeds of *C. jacea* are ejected from the seed head, and transported farther by wind, when wind gusts fling the seed head back and forth (Bouman et al. 2000). Seeds of *S. pratensis* are surrounded by their persistent calyx, which functions as a balloon (Bouman et al. 2000). After collection, the seeds were air-dried, weighed, and measured. The terminal velocity (v_t) of each seed was calculated using previously derived species-specific relationships between v_t, seed mass, and plume diameter (Soons and Heil 2002). Thus, the values of model input parameters v_t, H_0, $\bar{U}_{zref}$, z_{ref}, h, and LAI, and of model output D were known for each experimentally dispersed seed (Table 1). All other model parameters were computed from this set of input parameters.

Testing the models

We compared simulation results of the different models with measured dispersal distances and with each other to assess the accuracy and realism of the model simulations. For these comparisons, we carried out model simulations using the exact same input parameters as measured during the dispersal events in the field experiments. For the simple deterministic model, each set of input parameters yields a single dispersal distance. This allowed a one-to-one comparison between simulated and measured dispersal distances. For the stochastic models, we calculated a probability density function (PDF) of dispersal distances for each set of input parameters by simulating 5000 seed trajectories. We then compared the median values of the simulated PDFs to the measured distances. We compared the simulated and measured dispersal distances using linear regression analyses. To test for significant differences in regression coefficients and intercepts between the models, we carried out a linear multiple regression analysis with the models as groups and an interaction term "group × simulated distances."

The comparison of simulated median distances with measured distances assesses the accuracy of the simulated medians and provides a basis for cross-comparison with the deterministic model. However, there is no physical or statistical justification for expecting that the simulated medians represent the measured dispersal distances of the individual seed release experiments. For the two stochastic models, we therefore also calculated which percentage of the measured distances were within the range of the simulated PDFs (for both the full range of the PDFs and a more narrow range around the medians defined by the 25th- and 75th-percentile distances). To compare all models further, we combined the individual dispersal events to a PDF of measured dispersal distances. We compared this PDF to simulated PDFs based on the same input parameters (for the simple deterministic model we created a PDF by combining all simulated dispersal events). This comparison was made for each plant species separately,

because between-species variation in dispersal distance was large compared to within-species variation. We compared model performance between models and species using a Kolmogorov-Smirnov test for two independent samples. This test does not provide a measure of absolute model performance, however, because the measured distances are not a fully representative subset of the true PDFs of all species. For *C. dissectum* and *H. radicata*, the set of measured distances is biased towards shorter dispersal distances, because seeds that dispersed faster and further had a higher probability of being lost from sight and thus of being not included in the data set.

The ASC model could not be tested with the field data, because the temporal range of the temperature measurements was too low to calculate Q_H. Therefore, a separate sensitivity analysis was carried out for this model to determine the importance of incorporating stable atmospheric conditions (see next section). All statistical analyses were carried out in SPSS (1999).

Sensitivity analyses

For the simple deterministic model and the STG model, sensitivity analyses were carried out to assess which input parameters are the most important determinants of seed dispersal distances under natural conditions. No separate sensitivity analysis for the simple stochastic model was carried out, as results would be exactly the same as for the deterministic model. Table 1 lists the input parameters assessed per model. We studied the full natural range of variation of each of the input parameters to assess their importance under the full range of natural conditions. Therefore, we used a method for sensitivity analysis described by Nathan et al. (2001). Per model: (1) The natural range of values of each selected parameter was divided into 20 equal intervals. (2) A random set of 20 Latin hypercubes was created so that each interval of each selected parameter was selected once in each hypercube. (3) From each parameter interval in each hypercube, a random value was selected to be the parameter value in the model simulation. One simulation was carried out for each hypercube. Steps (2) and (3) were repeated 10 times, so that 200 parameter combinations were simulated. (4) The resulting 200 sets of independent variables (the input parameters) and dependent variables (the calculated distances) were rank-transformed and analyzed using stepwise multiple linear regression analysis in SPSS (1999). Sensitivity analyses were carried out for all species lumped together, and for each species separately (species specific v_t values from Table 1, species specific values of H_0 and h from Soons and Heil 2002).

A separate sensitivity analysis was carried out for the ASC model to assess the sensitivity of dispersal distances to Q_H. As the effect of Q_H changes with $\bar{U}$, we simulated seed dispersal for different combinations of Q_H and $\bar{U}$ (5000 dispersal trajectories for each combination). We carried out these simulations for three

TABLE 1. Summary of the values of the model input parameters as measured during the field experiments, and mean values and approximated value ranges under natural conditions.

| | Terminal velocity, v_t (m/s)† | | | |
Condition	Cd	Hr	Cj	Sp
Dispersal experiments	0.30–0.45	0.28–0.40	3.17–5.17	1.72–2.59
Natural conditions				
Mean	0.38	0.34	4.33	2.14
Range	0.30–0.51	0.24–0.54	3.17–5.57	1.64–2.60
S.A. simple	+	+	+	+
S.A. STG	+	+	+	+

Notes: Model input parameters included in the sensitivity analysis of the simple deterministic model (S.A. simple) or the Synthetic Turbulence Generation model (S.A. STG) are indicated by + symbols. The experimental parameter values are subsets of the full natural ranges, except for H_0, for which experimental values exceed the natural ranges of the species used in the experiments. Model sensitivity analyses were carried out using the full natural range of each parameter. Means and ranges are from Soons and Heil (2002), except LAI and wind velocity (see *Methods, Field data* and *Sensitivity analysis*).
† Species abbreviations: *Cd, Cirsium dissectum; Hr, Hypochaeris radicata; Cj, Centaurea jacea;* and *Sp, Succisa pratensis.*
‡ Horizontal wind velocity at reference height.

types of seeds: plumeless seeds of *C. jacea* with relatively high terminal velocity (4.33 m/s), plumed seeds of *H. radicata* with low terminal velocity (0.34 m/s), and *Cirsium arvense* plumes without achenes, which have a very low terminal velocity (0.15 m/s; Tackenberg 2001). Simulated levels of Q_H ranged from 0 to 300 W/m² and are representative of the full range of heat flux values in temperate grasslands during daytime (approximately −10 to 300 W/m²; Stull 1988). Simulated values of $\bar{U}$ ranged from 0.01 to 16 m/s at a reference height of 10 m, and are representative of the range of values in open landscapes in the inner area of The Netherlands (Wieringa and Rijkoort 1983) during the dispersal season (June to October).

RESULTS

Model predictions and field data

Figs. 1 and 2 demonstrate the differences between the models in simulating seed dispersal trajectories and vertical wind velocities. Performance of the models in simulating dispersal distances was assessed by comparing simulated dispersal distances to measured dispersal distances from the field experiments and comparing simulated distances among the models.

The first model test compares the simulated distances of the simple models and the STG model to the measured distance per dispersal event. Median dispersal distances simulated by the STG model are better predictors of the measured distances than median distances simulated by the simple stochastic model and distances simulated by the simple deterministic model: The median distances simulated by the STG model have a regression coefficient significantly closer to 1 (0.92 vs. 1.33 for the simple models; $P = 0.008$) and an intercept closer to 0 (0.36 vs. 0.61 and 0.62 for the simple models; not significant, all calculated intercepts not significantly different from 0). Statistics of the model comparison are presented in Table C1 (Appendix C).

Not only do the medians simulated by the STG model better predict the measured dispersal distances than the

medians simulated by the simple stochastic model. For the STG model, the probability is also higher that the measured dispersal distances are realizations of the PDFs simulated per dispersal event. Of all measured dispersal events, 92% are within the range simulated for them by the STG model, and 25% are even within the range defined by the simulated 25th- and 75th-percentile distances. For the simple stochastic model, these percentages are much lower: 21% and 3%, respectively.

The second model test compares the PDFs simulated by the stochastic models and the PDFs calculated for the simple deterministic model to the PDFs of the measured dispersal events (Fig. 3). For the species with plumed seeds (*C. dissectum* and *H. radicata*), adapted to LDD by wind, the stochastic models predict longer dispersal distances than measured in the field, due to limitation of measurements. The PDFs of these species are significantly different from the PDFs simulated by the stochastic models (Table C1). This is caused by an underestimation of the frequency of short-distance dispersal events (~2 m). For the species with short-distance seed dispersal by wind (*C. jacea* and *S. pratensis*), the PDFs simulated by the STG model are not statistically different from the measured PDFs. In contrast, the PDFs simulated by the simple stochastic model are significantly different from the measured PDFs (Table C1). For all species the PDFs for the deterministic model are most different from the measured PDFs (Fig. 3). These differences are not significant, however, because only ≤80 simulated distances per species could be used to calculate PDFs for the simple deterministic model (Table C1).

When comparing the models to each other, the main difference between the models is their ability to simulate LDD for the two species with plumed seeds. The STG model simulates more LDD events and LDD over longer distances (even >100 m) than the two simple models (Kolmogorov-Smirnov test, $P < 0.001$). The simple stochastic model is hardly able to simulate

Table 1. Extended.

Release height, H_0 (m)	Vegetation height, h (m)	Leaf area index, LAI	Horizontal wind velocity, $\bar{U}_{zref}$ (m/s)‡	Reference height, z_{ref} (m)
0.50–1.50	0.15–0.40	2.5–6.0	0–6.9 (per 10-s interval)	5.2
0.45	0.30	3.5	3.8 (per 1-h interval)	10
0.09–0.96	0.1–0.8	2.0–6.0	0–15.2 (per 1-h interval)	10
+	+		+	
+	+	+	+	

LDD: All simulated dispersal distances are <34 m. The simple deterministic model is not able to simulate LDD: All simulated dispersal distances are <12 m.

The effect of surface heating

To assess the importance of buoyantly produced fluctuations in wind velocity for dispersal distances, we carried out simulations with the ASC model for a series of mean horizontal wind velocities ($\bar{U}$) and heat fluxes (Q_H) (Fig. 4). Seed dispersal distances are longest at high $\bar{U}$. The large-scale buoyantly produced fluctuations in wind velocity that occur under highly unstable atmospheric conditions with high Q_H and low $\bar{U}$ have the potential to lift seeds with a low terminal velocity up high (relatively large w' and large autocorrelation time scale T_L; Fig. 5). However, even when such seeds are lifted up high, they are not transported very far in

a horizontal direction because of the low $\bar{U}$. The high values of $\bar{U}$ that occur under near-neutral atmospheric conditions have the greatest potential for transporting seeds horizontally. Even though the turbulent wind velocity fluctuations under these conditions are almost exclusively mechanically produced and have a lower potential to uplift seeds (large w', but small T_L; Fig. 5), seeds are dispersed much farther under stormy conditions than under unstable atmospheric conditions.

Sensitivity analyses

Results of the sensitivity analyses demonstrate that in the simple models and the STG model the same parameters are most important in determining seed dispersal distances. For each model, regression analyses were carried out on two groups of data. One group consisted of all data and the other consisted of a subset
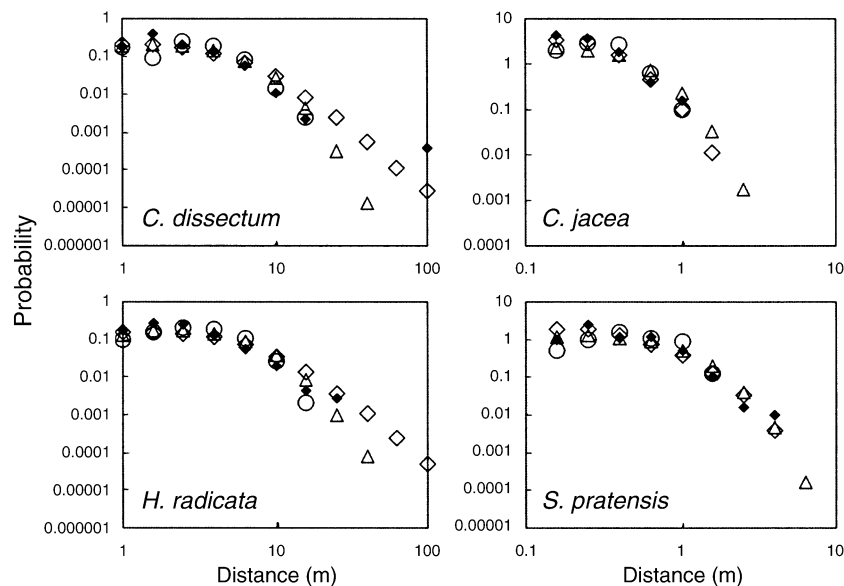

Fig. 3. Probability density functions (PDFs) of measured dispersal distances (solid diamonds) and simulated dispersal distances using the simple deterministic model (open circles), simple stochastic model (open triangles), and STG model (open diamonds) in four species. The STG model simulates dispersal over longer distances than the two simple models for the two species with plumed seeds adapted to LDD by wind (*C. dissectum* and *H. radicata*). For these two species, the models simulate PDFs that are significantly different from the measured PDFs. In contrast, for the two species with plumeless wind-dispersed seeds (*C. jacea* and *S. pratensis*), the PDFs simulated by the STG model are not significantly different from the measured PDFs. Probabilities are for log(distance categories) and per meter of distance (log scale). Zero probabilities are not plotted.
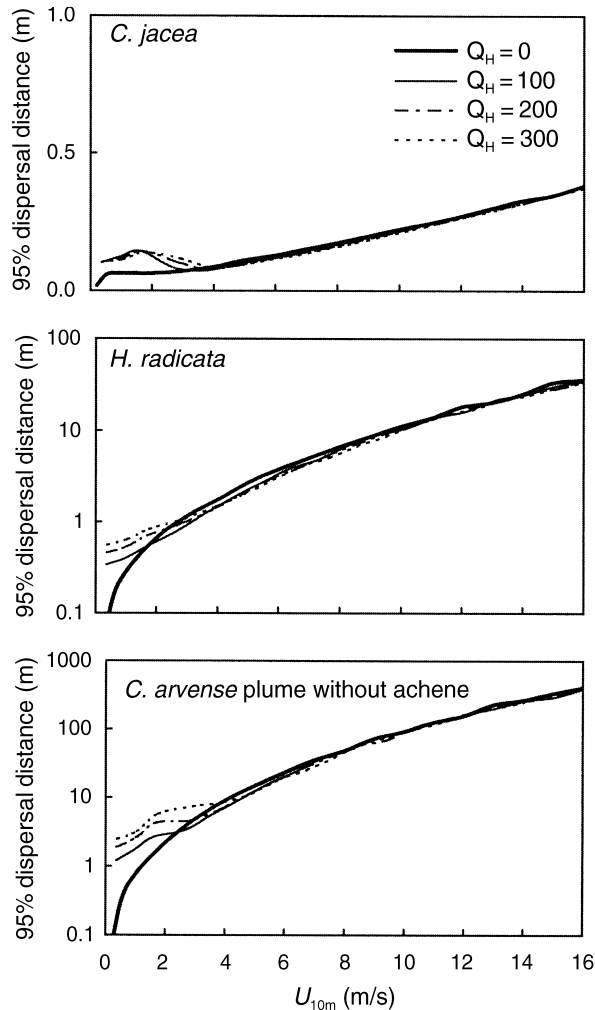
FIG. 4. The 95th-percentile dispersal distances simulated by the Markov chain ASC model increase strongly with increasing mean horizontal wind velocity ($\bar{U}_{10m}$). The 95th-percentile distances increase much less with increasing levels of sensible heat flux (Q_H), and only at low horizontal wind velocities. Sensible heat flux has a greater effect on dispersal distances for seeds with a lower terminal velocity. ASC model simulations are for plumeless seeds of *C. jacea* ($v_t = 4.33$ m/s), plumed seeds of *H. radicata* ($v_t = 0.34$ m/s), and *Cirsium arvense* plumes without achene (0.15 m/s; Tackenberg 2001); $H_0 = 0.45$ m, $h = 0.30$ m, LAI = 3.5. Distances of *H. radicata* seeds and *C. arvense* plumes are plotted on a log scale.

Appendix D). Seed terminal velocity (v_t) was only a significant determinant of dispersal distances in the analysis for all species together and for *S. pratensis*. This indicates that between-species variation in v_t is a significant source of variation in dispersal ability, but that within-species variation in v_t hardly contributes to variation in dispersal. The regression analysis including only the seeds with a probability of dispersal ($H_0 > (d + z_0)$) shows that $\bar{U}_{zref}$ is, overall, the most important determinant of dispersal distances, followed closely by H_0 and then h (Table D1 in Appendix D). Also, v_t is now a significant parameter for dispersal, especially when all species are analyzed together. Seed v_t is more important in determining LDD than median dispersal distances. In the STG model, the LAI is insignificant in determining median dispersal distances, but does contribute to determining LDD.

DISCUSSION

The processes that determine seed dispersal distances

The STG model performs better than the simple deterministic model and the simple stochastic model in simulating realistic dispersal distances. The STG model simulates measured dispersal distances generally more
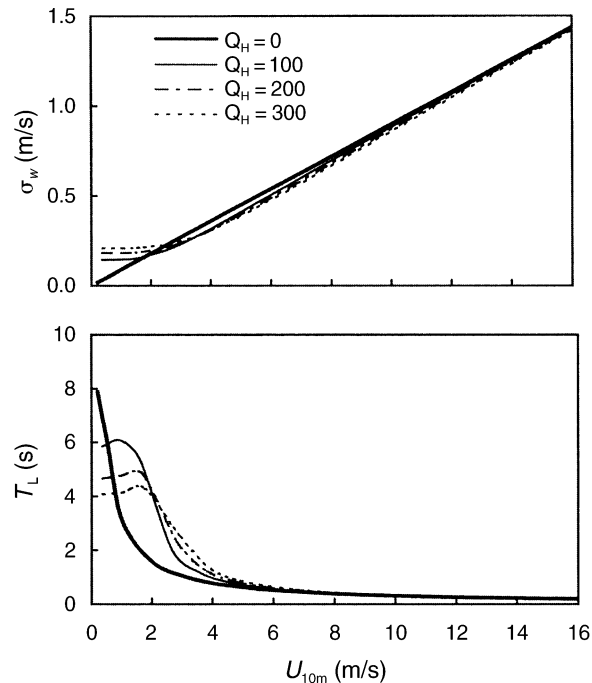
of the data including only the parameter combinations for which seed release height was above the height at which the wind velocity is zero, i.e., $H_0 > (d + z_0)$. This was done because a large number (28%) of the simulated parameter combinations resulted in conditions for which seeds did not disperse from the mother plant, because wind velocity was zero at the seed release height. The regression analysis including all simulated parameter combinations shows that seed release height (H_0) is the most important determinant of seed dispersal distances, followed by vegetation height (h) and mean horizontal wind velocity $\bar{U}_{zref}$ (Table D1, in

FIG. 5. The standard deviation of the fluctuations in vertical wind velocity (σ_w; top) increases strongly with increasing mean horizontal wind velocity ($\bar{U}_{10m}$) and increases to a much lower degree with increasing levels of sensible heat flux (Q_H). The autocorrelation time scale of the fluctuations in vertical wind velocity (T_L; bottom) declines rapidly with increasing mean horizontal wind velocity ($\bar{U}_{10m}$). This decline becomes less rapid with increasing levels of sensible heat flux (Q_H); $H_0 = 0.45$ m, $h = 0.30$ m, LAI = 3.5, $T = 20°C$.

accurately, although the difference in accuracy between the models is relatively small. Unfortunately, we could only test model performance for relatively short dispersal distances (measured dispersal distances range from 0 to 16 m, with one dispersal event of 80.4 m), as our field experiments again confirmed the difficulty in obtaining LDD data (Bullock and Clarke 2000, Cain et al. 2000, Nathan et al. 2003). When considering only relatively short dispersal distances (less than ± 15 m), the simple deterministic model may be the most suitable wind dispersal model in many situations, because it performs almost as well as the STG model and has a much lower complexity.

However, the two simple models cannot simulate LDD, whereas the STG model can. Simulation results from the STG model and the simple models show that adding spatially and temporally coherent fluctuations in vertical and horizontal wind velocity greatly increases model realism and allows simulation of LDD. Simulation of these (auto-) correlated fluctuations in wind velocity by the STG and ASC models creates more coherent dispersal trajectories. Some seeds experience coherent updrafts propelling them farther and farther as they experience stronger horizontal wind velocities at greater heights, while other seeds experience downdrafts until they land in the vegetation. The uplifting of seeds in coherent upward dispersal trajectories greatly increases their dispersal distance. Random vertical wind velocity fluctuations are also able to uplift seeds, but their upward trajectories are not sustained long enough in time to achieve LDD. These results are in agreement with the finding of Nathan et al. (2002*b*) and Tackenberg (2003) that seed uplifting is crucial in determining LDD ability. We add to their finding that it is not simply instantaneous uplifting, but the sustainability of this upward lifting for a sufficiently long time that is crucial.

1. *The importance of fluctuations in vertical wind velocity for LDD.*—The simulations with the Markov chain STG and ASC models show that autocorrelated upward deviations from the mean vertical wind velocity are the key mechanism for the coherent upward trajectories of uplifted seeds. All models used in this study simulated a zero mean vertical wind velocity ($\bar{W} = 0$), but the model results are very different based on the differences in the way the turbulent fluctuations in vertical wind velocity (w') are simulated. Our finding is in contrast, however, with Tackenberg's (2003) recent suggestion that a positive $\bar{W}$ under unstable atmospheric conditions is the key mechanism for seed uplifting and LDD. We here discuss three important differences between our modeling approach and Tackenberg's approach, which explain the different conclusions drawn by us and by Tackenberg.

First, values of $\bar{W}$ are usually too small to cause seed uplifting, even under unstable atmospheric conditions. Tackenberg (2001) published values of $\bar{W}$ for unstable atmospheric conditions, ranging from ± -0.10–

0.35 m/s. Although 0.35 m/s is an extremely high value (the natural range of values of $\bar{W}$ given by Stull (1988) is ± -0.2–0.3 m/s), it is only barely enough to uplift the seeds with the lowest terminal velocities (Table 1). Most plant seeds, even plumed seeds, have a terminal velocity that is too high to be dispersed over long distances by the rising parcels of warm air in convective plumes and thermals (two weather phenomena that may occur under unstable atmospheric conditions). In contrast, the amplitude of the fluctuations w' is usually much larger: Examples from Stull (1988) indicate ± -2.0–2.5 m/s, and Tackenberg (2001) reports ± -0.25–1.10 m/s. Thus, the turbulent fluctuations w' have a much greater potential to uplift seeds over significant distances than a positive $\bar{W}$, if the positive values of w' are sustained long enough in space and time. We simulated realistic autocorrelation of w', including the increase in the size of w' and the autocorrelation of w' with height. Thus, in our model, seeds that are uplifted experience the larger and more correlated turbulence that occurs at greater heights, and hence are likely to continue moving up and to disperse over a long distance. Tackenberg, however, used only time series of w' that he measured at a single height of 0.6 m, and which contain only the relatively damped and randomized fluctuations w' that occur at this low height. His extrapolation of these values to all heights greatly underestimates the sustainability of seed uplifting by w' and its importance for LDD.

Second, Tackenberg's (2003) conclusion is based on his use of a consistent positive $\bar{W}$ during simulation of seed dispersal under unstable atmospheric conditions. However, a consistent non-zero $\bar{W}$ is a local, and never a general, phenomenon (see *Methods, The simulation models, 3. The Markov chain model for Synthetic Turbulence Generation (STG model)*). A local positive $\bar{W}$ can occur due to a convective plume or thermal, but convective plumes and thermals move horizontally with $\bar{U}$ and are preceded and followed by air columns in which air flows downwards (Stull 1988). Assuming a local positive $\bar{W}$ for seed dispersal is unrealistic, because a large population of seeds will in reality experience local positive and local negative W during dispersal, with overall $\bar{W} = 0$. A positive $\bar{W}$ that is consistent in time and space can only occur under specific and spatially heterogeneous conditions, such as topography changes on uphill slopes (e.g., Nathan et al. 2001) or changes in landscape structure or vegetation type. The effect of a positive $\bar{W}$ on dispersal distances reflects specific and unique local situations, and overestimates the importance of a positive $\bar{W}$ in the general case.

Third, Tackenberg's (2003) conclusion depends critically on his assumption that $\bar{U}$ and $\bar{W}$ are linearly negatively correlated. This assumption is based on his measurement series from a single site and a single height, and is dependent on the local conditions (see

previous paragraph). In general, this relationship is not applicable.

We therefore conclude that strong turbulence, specifically large fluctuations in w', and sufficient sustainability of these fluctuations in space and time are the most important mechanism for seed uplifting and LDD. Incorporation of realistic turbulence in a mechanistic dispersal model is crucial for the simulation of coherent upward wind and seed movements and LDD of seeds.

2. *The importance of atmospheric stability conditions for LDD.*—Some authors suggested that strong buoyancy under unstable atmospheric conditions is the main mechanism for LDD by wind (Sheldon and Burrows 1973, Tackenberg 2003), while others suggested that storms (which occur during near-neutral conditions) are the main mechanism (Horn et al. 2001, Nathan et al. 2002*b*). Our graphical analysis of simulations with the ASC model clearly demonstrates the relative importance of Q_H and $\bar{U}$ (Figs. 4 and 5). Our results show that high wind velocities are the main mechanism for LDD by wind in grasslands. A strong heat flux increases dispersal distances, but only under low wind velocity conditions ($\bar{U}_{10m} < 4$ m/s), and then the dispersal distances are much lower than during stronger winds. Also, the increase in dispersal distance caused by even the strongest heat flux is very small (<1 m), even for plumed seeds with a very low terminal velocity (0.34 m/s).

It is conceivable, however, that under convective conditions a seed travels upwards to a very high elevation (even to the top of the atmospheric boundary layer) with a convective plume or thermal. This possibility is not included in the ASC model. Although the probability that this would happen is very low, and the probability that a seed rising up under convective conditions also disperses far horizontally is also very low, the ASC model thus underestimates dispersal distances under convective conditions. Quantification of this underestimation requires a dispersal model that simulates the full boundary layer dynamics under convective conditions (and not simply the addition of a constant positive $\bar{W}$). Ongoing model developments address this issue. So far, however, our results show that, for realistic simulation of LDD, a model for only near-neutral atmospheric conditions (such as the STG model) is highly suitable. Deviations from the results of such models due to different levels of sensible heat flux under low wind velocity conditions can be estimated from Fig. 4.

The parameters that determine seed dispersal distances

Our results show that the height of seed release (H_0) and of the surrounding vegetation (h) play a crucial role in determining seed dispersal in grasslands. H_0 and h determine whether a seed is released at a height where there is sufficient wind speed to transport it, determine the minimal falling time of a seed, and affect the level of turbulence, and hence probability of uplifting, at the location of seed release. The importance of plant height and vegetation height is often underestimated in seed dispersal studies; we are aware of only few studies in which both parameters were investigated (McEvoy and Cox 1987, Soons and Heil 2002).

For the seeds that are released at a height of nonzero wind velocity (i.e., $H_0 > (d + z_0)$), the most important parameter determining seed dispersal distances is $\bar{U}$, followed by H_0 and h. Augspurger and Franson (1987), Greene and Johnson (1992), Horn et al. (2001), and Nathan et al. (2001) attributed the greater importance of $\bar{U}$ for dispersal distances to its larger variation in comparison to other dispersal parameters. Our data confirm this observation: The natural range of $\bar{U}$ at 10 m height above grasslands in The Netherlands (excluding extremes) is much larger than the ranges of H_0, h, and LAI (Table 1). The between-species range of seed terminal velocity (v_t) is larger than that of H_0, and *between* species v_t is the second most important determinant of dispersal distance. *Within* species the ranges of v_t are relatively small (Table 1), and the importance of v_t for dispersal distances is relatively low. This same result was found for wind-dispersed tree seeds (Greene and Johnson 1992, Nathan et al. 2001). The importance of v_t for seed dispersal distances may be overestimated in dispersal studies that focus on only within-species variation in v_t (e.g., Augspurger 1988, Andersen 1992, Greene and Johnson 1992).

These results imply that within wind-dispersed grassland plant species, changing H_0 is the most important mechanism under the plant's control to affect seed dispersal distance. This not only holds for plants with a low H_0 relative to h, but also for plants with high protruding flowering stalks, because seeds that are released higher above the vegetation experience higher horizontal wind velocities, have a longer falling time, and have a higher probability of uplifting (for the same wind conditions). The great importance of a high release height for seed dispersal explains the large investment of many grassland plant species, especially rosette plants, in stalk length (Bazzaz et al. 2000).

Consequences for plant dispersal ability

Mean horizontal wind velocity, seed release height, vegetation height, and between-species variation in seed terminal velocity are crucial in determining seed dispersal distances. These are predominantly environmental and vegetation factors; even seed release height is important mainly in relation to vegetation height. Also, vegetation LAI plays a role in determining the probability of LDD. Changes in these environmental and vegetation parameters will affect seed dispersal. In species-rich grasslands in northwest Europe, the current process of eutrophication increases vegetation height (h) and seed interception height ($0.76 \times h$), also relative to the seed release height of wind-dispersed

plant species (Soons and Heil 2002). This will reduce wind dispersal ability in species that are not able to increase H_0 sufficiently. Management plans for grasslands should take this issue into account. Whenever a seed is dispersed, the most important determinant of the dispersal distance is, however, the horizontal wind velocity. Changes in the frequency of occurrence of extreme wind velocity events such as storms, therefore seem to have the highest potential to change the future dispersal of grassland plant seeds by wind.

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APPENDIX A

The calculation of the Markov chain dispersion process is available in ESA's Electronic Data Archive: *Ecological Archives* E085-101-A1.

APPENDIX B

The Markov chain Synthetic Turbulence Generation (STG) model is available in ESA's Electronic Data Archive: *Ecological Archives* E085-101-A2.

APPENDIX C

Results of the model comparisons (statistics) are available in ESA's Electronic Data Archive: *Ecological Archives* E085-101-A3.

APPENDIX D

Results of the sensitivity analyses (statistics) are available in ESA's Electronic Data Archive: *Ecological Archives* E085-101-A4.