

HUMAN EFFECTS ON LONG-DISTANCE WIND DISPERSAL AND COLONIZATION BY GRASSLAND PLANTS

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Abstract. Human effects on plant colonization capacity have not been studied mechanistically because a crucial component of colonization capacity, long-distance seed dispersal, could not be quantified. Now, development of mechanistic models has progressed sufficiently to estimate long-distance seed dispersal by wind. We used a recently developed mechanistic dispersal model to quantify seed dispersal by wind in grasslands for three important human effects on natural systems: habitat fragmentation, eutrophication, and an increase in extreme wind velocity events due to climate change. We combined the dispersal data with data on seed production and germination ability to estimate effects on colonization capacity. Habitat fragmentation decreases the number and size of populations. This does not affect the populations' seed dispersal ability, but it reduces the number and germinability of produced seeds, and hence the colonization capacity. Site eutrophication strongly reduces seed dispersal distances, but in some species it also increases seed production and germinability. Thus, long-distance colonization decreases, but short-distance colonization may increase. Wind velocity is the key determinant of dispersal distances. An increase in extreme winds increases long-distance dispersal and long-distance colonization capacity. However, increases in extreme winds predicted for climate change scenarios are not sufficient to compensate the reductions in long-distance colonization due to habitat fragmentation or eutrophication.

Key words: *anemochory; climate change; dispersal model; eutrophication; habitat fragmentation; mechanistic model; population size; productivity; long-distance seed dispersal; wind dispersal.*

INTRODUCTION

The survival of plant species restricted to (semi-) natural areas is strongly affected by human activities (Vitousek et al. 1997). Three of the most important human effects on (semi-) natural systems are habitat fragmentation, eutrophication, and anthropogenic effects on the global climate system. Habitat fragmentation reduces the number, size, and connectivity of plant populations and thereby reduces population and metapopulation survival (Saunders et al. 1991, Ouborg 1993, Tilman et al. 1994, Hanski 1998, Hanski and Ovaskainen 2000). Eutrophication increases site productivity, which reduces the local survival of species restricted to nutrient-poor sites because they are replaced by more competitive species (Thompson 1994, Bobbink et al. 1998, Aerts and Bobbink 1999, Neitzke 2001). Climate change alters local conditions for plant growth and population dynamics, which affects local survival of plant species (Easterling et al. 2000, Walther et al. 2002, Parmesan and Yohe 2003). Habitat fragmentation contributes to the eutrophication of nutrient-poor habitat patches, and eutrophication contributes to

habitat loss (Saunders et al. 1991, Neitzke 1998, 2001). Habitat fragmentation and eutrophication also interact with effects of climate change (Thompson 1994, Pitelka et al. 1997, Walther et al. 2002). In combination, habitat fragmentation, eutrophication, and climate change pose a severe threat to local and regional plant species survival.

Plant colonization capacity is an important determinant of regional species survival, especially in plant species of successional habitats. To date, however, direct effects of habitat fragmentation, eutrophication, and climate change on the colonization capacity of plant species have not been quantified. This is mainly because it is very difficult to quantify one crucial component of plant colonization capacity, namely long-distance seed dispersal (Bullock and Clarke 2000, Cain et al. 2000, Nathan et al. 2003). The effects of habitat fragmentation and eutrophication on the colonization characteristics of wind-dispersed grassland plants have been measured (Soons and Heil 2002). Habitat fragmentation and eutrophication were found to change the seed production, germination ability, and dispersal characteristics of grasslands plants. However, long-distance seed dispersal could not be measured and dispersal ability could only be estimated from measured dispersal characteristics (seed terminal velocity, seed release height, and vegetation height). Thus, the net

Manuscript received 9 June 2003; revised 19 March 2004; accepted 30 March 2004. Corresponding Editor: C. Martínez del Rio.

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TABLE 1. Measured relationships between plant colonization characteristics and population size or site productivity.

Colonization characteristic	Relationship with log-transformed population size		Relationship with site productivity	
	Plumed seeds	Plumeless seeds	Plumed seeds	Plumeless seeds
Seed				
Terminal velocity	0	+	0	+
Germination ability	+	+	-(Cd)	+
Plant				
Seed production	+	-(Sp)	0	+
Seed release height	0†	0	0	+
Variation in terminal velocity	+	-	0	0
Vegetation				
Height	0	0	+	+
Leaf area index (LAI)	NM	NM	NM	NM

Notes: Abbreviations are: +, positive relationship; -, negative relationship, and 0, no relationship. The relationships differ between species with different wind dispersal strategies: species with plumed seeds that facilitate long-distance dispersal by wind (*Cirsium dissectum* and *Hypochaeris radicata*), and species with plumeless seeds that are dispersed by wind over short distances (*Centaurea jacea* and *Succisa pratensis*). Species-specific relationships are indicated by Cd (*C. dissectum*) and Sp (*S. pratensis*). Data are from Soons and Heil (2002). "NM" indicates "not measured."

† Soons and Heil (2002) found a negative relationship for *H. radicata*. Because of the small sample size for *H. radicata* (only seven populations), this observed relationship may not reflect the general situation. Therefore, it is not used for the scenario analyses in this study.

effects on seed dispersal, especially long-distance dispersal, and colonization capacity could not be quantified.

The effects of climate change are likely to impact numerous characteristics of plant dispersal and colonization, but these appear to be species-specific and difficult to predict (Zangerl and Bazzaz 1984, Thompson 1994, Teughels et al. 1995, Korner 2000). When considering wind dispersal, however, there is one aspect of climate change that affects all species: increased frequency of occurrence of extreme wind velocity events. High wind velocities are the most important determinant of long-distance wind dispersal (see the companion article, Soons et al. 2004). Global warming is predicted to increase the frequency of storms, and especially high intensity storms, in the east Atlantic and in northwest Europe (Carnell et al. 1996, Lunkeit

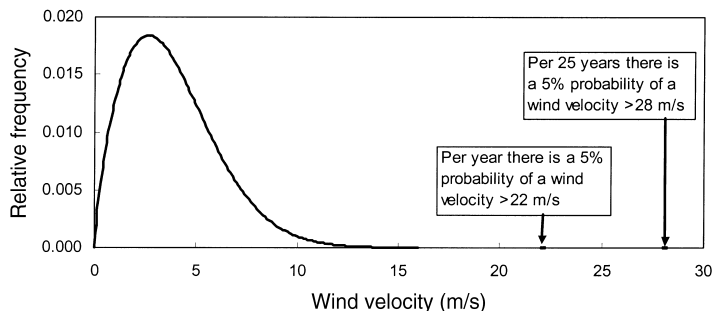
et al. 1996, Easterling et al. 2000, Knippertz et al. 2000). The Intergovernmental Panel on Climate Change (IPCC) stated that there is no general agreement among predictive models yet, but mention several studies that predict a shift from weak storms to heavier storms in the future (IPCC 2001).

Recently, the development of mechanistic models progressed sufficiently to predict long-distance seed dispersal by wind in a realistic way (Nathan et al. 2002, Tackenberg 2003, Soons et al. 2004). This opened up the opportunity to calculate seed dispersal distances from the dispersal characteristics measured by Soons and Heil (2002) and for different wind velocities. We used a mechanistic model to quantify, for the first time, the net effects of habitat fragmentation, eutrophication, and an increase in extreme wind velocities on the seed dispersal ability of wind-dispersed grassland plants. We

TABLE 2. Values of the model input parameters used in this study (species means, with ranges in parentheses).

Model parameter	<i>C. dissectum</i>	<i>H. radicata</i>	<i>C. jacea</i>	<i>S. pratensis</i>	Data source
Average terminal velocity (m/s)	0.38 (0.38–0.38)	0.34 (0.34–0.34)	4.3 (3.9–4.6)	2.1 (2.0–2.4)	Soons and Heil (2002)
Standard deviation in terminal velocity	0.03 (0.02–0.03)	0.01 (0.01–0.02)	0.45 (0.45–0.52)	0.20 (0.20–0.26)	Soons and Heil (2002)
Seed release height (m)	0.50 (0.50–0.50)	0.28 (0.28–0.28)	0.45 (0.22–0.65)	0.56 (0.46–0.67)	Soons and Heil (2002)
Vegetation height (m)	0.35 (0.11–0.64)	0.23 (0.11–0.38)	0.35 (0.11–0.64)	0.35 (0.11–0.64)	Soons and Heil (2002)
Leaf area index (m ² /m ²)	3.5	3.5	3.5	3.5	Fliervoet and Werger (1984), Werger et al. (1986)
Horizontal wind velocity (m/s)	3.8 (3.8–28.0)	3.8 (3.8–28.0)	3.8 (3.8–28.0)	3.8 (3.8–28.0)	Wieringa and Rijkooort (1983)

FIG. 1. The relative frequencies of wind velocities within the seed dispersal season follow a skewed distribution (Weibull distribution $f(U) = k/a(U/a)^{k-1}\exp(-(U/a)^k)$; $k = 1.74$; $a = 4.3$; data for the interior of The Netherlands; Wieringa and Rijkoort 1983). Wind velocities >16 m/s cannot be predicted reliably using the Weibull distribution. The frequencies of occurrence of two extreme wind velocities were derived from the Rijkoort-Weibull model (data for the interior of the Netherlands; Wieringa and Rijkoort 1983). These are indicated individually. All wind velocities are hourly averaged wind velocities at a reference height of 10 m.



thereby especially focused on long-distance dispersal. Although other dispersal mechanisms may also (accidentally) transport the seeds of wind-dispersed plant species, we focused on seed dispersal by wind only. We combined the dispersal data with data on seed production and germination ability to assess the effects on plant colonization capacity.

METHODS

We simulated and analyzed different fragmentation, eutrophication, and wind velocity scenarios for four wind-dispersed grassland forbs. These selected species represent common wind dispersal strategies in grasslands. *Cirsium dissectum* (L.) Hill and *Hypochaeris radicata* L. (both Asteraceae) have plumed seeds that facilitate long-distance wind dispersal (Bouman et al. 2000). *Centaurea jacea* L. (Asteraceae) and *Succisa pratensis* Moench (Dipsacaceae) have plumeless seeds that are dispersed by wind over short distances. The smooth-surfaced seeds of *C. jacea* are ejected from the seed head, and transported further by wind, when wind gusts move the seed head back and forth (Bouman et al. 2000). Seeds of *S. pratensis* are surrounded by a persistent calyx, which functions as a balloon by increasing the surface area of the seed without adding much weight (Bouman et al. 2000). All four species produce long flowering stalks that at the time of seed release protrude from the surrounding vegetation, at least under nutrient-poor conditions. The four species co-occur in species-rich, nutrient-poor grasslands in northwest Europe. More details on the species and their colonization characteristics are given in Tables 1 and 2 and by Soons and Heil (2002).

The simulation model

We used a mechanistic model to simulate seed dispersal by wind. The model simulates long-distance dispersal in a realistic way and has predicted measured dispersal distances accurately in previous studies (Nathan et al. 2002, Soons et al. 2004). The model simulates dispersal trajectories of individual seeds based on their terminal velocity, release height, the height at which they are intercepted by the vegetation, the hourly averaged horizontal wind velocity at a specified reference height, and wind turbulence. Wind turbulence

is simulated by spatially and temporally correlated stochastic fluctuations in horizontal and vertical wind velocity. The model generates these stochastic fluctuations and calculates their size and (auto-) correlation from input data on the hourly averaged horizontal wind velocity and the height and structure of the vegetation. The major advantage of this model over other mechanistic dispersal models is the realistic simulation of the turbulent wind movements that have the potential to uplift seeds. Seed uplifting is the main mechanism for long-distance wind dispersal (Horn et al. 2001, Nathan et al. 2002, Tackenberg 2003, Soons et al. 2004). A detailed model description is given by Soons et al. (2004): the Markov chain model for Synthetic Turbulence Generation. An overview of the model input parameters is given in Table 2.

Habitat fragmentation and eutrophication scenarios

For the habitat fragmentation and eutrophication scenarios, the plant colonization characteristics measured in field populations of the four selected species (Soons and Heil 2002) served as input data. These characteristics were measured for a range of isolated populations differing in degree of fragmentation (measured as current population size, in number of flowering rosettes per population) and eutrophication (measured as current site productivity, in grams aboveground dry biomass per square meter). The population sizes and site productivities of the measured populations span the full range found in the Pleistocene soil areas of The Netherlands (population sizes = 2–400 000 flowering rosettes, site productivities = 96–786 g/m²). Table 1 gives an overview of the significant relationships between the colonization characteristics and population size or site productivity. For a detailed description of the measurements and relationships, we refer to Soons and Heil (2002). One model parameter, vegetation leaf area index (LAI), was estimated from literature (Fliervoet and Werger 1984, Werger et al. 1986).

For the habitat fragmentation scenarios, we focused on the range of population sizes that represent the decrease of relatively large to very small populations: from 1000 to 10 flowering rosettes. For population sizes in this range, we calculated the values of the colonization characteristics by interpolating the measured

TABLE 3. Habitat fragmentation, eutrophication, and an increase in extreme wind velocities change the colonization capacity of wind-dispersed grassland plants (*Cirsium dissectum*, *Hypochaeris radicata*, *Centaurea jacea*, and *Succisa pratensis*).

Species	Seed production per population ($\times 10^3$) [†]				Germination percentage (%) [‡]			
	O	HF	EU	W	O	HF	EU	W
<i>C. dissectum</i>	30	2.6	30	30	52	48	34	52
<i>H. radicata</i>	160	14	160	160	61	54	61	61
<i>C. jacea</i>	190	19	340	190	85	81	91	85
<i>S. pratensis</i>	220	32	390	220	19	13	30	19

Notes: Abbreviations are: O, "original" scenario, unfragmented populations of 1000 flowering rosettes, at sites of average productivity (*C. dissectum* 460 g/m², *H. radicata* 180 g/m², *C. jacea* 500 g/m², *S. pratensis* 400 g/m²; Soons and Heil 2002), for an extreme storm with wind velocity 22 m/s; HF, high habitat fragmentation scenario, population size reduced to 100 flowering rosettes; EU, high eutrophication scenario, site productivity increased to 800 g/m², for *H. radicata* to 450 g/m²; W, increased wind velocity scenario, extreme wind velocity increased to 24.2 m/s. In combination, the total number of germinable seeds to be dispersed and the 95th percentile dispersal distance give an estimate of plant colonization capacity.

[†] For *H. radicata*, *C. jacea*, and *S. pratensis*, these values can be used for comparisons between species and scenarios only, because they are based on the assumption that each flowering rosette produces only one flowering stalk with all seed heads equal to the top seed head. At more productive sites, rosettes generally produce more than one stalk. Lower seed heads generally produce fewer seeds than the top head. Data are from Soons and Heil (2002).

[‡] Data are from a greenhouse germination experiment (Soons and Heil 2002).

relationships between the colonization characteristics and population size. For the eutrophication scenarios, we focused on the full range of site productivities over which the selected species were found to occur: ~100–800 g/m² (except for *H. radicata*: ~100–450 g/m²). For site productivities in this range, we calculated the colonization characteristics by interpolating the measured relationships between these characteristics and site productivity.

Wind velocity scenarios

Regional increases in extreme wind velocities have been predicted for various climate change scenarios. However, there is no general agreement yet on their precise magnitude and geographic location. Therefore, we used a wide range of plausible wind velocities for the wind velocity scenarios. We selected wind velocities from the distribution of horizontal wind velocities for the seed dispersal season (July–October) in the interior of The Netherlands (approximately the area where we carried out the field measurements). These velocities follow a Weibull distribution up to ~16 m/s (Fig. 1; Wieringa and Rijkoort 1983). We obtained the frequencies of occurrence of extreme wind velocities (>16 m/s) from the Rijkoort-Weibull model (Wieringa and Rijkoort 1983). To assess seed dispersal under extreme wind velocities, we selected two extreme wind velocities for the scenario simulations: 22 and 28 m/s (Fig. 1). To assess seed dispersal under less extreme conditions, we also selected the average wind velocity (3.8 m/s) and a set of intermediate wind velocities. All wind velocities are hourly averaged wind velocities at a reference height of 10 m.

Quantification of dispersal ability and colonization capacity

Seed dispersal distances were quantified for all scenarios using the mechanistic dispersal model. To quan-

tify the effects of the habitat fragmentation and eutrophication scenarios under realistic dispersal conditions, we simulated these scenarios for each wind velocity scenario. Vegetation parameters were held constant in space to keep model simulation results tractable. All simulations (i.e., each parameter combination) were carried out for 10 000 seeds. The simulation results should be viewed as dispersal probabilities, because in reality populations of different sizes produce different numbers of seeds.

We estimated population colonization capacity for four scenarios: the "original" undisturbed scenario, a highly fragmented scenario, a highly eutrophied scenario, and a scenario with highly increased extreme wind velocity (Table 3). To estimate the net effects of these four scenarios on long-distance colonization capacity, we combined simulated dispersal distances with seed production and germination ability calculated for the scenarios. The relationships of seed production and germination ability with population size and site productivity are indicated in Table 1. Changes in extreme wind velocity are assumed not to affect seed production or germinability.

RESULTS

The effects of population size and wind velocity on seed dispersal distances are plotted in Figs. 2 and 3. Despite the effects of population size on seed terminal velocity, population size has almost no effect on dispersal distance. An increase in wind velocity increases dispersal distances. The increase in median dispersal distances is almost linear, but the increase in long-distance dispersal is larger at higher wind velocities. The effects of site productivity and wind velocity are presented in Figs. 4 and 5. An increase in site productivity reduces median and long-distance dispersal distances greatly in *C. dissectum*, *H. radicata*, and *S. pratensis*. In *C. jacea*, an increase in site productivity does

TABLE 3. Extended.

Germinable seeds per population ($\times 10^3$)				95th-percentile dispersal distance (m)			
O	HF	EU	W	O	HF	EU	W
16	1	10	16	81	81	25	110
98	8	98	98	36	36	13	49
162	15	309	162	0.56	0.56	0.57	0.62
42	4	117	42	2.4	2.4	1.2	2.8

not affect median dispersal distances and long-distance dispersal.

For the quantification of long-distance dispersal, we used 95th-percentile dispersal distances instead of maximum dispersal distances, because in all species the maximum dispersal distances are highly stochastic. The maximum dispersal distances demonstrate the stochasticity in the long-distance dispersal process and show no consistent changes with population size or site productivity. Maximum dispersal distances do increase more than proportionally with increasing wind velocity, however. A very small number of seeds experience upward turbulent fluctuations in vertical wind velocity that are sustained long enough to uplift the seeds very high. These few seeds are dispersed much further than the 95th-percentile distances; they are rare long-distance dispersal events. At a wind velocity of 22 m/s, the maximum dispersal distance is, on average, 3400 m for *C. dissectum*, 2300 m for *H. radicata*, 1.2 m for *C. jacea*, and 11 m for *S. pratensis* (averages over all population sizes and site productivities). At a wind velocity of 28 m/s, the maximum dispersal distances are, on average, 6000 m for *C. dissectum*, 3900 m for *H. radicata*, 1.7 m for *C. jacea*, and 30 m for *S. pratensis*.

The effects of a sharp reduction in population size, large increase in site productivity, or large increase in extreme wind velocity on long-distance colonization capacity are presented in Table 3. The 95th-percentile dispersal distances are presented because these show consistent changes with the scenarios, whereas maximum distances show much more stochasticity. A 90% reduction in population size reduces the number of germinable seeds per population more than proportionally (by ~92%) in all species except *S. pratensis*. This is due to a reduction in number and germinability of seeds in all species except *S. pratensis*. In *S. pratensis*, seed germinability is also reduced, but seed production is slightly increased. A 90% reduction in population size does not affect 95th-percentile dispersal distances. Because there are fewer seeds that can disperse, however, the reduction in population size reduces the colonization capacity of all species. An increase in site productivity to the maximum productivity at which the species occur (an increase by roughly 50%) increases the numbers of germinable seeds in *C. jacea* and *S. pratensis* by 92% and 180%, respectively. It decreases

the number of germinable seeds in *C. dissectum* by 38%. In all species except *C. jacea*, it also greatly decreases 95th-percentile dispersal distances (by 50–69%). Thus, in all species except *C. jacea*, site eutrophication decreases long-distance colonization. In *H. radicata* and *S. pratensis*, this may increase short-distance colonization, but in *C. dissectum* all colonization is reduced. An increase in extreme wind velocity by 10% increases 95th-percentile distances by 11–36%, and thus increases long-distance colonization capacity.

DISCUSSION

Seed dispersal ability

This study shows how measured changes in plant dispersal characteristics translate to changes in seed dispersal distances. Soons and Heil (2002) found that small isolated populations of species with plumed seeds have a reduced variation in seed terminal velocity, whereas small isolated populations of species with plumeless seeds have a reduced average terminal velocity and increased variation in terminal velocity. Our results show that these effects of reduced population size, although significant, are too small to affect seed dispersal ability. This finding is in agreement with sensitivity analyses of mechanistic wind dispersal models, which showed that seed dispersal distances are not very sensitive to intraspecific variation in seed terminal velocity (Soons et al. 2004). Thus, habitat fragmentation does not affect plant seed dispersal ability by reducing the size of isolated populations.

Eutrophication greatly affects seed dispersal by wind. It reduces median and long-distance dispersal distances in *C. dissectum*, *H. radicata*, and *S. pratensis*, because in these species the seed release height decreases relative to the vegetation height (Soons and Heil 2002). Due to eutrophication, the vegetation composition changes and vegetation height increases. The seed release height of the studied species also increases, but less than the vegetation height (though hardly less in *C. jacea*). The increase in seed release height is lowest in *C. dissectum* and *H. radicata*, which have leaf rosettes. Seeds that are released from a lower height above the vegetation are generally dispersed over shorter distances. Firstly, they experience lower wind velocities. Secondly, they fall over a shorter distance and hence have a shorter flight time. Thirdly, they

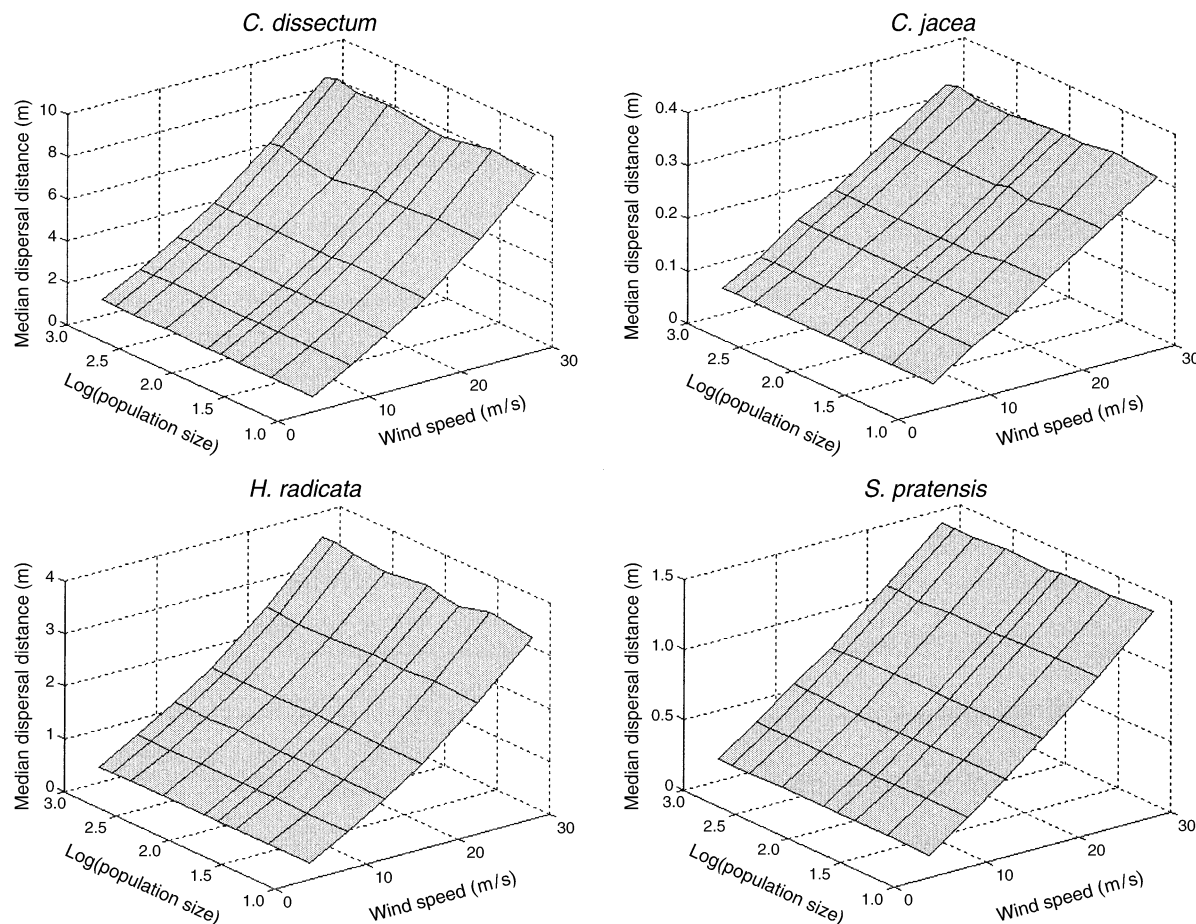


FIG. 2. Population size (log-transformed) has no effect on median seed dispersal distances, but an increase in horizontal wind velocity increases median seed dispersal distances.

experience less organized wind turbulence and hence the probability of uplifting is lower. Our results confirm that seed release height and vegetation height greatly affect dispersal ability (Soons et al. 2004).

An increase in horizontal wind velocity has the greatest effect on seed dispersal distances, and especially long-distance dispersal. This is caused by two mechanisms. Firstly, higher wind velocities transport seeds further during their flight time. Secondly, higher wind velocities increase mechanically produced turbulence and hence the probability of seed uplifting. Seed uplifting is the most important mechanism for long-distance dispersal by wind (Horn et al. 2001, Nathan et al. 2002, Tackenberg 2003, Soons et al. 2004). This is illustrated by the strong positive correlation between seed uplifting percentages and 95th-percentile distances found in this study (Spearman's $\rho = 0.965$, $P < 0.001$, two-tailed).

There are still many uncertainties in the predicted changes in extreme wind velocity events. Predicted changes include increases in extreme wind velocities by 4–12% (Knutson et al. 1998, Knippertz et al. 2000), shifts of the entire wind velocity distribution to higher

velocities at the expense of lower velocities (Carnell et al. 1996, Lunkeit et al. 1996), and local increase in the frequency of occurrence of gales (16–24 m/s) by 30–40% (Carnell et al. 1996). The WASA Group (1998), however, argues that predicted changes fall within the natural variation in north Atlantic storminess. Due to the relatively short measurement period, detected increases in the frequency of storms also fall within natural fluctuations. This makes it difficult to assess the accuracy of predictions made by climate change models (WASA Group 1998, IPCC 2001). Also, predicted increases in extreme wind velocity events are for the winter season and may be lower for the seed dispersal season. Overall, the exact changes still remain unknown. However, for any possible change in wind velocity, the resultant change in grassland seed dispersal by wind can be estimated using methods developed here.

The quantified effects of habitat fragmentation, eutrophication, and an increase in extreme wind velocities on the seed dispersal ability and colonization capacity of wind-dispersed grassland plants apply to the future circa <100 years from now. Over longer time periods,

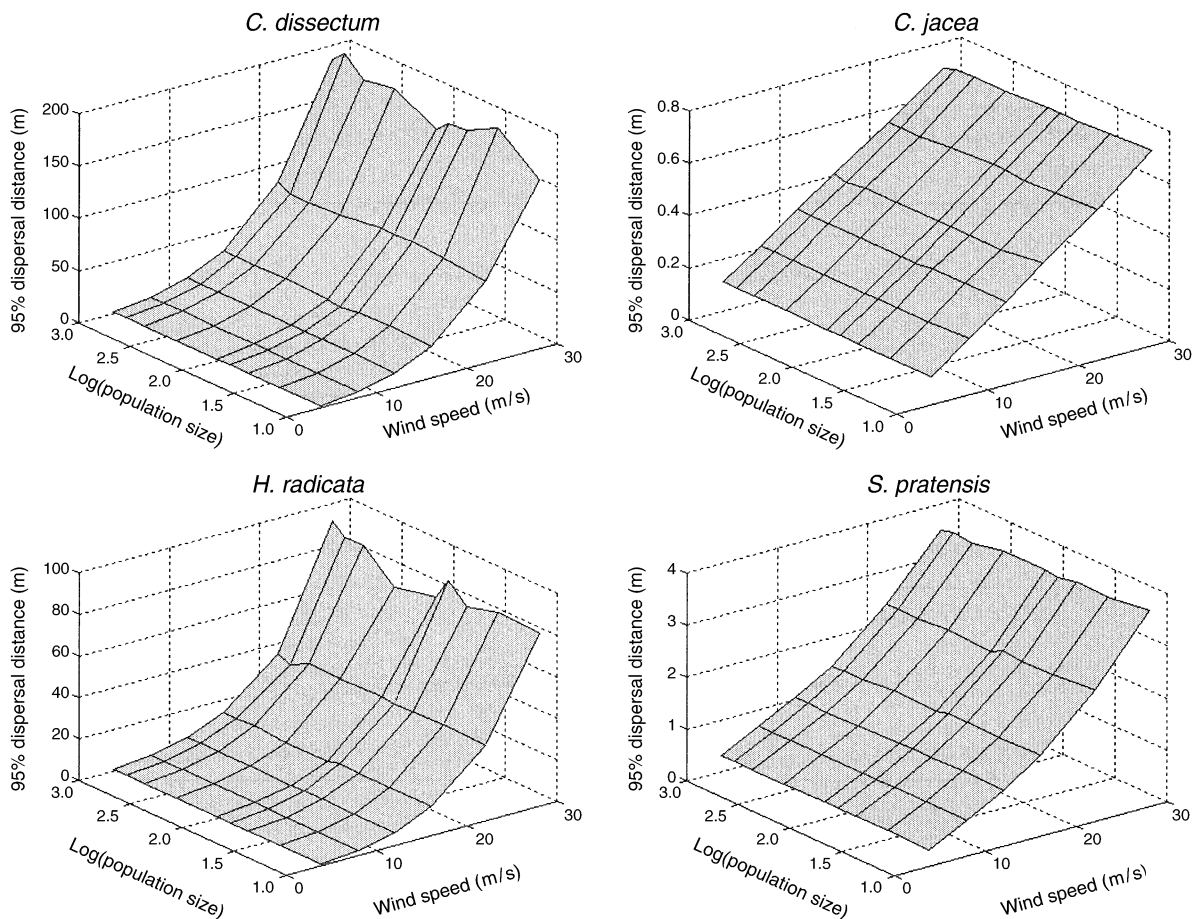


FIG. 3. Population size (log-transformed) has no effect on 95th-percentile seed dispersal distances, but an increase in horizontal wind velocity increases 95th-percentile seed dispersal distances.

evolutionary processes may change the plant species' dispersal characteristics, and such changes were not included in this study. Cody and Overton (1996) suggested that in small populations rapid evolution of dispersal characteristics may take place, but in the plant species that were used in this study no evidence for rapid evolution (within 25–50 years) of dispersal characteristics has been found (Soons and Heil 2002).

Are the simulated dispersal distances realistic?

In this study we quantified long-distance seed dispersal for species with different wind dispersal strategies. Especially for the species with plumed seeds, simulated maximum dispersal distances are high. Only very few data on long-distance dispersal under natural conditions are available for comparison. In most studies on wind dispersal of (grassland) herbs, field measurements are limited to <45 m (the maximum in a review by Cain et al. 1998). Bullock and Clarke (2000) measured the longest distances in grassland using seed traps (80 m). To assess whether our maximum dispersal distances are realistic, we therefore compare them to

data on long-distance colonization events and species migration.

From 1930 to 1933, *Aster tripolium* colonized newly reclaimed land in The Netherlands through seed dispersal during storms (Feekes 1936). During that period, the maximum dispersal distance of the species was ~5 km per dispersal season (September). The maximum wind velocity was ~23 m/s per dispersal season (Royal Netherlands Meteorological Institute, *available online*).⁵ Terminal velocity of the plumed seeds of *A. tripolium* was ~0.3 m/s, the vegetation was open and homogeneous, and seed germination and establishment was high (Feekes 1936). Given these conditions, the maximum dispersal distance of *A. tripolium* can be compared to the maximum distances predicted for *C. dissectum* and *H. radicata* at a wind velocity of 22 m/s. The 5 km of *A. tripolium* is in the same order of magnitude as the ~3.4 and 2.3 km for *C. dissectum* and *H. radicata*. The higher distance reached by *A. tripolium* is partly due to its lower seed terminal ve-

⁵ (<http://www.knmi.nl>)

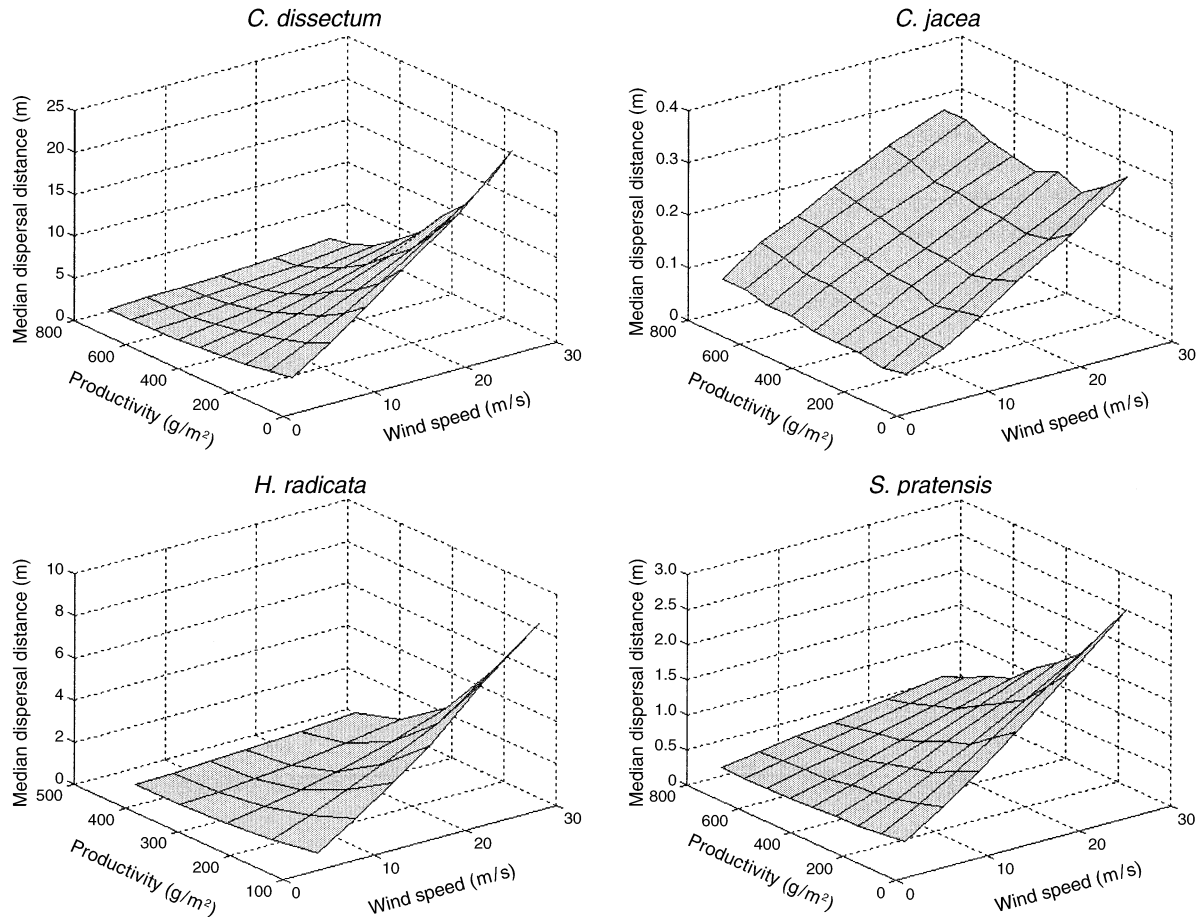


FIG. 4. An increase in site productivity reduces median seed dispersal distances in most species, but an increase in horizontal wind velocity increases median seed dispersal distances.

locity. Also, *A. tripolium* has a higher maximum seed release height (up to 1.5 m; Feekes 1936). Also, *A. tripolium* produced much more seeds than the 10 000 seeds simulated for *C. dissectum* and *H. radicata* (maximum density of trapped seeds at the seed source was 1 million seeds/m²; Feekes 1936), so that the probability of long-distance dispersal events was higher.

For a comparison to species migration rates, we made rough approximations of the migration rates of the studied species. In The Netherlands, wind velocities ≥ 22 m/s occur almost certainly at least once every 20 years. Thus, a population producing 10 000 viable seeds per year (for *C. dissectum* ± 390 flowering rosettes, for *H. radicata* < 60 flowering rosettes) may disperse ~ 500 seeds per 20-year time interval over a distance between the 95th-percentile and the maximum dispersal distance simulated for a 22 m/s wind velocity. We assume that some of these 500 seeds land at favorable sites and establish populations large enough to produce another 10 000 seeds per year during the next 20-year time interval. Then, the migration rate lies between the 95th-percentile distance divided by 20 and the maximum distance divided by 20. Under average

productivity and vegetation conditions, the migration rates are then: 4–170 m/yr for *C. dissectum* and 2–115 m/yr for *H. radicata*. These rough approximations underestimate migration rates when population growth and/or seed production are higher, or higher wind velocities occur. They overestimate migration rates in landscapes with low habitat availability and/or low population growth. Vegetation heterogeneity, wind barriers, or other obstacles in the landscape may also reduce the migration rates. But overall, the estimated rates are roughly representative of migration through open and suitable landscapes, as may have been the case during Holocene migrations. The estimated migration rates for *C. dissectum* and *H. radicata* are comparable to the range of Holocene migration rates estimated for tree species in the Northern hemisphere: 25–500 m/yr (for a few species, up to 2000 m/yr; Macdonald 1993).

The maximum dispersal distances predicted by the model are thus within realistic ranges. Our results indicate that wind dispersal of plumed seeds may be sufficient for explaining long-distance dispersal events and relatively rapid migrations through open, suitable

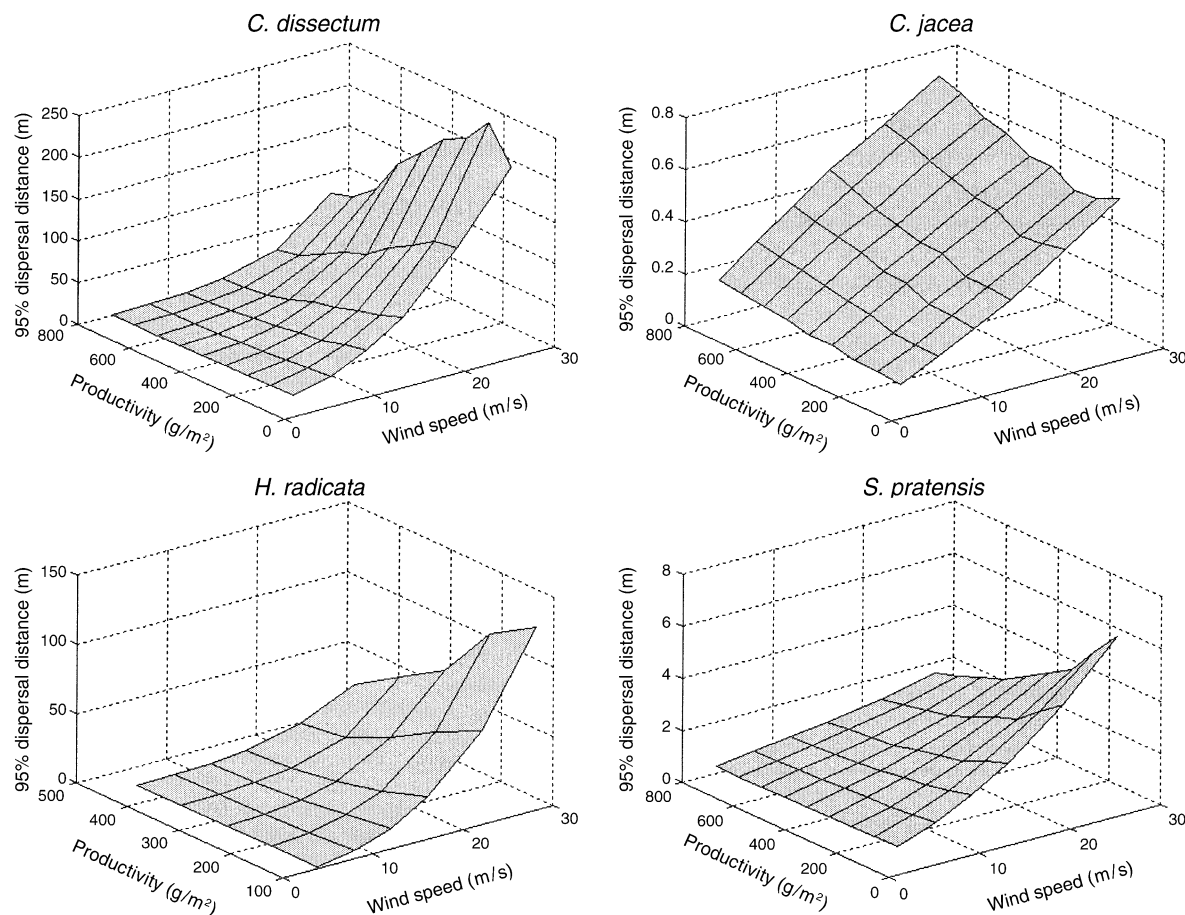


FIG. 5. An increase in site productivity reduces 95th-percentile seed dispersal distances in most species, but an increase in horizontal wind velocity increases 95th-percentile seed dispersal distances.

landscapes. In highly fragmented and largely unsuitable landscapes, however, seed dispersal plays a less important role in determining migration potential (Thompson 1994, Pitelka et al. 1997).

Colonization capacity

Plant colonization capacity is determined by seed dispersal ability, seed production, and seed germination ability. Although a reduction in population size does not affect seed dispersal distances, it strongly reduces the number and germinability of the dispersed seeds. Thus, habitat fragmentation reduces the colonization capacity. Eutrophication reduces long-distance colonization because long-distance dispersal is reduced, but may increase short-distance colonization because more germinable seeds are dispersed. In *C. dissectum*, eutrophication reduces seed germinability (Soons and Heil 2002) and colonization is reduced for all distances. An increase in extreme wind velocity increases long-distance dispersal and hence, long-distance colonization. Seed production and germination ability are unlikely to be affected by a change in extreme wind velocities. They are affected by other aspects of climate

change (e.g., LaDeau and Clark 2001, Korner 2000), but no general relationships have yet been established (Korner 2000), and further research is required.

Our results indicate how, and by how much, habitat fragmentation and eutrophication can affect long-distance seed dispersal and the long-distance colonization capacity of wind-dispersed grassland plants. The studied scenarios are realistic. Habitat fragmentation continues to reduce the size of local populations. Many populations of once-common grassland plants now consist of <100 flowering rosettes (e.g., Ouborg and Vantreuren 1995, Fischer and Matthies 1998, Kery et al. 2000, Soons and Heil 2002). Eutrophication also continues and local productivities continue to increase, especially at sites that lack management aimed at nutrient removal (Berendse et al. 1992, Bobbink et al. 1998, Neitzke 1998). Eventually, ongoing habitat fragmentation and eutrophication cause extinction of local populations of species restricted to nutrient-poor grasslands. But before this happens, the populations suffer from reduced capacity to colonize new sites, and especially distant sites. For species with only short-distance dispersal by wind, such as *C. jacea*, reduced long-

distance colonization capacity is not likely to affect species survival greatly. Our results show that for such species, dispersal by wind is <2 m. This is generally not sufficient to colonize new, unoccupied habitat patches. But for species adapted to long-distance dispersal by wind, such as *C. dissectum* and *H. radicata*, the reductions in long-distance colonization capacity may make the difference between colonization of new, unoccupied, habitat patches or "colonization" of sites within the source patch only. Even *S. pratensis* occasionally disperses over >30 m, which may be sufficient to colonize new habitat patches. In these species, reduced long-distance colonization capacity may pose a serious threat to regional species dynamics and survival.

An increase in extreme wind velocity by 10% increases long-distance dispersal and colonization more than proportionally. However, an increase in extreme wind velocity events in the future is unlikely to compensate reductions in long-distance colonization capacity due to habitat fragmentation or eutrophication. An increase in extreme winds or extreme wind events by 10% is large given the current predictions (see *Results; Seed dispersal ability*). And even if such an increase would occur, its effects are still smaller than the reduction in dispersal ability due to eutrophication. If habitat fragmentation and eutrophication continue and their effects are not ameliorated by management, a net decrease in long-distance dispersal and colonization of wind-dispersed grassland plants is the dominant trend for the future.

ACKNOWLEDGMENTS

This research was supported by the Research Council for Earth and Life Sciences (ALW), with financial aid from the Netherlands Organization for Scientific Research (NWO), the Schure-Beijerinck-Popping Fonds, Stichting Hugo de Vries Fonds, and Miquel Fonds. R. Nathan acknowledges support from the National Science Foundation (NSF-IBN), German-Israeli Foundation (GIF), and Israeli Science Foundation (ISF). G. Katul acknowledges support from the National Science Foundation (NSF-EAR, NSF-DMS) and the Department of Energy through the NIGEC-SERC, FACE, and TCP programs for developing the Markov chain STG model. The Park Rangers of Staatsbosbeheer kindly permitted M. Soons to take measurements and collect seeds in their nature reserves. Marinus Werger and two anonymous reviewers improved the manuscript with their valuable comments.

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