4. Human effects on long-distance wind dispersal and colonization by grassland plants

M.B. Soons, R. Nathan, G.G. Katul

**Summary**

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 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 reduces the number and germinability of produced seeds, and hence the colonization capacity. Site eutrophication strongly reduces seed dispersal distances, but in many species also increases seed production and germinability. Thus, long-distance colonization decreases but short-distance colonization increases. 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. This 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. This reduces 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). Habitat fragmentation contributes to the eutrophication of nutrient-poor habitat patches, and eutrophication contributes to habitat loss (Saunders et al. 1991; Neitzke 1998, 2001). Climate change alters local conditions for plant growth and population dynamics, and affects local survival of plant species (Easterling et al. 2000; Walther et al. 2002; Parmesan and Yohe 2003). 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. 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 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 (this thesis, Chapter 3). Global warming is predicted to increase the frequency of storms, and especially high intensity storms, in the east Atlantic and in north-west 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, development of mechanistic models progressed sufficiently to predict long-distance seed dispersal by wind in a realistic way (Nathan et al. 2002; Tackenberg 2003; this thesis, Chapter 3). 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 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 thereby focused especially on long-distance dispersal. 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 increases 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 for seed dispersal by wind that simulates long-distance dispersal in a realistic way and predicted measured dispersal distances accurately in previous studies (Nathan et al. 2002; this thesis, Chapter 3). 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 horizontal wind velocity, and wind turbulence. Turbulence is simulated by spatially and temporally correlated stochastic fluctuations in horizontal and vertical wind velocity. The size and (auto-) correlation of these fluctuations are dependent on the mean 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; this thesis, Chapter 3). A detailed model description is given in Chapter 3 of this thesis (the Markov chain Synthetic Turbulence Generation model). 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 g aboveground dry biomass per m²). 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

### Table 1. Measured relationships between plant colonization characteristics and population size or site productivity. Relationships are presented per wind dispersal strategy (species with plumed seeds: C. dissectum and H. radicata; with plumeless seeds: C. jacea and S. pratensis), unless a species-specific relationship is indicated (Cd = C. dissectum, Sp = S. pratensis). Data from Soons and Heil (2002). + = Positive relationship, - = negative relationship, o = no relationship.

<table>
<thead>
<tr>
<th>Colonization characteristic</th>
<th>Relationship with log transformed population size</th>
<th>Relationship with site productivity</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Plumed seeds</td>
<td>Plumeless seeds</td>
</tr>
<tr>
<td><strong>Seed</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Terminal velocity</td>
<td>o</td>
<td>+</td>
</tr>
<tr>
<td>Germination ability</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><strong>Plant</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Seed production</td>
<td>+</td>
<td>- (Sp)</td>
</tr>
<tr>
<td>Seed release height</td>
<td>o</td>
<td>o</td>
</tr>
<tr>
<td>Variation in terminal velocity</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td><strong>Vegetation</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Height</td>
<td>o</td>
<td>o</td>
</tr>
<tr>
<td>Leaf area index</td>
<td>Not measured</td>
<td>Not measured</td>
</tr>
</tbody>
</table>

1 Soons and Heil found a negative relationship for H. radicata. Because of the small sample size in H. radicata (only 7 populations), this observed relationship may not reflect the general situation. Therefore, it is not used for the scenario analyses in this study.
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Table 2. Values of the model input parameters used in this study (species average and range).

<table>
<thead>
<tr>
<th>Model parameter</th>
<th>C. dissectum</th>
<th>H. radicata</th>
<th>C. jacea</th>
<th>S. pratensis</th>
<th>Data source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Average terminal velocity (m/s)</td>
<td>0.38</td>
<td>0.34</td>
<td>4.3</td>
<td>2.1</td>
<td>Soons and Heil 2002</td>
</tr>
<tr>
<td>Standard deviation in velocity</td>
<td>0.03</td>
<td>0.01</td>
<td>0.45</td>
<td>0.20</td>
<td>Soons and Heil 2002</td>
</tr>
<tr>
<td>Seed release height (m)</td>
<td>0.50–0.50</td>
<td>0.28–0.28</td>
<td>0.22–0.65</td>
<td>0.46–0.67</td>
<td>Soons and Heil 2002</td>
</tr>
<tr>
<td>Vegetation height (m)</td>
<td>0.35–0.35</td>
<td>0.23–0.23</td>
<td>0.35</td>
<td>0.35</td>
<td>Soons and Heil 2002</td>
</tr>
<tr>
<td>Leaf area index (m²/m²)</td>
<td>3.5</td>
<td>3.5</td>
<td>3.5</td>
<td>3.5</td>
<td>Fliervoet and Werger 1984; Werger et al. 1986</td>
</tr>
<tr>
<td>Horizontal wind velocity (m/s)</td>
<td>3.8–28.0</td>
<td>3.8–28.0</td>
<td>3.8–28.0</td>
<td>3.8–28.0</td>
<td>Wieringa and Rijkoort 1983</td>
</tr>
</tbody>
</table>

(2002). One model parameter, vegetation 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 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: ca. 100-800 g/m² (except for H. radicata: ca. 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 realistic 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 ca. 16 m/s (Fig. 1; Wieringa and Rijkoort 1983). The frequencies of occurrence of extreme wind velocities (>16 m/s) were obtained from the Rijkoort-Weibull model (Wieringa and Rijkoort 1983). For the scenario simulations we selected two extreme wind velocities (22 and 28 m/s; Fig. 1) and a set of intermediate velocities in between the extremes and the average (3.8 m/s).
Quantification of dispersal ability and colonization capacity

Seed dispersal distances were quantified for all scenarios using the mechanistic dispersal model. To quantify 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 calculated the average number of seeds per year that would colonize sites at a distance greater than the 95-percentile distance if all seeds land at sites suitable for germination. We thus combined the 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.

Figure 1. Relative frequencies of hourly-averaged wind velocities at 10 m height for the interior of The Netherlands (Weibull distribution \( f(U) = k/a \cdot (U/a)^{k-1} \cdot \exp(-((U/a)^k); k = 1.74; a = 4.3 \)). Wind velocities >16 m/s cannot be predicted reliably using the fitted Weibull distribution, so two extreme wind velocities derived from the Rijkoort-Weibull model are plotted additionally (Wieringa and Rijkoort 1983).
RESULTS

The effects of population size and wind velocity on seed dispersal distances are plotted in Figs. 2-4. 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 graphs of the maximum dispersal distances demonstrate the stochasticity in the long-distance dispersal process, especially at the highest wind velocities. 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 95-percentile distances; they are rare long-distance dispersers.
dispersal events. The maximum dispersal distances are shown to indicate over what distances such seeds can be dispersed. The effects of site productivity and wind velocity are presented in Figs. 5-7. An increase in site productivity reduces median and 95-percentile dispersal distances greatly in *C. dissectum*, *H. radicata*, and *S. pratensis*. In *C. jacea* an increase in site productivity does not affect median distances and increases 95-percentile distances. In all species maximum dispersal distances are highly stochastic and show no consistent changes with site productivity.

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. 95-Percentile dispersal distances are presented, because these show consistent changes with the scenarios whereas maximum distances show much more stochasticity. Estimates of the maximum dispersal distances can be
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obtained from Figs. 4 and 7. A 90% reduction in population size reduces the number of seeds that colonize sites farther away than the 95-percentile dispersal distance more than proportionally (ca. 92%) in all species except *S. pratensis*. This is due to a reduction in number and germinability of the dispersed seeds in all species except *S. pratensis*. In *S. pratensis* seed germinability is also reduced, but seed production increased. An increase in site productivity to the species’ extremes (by roughly 50%) increases the number of seeds that may colonize sites further away than the 95-percentile distance in *C. jacea* and *S. pratensis* by 92% and 180%. But in all species it greatly decreases 95-percentile dispersal distances (by 50-69%). Thus, site eutrophication increases short-distance colonization at the expense of long-distance colonization. An increase in extreme wind velocity by 10% increases 95-percentile distances by 11-36%, and thus increases long-distance colonization capacity.

Figure 4. Maximum dispersal distances for different population sizes (log transformed) and wind velocities.
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

Figure 5. Median dispersal distances for different site productivities and wind velocities.
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Distances are not very sensitive to intraspecific variation in seed terminal velocity (this thesis, Chapter 3). 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 95-percentile 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 infructescence height of the studied species also increases, but less than the vegetation height (though hardly less in *C. jacea*). The increase in infructescence 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 distance. Firstly, they experience lower wind velocity. Secondly, they fall over a shorter distance and hence have a shorter flight time. Thirdly,
they experience less organized wind turbulence and hence their probability of uplifting is lower. Our results confirm that seed release height and vegetation height greatly affect dispersal ability (this thesis, Chapter 3).

An increase in mean 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 (Horn *et al.* 2001; Nathan *et al.* 2002; Tackenberg 2003; this thesis, Chapter 3). This is illustrated by the strong positive correlation between seed uplifting percentages and 95-percentile distances found in this study (Spearman’s $\rho =0.965$, $p<0.001$, 2-tailed).

Figure 7. Maximum dispersal distances for different population sizes (log transformed) and wind velocities.
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 (The 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 yet remain unknown. However, for any possible change in wind velocity the resultant change in grassland seed dispersal by wind can be estimated from Figs. 2-7.

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 ca. 5 km per dispersal season (September). The maximum wind velocity was ca. 23 m/s per dispersal season (Royal Netherlands Meteorological Institute, www.knmi.nl). Terminal velocity of the plumed seeds of *A. tripolium* was ca. 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 ca. 2.5 and 3.5 km for *H. radicata* and *C. dissectum*. The higher distance reached by *A. tripolium* is partly due to its lower seed terminal velocity. Also, *A. tripolium* has a higher maximum seed release height (up to 1.5 m; Feekes 1936). And, *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
Table 3. Changes in plant colonization capacity for different scenarios. 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. The 95-percentile dispersal distance and the number of germinable seeds that disperse further than this distance give an estimate of colonization capacity.

<table>
<thead>
<tr>
<th>Species</th>
<th>Seed production per population (× 10^3)</th>
<th>Germination percentage (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>O</td>
<td>HF</td>
</tr>
<tr>
<td>C. dissectum</td>
<td>30</td>
<td>2.6</td>
</tr>
<tr>
<td>H. radicata</td>
<td>160</td>
<td>14</td>
</tr>
<tr>
<td>C. jacea</td>
<td>190</td>
<td>19</td>
</tr>
<tr>
<td>S. pratensis</td>
<td>220</td>
<td>32</td>
</tr>
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<table>
<thead>
<tr>
<th>Species</th>
<th>95-Percentile dispersal distance (m)</th>
<th>Germinable seeds at distance &gt; 95-perc. (× 10^3)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>O</td>
<td>HF</td>
</tr>
<tr>
<td>C. dissectum</td>
<td>81</td>
<td>81</td>
</tr>
<tr>
<td>H. radicata</td>
<td>36</td>
<td>36</td>
</tr>
<tr>
<td>C. jacea</td>
<td>0.56</td>
<td>0.56</td>
</tr>
<tr>
<td>S. pratensis</td>
<td>2.4</td>
<td>2.4</td>
</tr>
</tbody>
</table>

* 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 from Soons and Heil (2002).

* Data from greenhouse germination experiment (Soons and Heil 2002).

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) disperses ca. 500 seeds per 20-year time interval over a distance between the 95-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 95-percentile distance divided by 20 and the maximum distance divided by 20. Under average productivity and vegetation conditions, the migration rates are then: 4-180 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
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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 over all, 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 within the range of Holocene migration rates estimated for tree species in the Northern hemisphere: 25–500 (for a few species -2000) m/yr (Macdonald 1993).

The maximum dispersal distances predicted by the model thus are 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 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 increases short-distance colonization because more germinable seeds are dispersed, but reduces long-distance colonization because long-distance dispersal is reduced. 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 show how, and by how much, habitat fragmentation and eutrophication 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; this thesis, Chapter 5). 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; this thesis, Chapter 5). 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 >20 m, which may be sufficient to colonize new habitat patches. In these species reduced long-distance colonization capacity poses a 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 *Seed dispersal ability* section). 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.

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