Habitat fragmentation and connectivity

Spatial and temporal characteristics of the colonization process in plants

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Habitatversnippering en connectiviteit

Kolonisatieprocessen bij planten

(met een samenvatting in het Nederlands)

Proefschrift

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Promotor:	Prof. Dr. M.J.A. Werger
Co-promotor:	Dr. G.W. Heil
	Faculty of Biology, Plant Ecology Group Utrecht University

M.B. Soons
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Voor mijn ouders
Voor Eric

“*Mais, bien sûr, nous qui comprenons la vie,*
nous nous moquons bien des numéros! ”

Antoine de Saint-Exupéry, *Le petit prince*

Contents

Preface

This thesis presents the most important results from my Ph.D. research project. I have enormously enjoyed working on this project, especially the opportunity to combine field and lab experiments with theoretical work. Many people have contributed to my research, and I would like to use this opportunity to thank them.

Gerrit Heil, my *co-promotor*, supervised my Ph.D. research. I thank him for the many inspiring discussions, his practical advice on all aspects of the research as well as life in general, and his unconditional optimism. I am glad that I had the opportunity to carry out my Ph.D. research under his supervision. I am grateful to Marinus Werger for acting as my *promotor*, providing me with my base at the Plant Ecology Group, and giving me complete freedom in my research, education, and teaching activities, which I have greatly appreciated. My research project has been part of the national research program ‘Survival of Plant Species in Fragmented Landscapes’. Jan van Groenendael, the program leader, has guided the progress of the research carried out within the program and found practical solutions for difficulties that came along. I also thank him for his interest in my work and his many useful suggestions and comments on my manuscripts. Ecologists with different fields of expertise have worked together in the research program. I greatly enjoyed, and learned a lot from, this collaboration and the interesting discussions I had with the other researchers involved in the program: Carla Grashof-Bokdam, Carolin Mix, Eelke Jongejans, Felix Knauer, Hans de Kroon, Jana Verboom-Vasiljev, and Joop Ouborg. I carried out much of my fieldwork with Carolin and, especially, Eelke and thank them for their good company.

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Bart Timmermans, Lennart Turlings, Liesbeth Brouwer, Maarten Mouissie, Marloes Vermeer, and Rob Messelink carried out M.Sc. research projects under my supervision. They all contributed to my research in one way or another, and I thank them for their creativity, hard work, and pleasant work relations (and, some of them, for daring to get in the car when I was driving to the field sites).

I carried out a part of my research in the lab of Gabriel Katul, Nicholas School of the Environment and Earth Sciences, Duke University. Gabriel Katul developed the Markov chain models described in Chapter 3. I thank him for his hospitality, great help with the modeling work, and introducing me to the world of boundary layer dynamics. I thank Ran Nathan for introducing me to Gaby, for thinking along with us on the research and writing of manuscripts, and improving the manuscripts with his perceptive comments. I thank all the ‘BATlab’ people and Erin O’Reilly for providing a great scientific environment and making my stay in Durham a very pleasant one.

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Merel

The research program ‘Survival of Plant Species in Fragmented Landscapes’

The study that resulted in this thesis is part of the Dutch national research program ‘Survival of Plant Species in Fragmented Landscapes’ (1998-2004). This program is a collaborative research effort of Utrecht University, Wageningen University, the University of Nijmegen, and ALTERRA and is funded by the Netherlands Organization for Scientific Research – Earth and Life Sciences (NWO-ALW). The aim of the research program is to obtain detailed information on the mechanisms that determine extinction and survival of plant species in fragmented landscapes and to provide guidelines for their conservation. To achieve this goal, ecologists from different sub-disciplines work together in close cooperation to facilitate exchange of information and integration of study results. The selected study system consists of nutrient-poor, species-rich, moist grasslands. Special focus was placed on four selected plant species that represent two common dispersal strategies and two life-history strategies. The following three Ph.D. studies and postdoc study are carried out within the research program.

1. The study ‘Fragmentation and connectivity: spatial and temporal characteristics of the colonization process in plants’ resulted in this thesis. The main focus of this study is on the potential of fragmented populations to disperse seeds and colonize habitat fragments.

2. The study ‘Establishment and extinction: the dynamics of local plant populations in a regional perspective’ will result in a thesis by Eelke Jongejans (Wageningen University). The main focus of that study is on the local population processes that drive extinction or survival of the fragmented populations.

3. The study ‘Inbreeding and outbreeding: effects of gene flow and local adaptation on the survival of small isolated populations of plants in a regional context’ will result in a thesis by Carolin Mix (University of Nijmegen). The main focus of that study is on the genetic effects of habitat fragmentation on the small and isolated remnant populations. These effects may change the colonization capacity and the local survival probability of fragmented populations.

4. Felix Knauer (ALTERRA) carries out the research project ‘Integration and application: regional survival in changing landscapes’, in which information from the above three studies is integrated to provide landscape-scale guidelines for the conservation of rare grassland species in fragmented landscapes.

Staff members of the research institutions involved in the research program are:
Prof.Dr. J.M. van Groenendael (program leader) – University of Nijmegen
Dr. G.W. Heil and Prof.Dr. M.J.A. Werger - Utrecht University
Prof.Dr. H. de Kroon and Dr. N.J. Ouborg - University of Nijmegen
Dr. C.J. Grashof-Bokdam and Dr. J. Verboom-Vasiljev – ALTERRA

1. Introduction

HABITAT FRAGMENTATION AND PLANT SPECIES SURVIVAL

Habitat fragmentation is the process of subdivision of large, connected habitat areas into increasingly smaller and less connected habitat areas, which are commonly referred to as habitat patches. Habitat fragmentation has a major impact on the regional survival of plant species (Saunders *et al*. 1991; Tilman *et al*. 1994; Hanski and Ovaskainen 2000; Ney-Nifle and Mangel 2000), and is one of the most important causes of world-wide loss of biodiversity (Vitousek *et al*. 1997). Firstly, habitat fragmentation almost always goes together with habitat loss. When less habitat is available, fewer individuals of a species restricted to that habitat can survive. Secondly, habitat fragmentation reduces the area of individual habitat patches. This decreases the survival probability of the populations in habitat patches, through mechanisms which are discussed below. Thirdly, habitat fragmentation reduces the connectivity between habitat patches. This has several negative consequences for local and regional species survival, which are also discussed below. The effects of reduced habitat patch area and connectivity interact, and have more serious consequences for regional plant species survival when occurring in combination than when occurring separately.

Reduced area of habitat patches

A reduction in the area of habitat patches decreases the survival probability of the populations in these patches through two main mechanisms. Firstly, a reduction in the area of habitat patches decreases the size of the populations in these patches. Smaller populations have a higher probability to go extinct due to environmental, demographic, or genetic stochasticity. Environmental stochasticity (*e.g.* a prolonged inundation at the site of the population) or demographic stochasticity (*e.g.* a year with very low seed set) may abruptly end the existence of a small population. Genetic stochasticity results in loss of genetic variation, which decreases the population’s ability to adapt to changing environmental conditions, and may even result in genetic fixation of deleterious alleles (Ellstrand and Elam 1993; Booy *et al*. 2000). Genetic stochasticity reduces the long-term survival probability of small populations. When the connectivity of small populations is low, their survival is threatened by additional mechanisms. Small and isolated populations produce fewer seeds and seeds with lower germination ability (see next section). This threatens the rejuvenation of such populations. In addition, small and isolated populations have a greater probability of genetic loss or genetic fixation, and may suffer from inbreeding depression (see next section).

Secondly, a reduction in the area of habitat patches increases the vulnerability of the conditions in the patches to external influences (Saunders *et al*. 1991). Smaller patches have a larger contact zone with their surroundings, relative to their inner area, than larger patches. Through this contact zone habitat patches are exposed to influences from their surroundings, which may include decreasing water tables, pollution, and eutrophication (Vos and Zonneveld 1993; Neitzke 1998, 2001; Bakker and Berendse 1999). Changed habitat patch conditions affect the survival, the colonization capacity, and the potential for gene flow of the populations in the habitat patches. Eventually, the external influences may change the conditions in habitat patches so much that they become unsuitable as habitat.

Reduced connectivity of habitat patches

For a plant species the functional connectivity (sensu Tischendorf and Fahrig 2000) of habitat patches is determined by the probability that i) patches not occupied by that species are colonized by populations of that species in other patches, and ii) there is gene flow between populations of that species in different patches. Habitat patches can be colonized by seed dispersal, followed by successful germination and establishment. Alternatively, habitat patches can be re-colonized by germination from a persistent seed bank, followed by successful establishment. Gene flow between populations in habitat patches is achieved by between-patch seed or pollen dispersal, followed by successful germination and establishment, or pollination. The functional connectivity of habitat patches is different for different species, even if they share the same habitat, because colonization and gene flow differ between species. From here on, we refer to ‘functional connectivity’ as ‘connectivity’.

Habitat fragmentation reduces the connectivity of habitat patches, because it increases the distance and/or presence of barriers between habitat patches. This reduces seed and pollen dispersal between patches. The reduction in seed and pollen dispersal is stronger when habitat fragmentation also decreases the area of habitat patches. Firstly, smaller and more isolated populations produce fewer seeds and pollen. In many species seed production is even reduced per individual (Fischer and Matthies 1998a; Groom 1998; Cunningham 2000; Kery *et al*. 2000), although this is generally not the case in self-compatible species (Mustajarvi *et al*. 2001). Secondly, such populations attract fewer seed and pollen dispersers (Groom 1998; Steffan-Dewenter and Tscharntke 1999; Santos *et al*. 1999). Thirdly, in many species the germinability of seeds is reduced in such populations due to inbreeding or negative maternal effects (Charlesworth and Charlesworth 1987; Menges 1991; Kahmen and Poschlod 2000).

A reduction in the connectivity of habitat patches decreases the long-term local and regional survival of species restricted to that habitat. A reduction in patch colonization disturbs the extinction-colonization balance in metapopulations, decreases migration and range expansion, and impedes the colonization of new or restored nature areas. A reduction in gene flow decreases the genetic variation within populations. In small and isolated populations the genetic variation may be further reduced by inbreeding, genetic fixation, or genetic loss (Vantreuren *et al*. 1991; Ellstrand and Elam 1993; Fischer and Matthies 1998b; Booy *et al*. 2000). This may reduce the survival probability of the populations by inbreeding depression (Charlesworth and Charlesworth 1987; Husband and Schemske 1996), fixation of deleterious alleles, or a reduced capacity to adapt to changing environmental conditions (Booy *et al*. 2000). These genetic effects may also change plant characteristics affecting seed and/or pollen dispersal, and reduce the connectivity further. In addition, reduced gene flow prevents 'rescue effects' in small populations (increases in population size and genetic variation due to successful seed and pollen dispersal) and increases their probability of extinction.

Fragmented habitat versus patchy habitat

All above-mentioned effects of habitat fragmentation reduce the regional survival of plant species restricted to habitat patches. This does not mean that habitat patchiness in general has negative consequences for species survival. Regional survival of species adapted to naturally patchy habitats benefits from a certain level of habitat patchiness. Isolation of patches reduces the spread of pests or pathogens between populations (Hess 1994, 1996; Grenfell and Harwood 1997). It also reduces the spatial synchronization of populations (Bjornstad *et al*. 1999; Koenig 1999; Kendall *et al*. 2000), and thereby reduces the vulnerability of regional species survival to environmental or demographic stochasticity. However, the fast rate, vast spatial extent, and sharp decrease in habitat area and connectivity of the current habitat fragmentation process prohibit adjustment to the new situation in most species. Thus, for most species the negative consequences of habitat fragmentation overrule the benefits of increased habitat patchiness.

CONNECTIVITY

This study focuses on the effects of habitat fragmentation on connectivity. Habitat fragmentation reduces the connectivity of habitat patches directly, because it increases the distance and/or presence of barriers between habitat patches. Habitat fragmentation can also affect the connectivity of habitat patches indirectly, by changing the colonization and/or gene flow characteristics of populations of the species that inhabit the habitat patches. On the other hand, the colonization and/or gene flow characteristics of a species determine how much impact habitat fragmentation has on the connectivity of habitat patches for that species. For example, if habitat fragmentation increases the average distance between habitat patches from 25 to 75 m, habitat connectivity is greatly reduced for a species with seed dispersal distances up to 50 m, somewhat reduced for a species with dispersal distances up to 1000 m, and not affected for a species with dispersal distances up to 2 m. The study of connectivity thus requires information on the spatial and temporal distribution of habitat area, on the colonization and/or gene flow characteristics of plant species, and on their interaction. This study focuses on the distribution of habitat area, plant species' colonization capacity, and the interaction between these two.

Habitat distribution

Both the spatial and temporal distribution of habitat area are important for connectivity. The spatial and temporal scales of the habitat area dynamics need to be related to the spatial and temporal scales of the relevant plant species processes to assess their effects on connectivity (Tischendorf and Fahrig 2000; Vos *et al*. 2001; Moilanen and Nieminen 2002). If habitat patches are more ephemeral, patch turnover rate relative to species' seed bank longevity becomes more important as determinant of connectivity. If the distribution of habitat patches is more temporally stable, the spatial configuration of the patches in relation to species' seed dispersal ability is a more important determinant of connectivity (Fahrig 1992; Keymer *et al*. 2000). When habitat fragmentation is concerned, the change in spatial habitat configuration in relation to species' seed dispersal ability is generally the most important determinant of connectivity.

Plant colonization capacity

The colonization capacity of plant species is determined primarily by their seed production, seed dispersal, and seed germination ability. If plants produce more seeds, disperse seeds over a wider range of distances, and/or disperse seeds with a higher germination ability, the probability of successful colonization increases. Seed bank longevity is of great importance for the re-colonization of previously occupied sites after an unfavorable period (Bakker *et al*. 1996; Bakker and Berendse 1999), but does not contribute to the colonization of previously unoccupied patches. Within connected habitat areas vegetative dispersal by clonal growth is a common and important mechanism for colonization of nearby sites (Cain and Damman 1997; Donohue *et al*. 2000), but for the colonization of discrete patches it is of little importance. The dispersal of vegetative plant parts may also play a role in colonization, but this is in specific cases only and not further discussed here.

1. Seed production and seed germination ability

Seed production and germination ability are plant traits that can relatively easily be quantified by measurements in the field or under controlled conditions. Differences in seed production and germinability contribute to different colonization strategies (*e.g.* Olff *et al*. 1994; Kelly and Sork 2002). The effects of many environmental conditions on seed production and germinability have been measured. Habitat fragmentation has been found to reduce seed production per individual in species in which outcrossing is normally high (Fischer and Matthies 1998a; Groom 1998; Cunningham 2000; Kery *et al*. 2000) and to reduce seed germination ability when population size becomes very small (Charlesworth and Charlesworth 1987; Menges 1991; Kahmen and Poschlod 2000). Changes in habitat patch conditions also affect seed production and germinability. For example, eutrophication initially increases nutrient availability for parent plants and generally increases seed production (Sugiyama and Bazzaz 1997; Bazzaz *et al*. 2000; Galloway 2001). Seed germination ability also commonly increases (Roach and Wulff

1987), but may also decrease in some species (Wulff and Bazzaz 1992; Galloway 2001). The net changes in seed production and germination in fragmented populations are dependent on the degree of fragmentation and its effect on the local conditions, and require further investigation.

2. Seed dispersal

Seed dispersal ability is a component of plant colonization capacity that is of major ecological importance for (meta-)population dynamics (Hamilton and May 1977; Venable and Brown 1993; Ezoe 1998; Levin and Muller-Landau 2000), recruitment and species diversity (Tilman 1994; Howe and Miriti 2000; Nathan and Muller-Landau 2000; Hubbell 2001), metapopulation survival (Hanski 1998; Brachet *et al*. 1999), migration of species under changing climatic conditions (Pitelka *et al*. 1997; Cain *et al*. 1998; Clark *et al*. 1998; Higgins and Richardson 1999), invasion biology (Shigesada *et al*. 1995; Higgins *et al*. 1996; Kot *et al*. 1996), and the success of nature restoration projects (Bakker *et al*. 1996; Bakker and Berendse 1999). Long-distance dispersal is considered a very important component of seed dispersal (above references; Cain *et al*. 2000; Nathan 2001a).

However, many of the findings on the importance of (long-distance) dispersal are based on theoretical studies and/or inspired by observational data. Observational data suggest that long-distance dispersal events occur in many species (Cain *et al*. 1998, 2000; Nathan 2001a). But it is extremely difficult to measure seed dispersal ability, especially long-distance dispersal ability (Cain *et al*. 2000; Nathan 2001b; Nathan *et al*. 2003). There are many different seed dispersal mechanisms (for overviews see Howe and Smallwood 1982; Van der Pijl 1982), and many species are dispersed by multiple mechanisms (Hughes *et al*. 1994). Typical long-distance dispersal mechanisms are dispersal by wind, by large mammals or birds, or by water. Many plant species have seeds with specific adaptations for long-distance dispersal by these mechanisms (Howe and Smallwood 1982; Van der Pijl 1982; Bouman *et al*. 2000). But even without specific adaptations, seeds may be dispersed over very long distances; *e.g.* in mud on animal hooves, or by humans (Poschlod and Bonn 1998). The longest measured seed dispersal distributions under natural conditions range from 80 m for heather seeds (Bullock and Clarke 2000) to 1600 m for tree seeds (Pickford in Greene and Johnson 1995). Future progress in the measurement of long-distance dispersal may come from genetic analyses (Ouborg *et al*. 1999; Cain *et al*. 2000).

Because of the difficulty in measuring long-distance seed dispersal, researchers have reverted to modeling approaches. These approaches range from fitting statistical functions to short- to intermediate-distance dispersal data (Ribbens *et al*. 1994; Clark *et al*. 1999), to simulations with mechanistic diffusion models (Okubo and Levin 1989; Andersen 1991) and mechanistic trajectory models (Andersen 1991; Greene and Johnson 1995; Nathan *et al*. 2002; Tackenberg 2003). The mechanistic models can simulate (relatively) long-distance dispersal, and allow researchers to simulate specific mechanisms and assess their effects on dispersal distances. Especially for wind dispersal this approach works well (Nathan *et al*. 2002; Tackenberg 2003; Tackenberg *et al*.

2003). Wind dispersal is one of the most common long-distance dispersal mechanisms (Van der Pijl 1982; Fenner 1985). It is an inanimate process and therefore presumably less complicated than long-distance dispersal by large mammals or birds. However, even for long-distance dispersal by wind there is still uncertainty regarding the optimal modeling approach and the exact processes that should be simulated. Further model development and analysis, as well as dispersal measurements, are required to increase our knowledge of the causes and consequences of long-distance seed dispersal.

AIMS AND OUTLINE OF THIS THESIS

The degree to which species are affected by habitat fragmentation depends for an important part on the reduction in habitat connectivity. To assess the consequences of habitat fragmentation for regional species survival and to ameliorate these consequences in the future, more detailed knowledge of the effects of habitat fragmentation on connectivity is required.

The aims of this study are:

- To provide detailed information on the mechanisms that determine the colonization capacity of plant species in fragmented landscapes, with special emphasis on the (long-distance) seed dispersal component of colonization capacity.
- To estimate the current and future colonization capacity of plant species in fragmented landscapes.
- To combine information on habitat fragmentation and plant colonization capacity to estimate the effects of habitat fragmentation on connectivity.
- To use this information to provide guidelines for the conservation of plant species in fragmented landscapes.

To achieve these aims within a single thesis study, one specific study system was selected as the focus of research: nutrient-poor semi-natural grasslands. These grasslands have become highly fragmented in north-west Europe and many other areas in the world. Their continuing loss and fragmentation, and the concomitant loss of endangered species and biodiversity, are reason for concern and advocated the selection of this system as subject of study. In grasslands, as in other early successional and open vegetation types, seed dispersal by wind is a common dispersal mechanism (Van der Pijl 1982; Fenner 1985; Cheplick 1998). Possibly, wind dispersal is now the most common long-distance dispersal mechanism, since dispersal by animals and by other mechanisms has been interrupted by landscape fragmentation and changes in land use (Poschlod and Bonn 1998). The importance of these grasslands for nature conservation, their current degree of fragmentation, their predominant seed dispersal mechanism, and their open and relatively homogeneous character all qualify these grasslands as an ideal system to study the colonization capacity of wind-dispersed grassland plants in fragmented habitats.

Chapter 2

Habitat fragmentation reduces the connectivity of habitat patches, because it increases the distance and/or presence of barriers between habitat patches. In addition, the consequences of habitat fragmentation may change the colonization characteristics of plant populations in habitat patches. This may further reduce the connectivity. In Chapter 2 this effect is investigated in four wind-dispersed grassland plant species. The effects of habitat fragmentation on three components of plant colonization capacity, *i.e.* seed production, seed dispersal characteristics, and seed germination ability, are quantified.

Chapter 3

The component of plant colonization capacity that is most difficult to quantify is long-distance seed dispersal. Measurement of long-distance seed dispersal is extremely difficult. Simulation of dispersal with a mechanistic model is the best approach currently available for the quantification of dispersal distances under different conditions. However, existing models have not led to agreement regarding the optimal modeling approach and the key processes required for simulating long-distance seed dispersal. In Chapter 3 mechanistic models and field data are used to assess which aspects of wind flow and which plant and vegetation characteristics are required for realistic simulation of long-distance seed dispersal by wind in grasslands. The effects of these wind, plant, and vegetation characteristics on seed dispersal distances are assessed.

Chapter 4

The most important disturbances of (semi-)natural grasslands in the future are expected to include habitat fragmentation, eutrophication, and anthropogenically induced rapid climate change. These disturbances are likely to affect the colonization capacity of plant species. In Chapter 4 the effects of these disturbances on the colonization capacity of wind-dispersed grassland plant species are estimated. The dispersal characteristics that are quantified in Chapter 2 (and information on potential effects of climate change) are used as input data in a mechanistic dispersal model that was presented in Chapter 3. The resulting dispersal data are combined with data on seed production and germination ability from Chapter 2 to estimate colonization capacity.

Chapter 5

To estimate the effects of habitat fragmentation on connectivity, estimates of habitat fragmentation and plant colonization capacity need to be combined. In Chapter 5 the habitat fragmentation of nutrient-poor semi-natural grasslands during the last century is reconstructed. Based on habitat maps, the rate and spatial pattern of habitat fragmentation are quantified. This information is combined with estimates of plant colonization capacity that were calculated using a mechanistic dispersal model presented in Chapter 3. From this information the change in habitat connectivity and the current habitat connectivity are quantified for wind-dispersed grassland plants.

Chapter 6

In Chapter 6 the results of the previous chapters are summarized. The information on colonization capacity and habitat fragmentation from the previous chapters is used to suggest management strategies for the regional conservation of wind-dispersed plant species restricted to nutrient-poor grassland fragments. Given the focus of this study, these strategies mainly concern improvement of connectivity. The chapter is concluded with perspectives for future research.

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2. Reduced colonization capacity in fragmented populations of wind-dispersed grassland forbs

M.B. Soons and G.W. Heil

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SUMMARY

1. Habitat fragmentation as a result of intensification of agricultural practices decreases the population size and increases the site productivity of remnant populations of many plant species native to nutrient-poor, species-rich grasslands. Little is known about how this affects the colonization capacity of populations, which is highly important for regional species survival. We studied the effects on four wind-dispersed forbs that represent two major dispersal strategies in grasslands: *Cirsium dissectum* and *Hypochaeris radicata*, which have plumed seeds and are adapted to long-distance dispersal by wind, and *Centaurea jacea* and *Succisa pratensis*, which have plumeless seeds and are adapted to only short-distance dispersal by wind.

2. Colonization capacity decreased with decreasing population size. This was due to lower seed germination ability in all species, and a lower seed production and a narrower range of seed dispersal distances in the species with plumed seeds. Inbreeding depression is the most likely cause of this. We found no evidence for a stronger selection for reduced dispersal in smaller populations.

3. Increasing site productivity changed the colonization capacity of all species. The capacity for colonization of nearby sites increased, due to higher seed production and seed germination ability, but the capacity for colonization of distant sites decreased, due to a lower long-distance dispersal ability.

4. Seed dispersal ability and germination ability were negatively correlated in the species with plumeless seeds, but not in the species with plumed seeds. The dispersal ability of individual plumed seeds remained constant under changes in population size and site productivity. This indicates a strong selection pressure for long-distance dispersal ability in these species.

5. When habitat fragmentation results in a simultaneous decrease in population size and increase in site productivity, both the local survival probability and the colonization capacity of remnant populations of wind-dispersed grassland forbs are likely to be severely reduced. This increases regional extinction risks of the species.

Keywords: germination, habitat fragmentation, population size, seed production, site productivity, wind dispersal

INTRODUCTION

Nutrient-poor, species-rich grasslands in north-west Europe are becoming highly fragmented due to the intensification of agricultural practices (Vos and Zonneveld 1993; Bakker and Berendse 1999). As a result, populations of plant species that are restricted to this habitat are becoming ever smaller and more isolated and consequently their extinction probabilities rise (Ellstrand and Elam 1993; Ouborg 1993). Habitat fragmentation also increases the extinction probabilities of these populations indirectly by decreasing the quality of the remaining habitat patches: as the patches become smaller and more isolated, they become more vulnerable to influences from the surrounding agricultural landscape (*e.g.* Neitzke 2001). This primarily results in a higher productivity due to an increased inflow of nutrients (Bakker and Berendse 1999), often accompanied by acidification and lowering of the water table (Vos and Zonneveld 1993).

Despite the increasing extinction risks of local populations, a species may survive regionally if there is sufficient colonization of unoccupied habitat patches (Van der Meijden *et al*. 1992; Ouborg 1993; Husband and Barrett 1996). Little is known however, about the effects of decreasing population size and increasing site productivity on the colonization capacity of isolated remnant populations. We define colonization capacity of a population as the capacity to establish seedlings at suitable sites not occupied by individuals from that population. Whilst re-colonization from the seed bank also plays an important role in this capacity (Bakker *et al*. 1996; Strykstra *et al*. 1998a), this study focuses only on colonization through spatial seed dispersal. This colonization capacity is determined by seed production, dispersal ability and germination ability.

Decreasing population size and increasing site productivity appear to have opposite effects on both seed production and germination ability. It has been found that seed production per individual was lower in small fragmented populations than in large populations (Kery *et al*. 2000; Fischer and Matthies 1998a), due to inbreeding depression (Charlesworth and Charlesworth 1987; Fischer and Matthies 1998b) or reduced pollination (Cunningham 2000; Groom 2001; Moody-Weis and Heywood 2001). In small fragmented populations, the germination ability of seeds may also be reduced by inbreeding depression (Charlesworth and Charlesworth 1987), or by maternal environmental effects (Kahmen and Poschlod 2000). In contrast, increasing site productivity has been shown to result in larger plants that produce more and heavier seeds (Sugiyama and Bazzaz 1997; Bazzaz *et al*. 2000; Galloway 2001) with higher germinability (Roach and Wulff 1987).

The effects on dispersal ability are, however, less clear. Wind is the main dispersal agent in early successional vegetation types such as grasslands (Fenner 1985; Van der Pijl 1982). Because long-distance dispersal is a very important aspect of dispersal ability, but almost impossible to measure (Bullock and Clarke 2000; Cain *et al*. 2000), various mechanistic models have been developed that predict wind dispersal from physical laws (*e.g.* Okubo and Levin 1989; Andersen 1991; Nathan *et al*. 2002a, 2002b; Tackenberg 2003). These models describe the flight of seeds based on seed, plant, vegetation and wind characteristics. The plant-controlled characteristics that determine wind dispersal distance are seed terminal velocity (v_t) and seed release height. Release height is only relevant, however, when the seed is released above the directly surrounding vegetation (Sheldon and Burrows 1973) and above the height at which horizontal wind speed is zero. We therefore use relative seed release height (H_{rel}, the difference between seed release height and the height at which wind speed is zero) as the second plant-controlled dispersal parameter.

Decreased population size and increased site productivity might be expected to have a negative impact on dispersal ability. First, it has been suggested that isolated populations experience selection for reduced dispersal ability, as only seeds that disperse nearby contribute to the genetic pool (Carlquist 1966). In small populations such selection would be stronger than in large populations. Cody and Overton (1996) found measurable effects of selection for reduced dispersal in small isolated populations after less than six plant generations; these effects consisted of changes in seed traits that determine v_t. Secondly, in small fragmented populations genetic drift may reduce the variation in plant traits (Ellstrand and Elam 1993; Booy *et al*. 2000). If the variation in traits that determine v_t is reduced, this results in a narrower range of dispersal distances (Augspurger and Franson 1993), and thus lower dispersal ability. Thirdly, if plants at more productive sites produce heavier seeds, their wind dispersal ability may be lower, as heavier seeds are likely to have a higher v_t (*e.g.* Greene and Johnson 1993). In addition, wind dispersal may be hampered by tall vegetation at a productive site if the flowering stalks are shorter than the surrounding vegetation, *i.e.* H_{rel} is low.

Effects on seed production, dispersal ability and germination ability are not independent of each other. In particular, changes in dispersal and germination ability may be correlated: lighter seeds are better dispersed by wind but have a lower germination ability in *Arnica montana* (Strykstra *et al*. 1998b). So far, the mechanisms by which changes in seed production, dispersal and germination ability influence each other remain unknown, as the three have not been studied together. Furthermore, the effects of decreasing population size and increasing site productivity on seed dispersal ability have not been studied, and differences between species with different dispersal strategies are unknown. The purpose of this study is to fill in these gaps and to clarify the effects on the colonization capacity of fragmented populations. We studied isolated remnant populations of grassland forbs with two different wind-dispersal strategies, *i.e.* long-distance and short-distance seed dispersal. Specifically, we addressed the following questions:

- Does a decrease in population size reduce colonization capacity by decreasing the number of viable seeds produced per plant, variation in v_t of the seeds, and/or germination ability of the seeds?
- Does a decrease in population size result in stronger selection for reduced dispersal, so that smaller populations have lower H_{rel} and/or higher seed v_t ?
- Does an increase in site productivity change colonization capacity by increasing the number of viable seeds produced per plant, decreasing H_{rel}, and/or increasing v_t and germination ability of the seeds?

- Do seeds with a higher ability for long-distance dispersal due to a lower v_t have a lower germination ability?

METHODS

Study species

Four wind-dispersed grassland forbs confined to nutrient-poor, species-rich grasslands were selected as study species. All species are outcrossing (Grime *et al*. 1988; Smulders *et al*. 2000) and were common in The Netherlands before the rapid fragmentation and destruction of their habitat. Two of the study species, *Cirsium dissectum* (L.) Hill and *Hypochaeris radicata* L. (both *Asteraceae*), have plumed seeds and are adapted to long-distance dispersal by wind (Fig. 1). The other two study species, *Centaurea jacea* L. (*Asteraceae*) and *Succisa pratensis* Moench (*Dipsacaceae*), are also classified as wind-dispersed, but have plumeless seeds that are dispersed by wind only over short distances. The plumeless, smooth-surfaced seeds of *C. jacea* (Fig. 1) are ejected from the seed head, and transported further by wind, when strong winds fling the seed head back and forth (Bouman *et al*. 2000). Seeds of *S. pratensis* are surrounded by a persistent calyx (Fig. 1), which is dry and hairy and increases the surface area of the seed without adding much weight (Bouman *et al*. 2000).

All four species are hemicryptophytes that overwinter as leaf rosettes (Van der Meijden 1990; Grime *et al*. 1988). In summer they produce long flowering stalks that (at least under nutrient-poor conditions) protrude from the surrounding vegetation. Rosettes of *C. dissectum* produce one flowering stalk that carries one, rarely two, flower heads. Rosettes of the other species may produce multiple branched stalks, with various numbers of flower heads. All species propagate both sexually via seeds and asexually by side-rosettes and clonal extension (especially *C. dissectum*). *C. dissectum*, *S. pratensis* and *C. jacea* are long-lived species, while individuals of *H. radicata* live for a decade at most. All species have transient seed banks (Thompson *et al*. 1997).

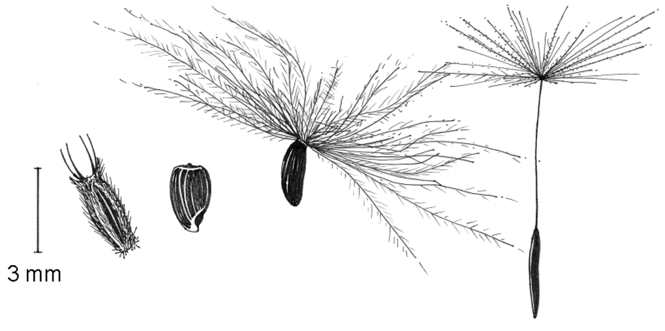

Figure 1. Seeds of (from left to right) *S. pratensis*, *C. jacea*, *C. dissectum* and *H. radicata*.

Collection of field data and sampling

Ten fragmented populations, representative of the full range of population sizes and site productivities in the Pleistocene soil areas in The Netherlands, were selected for each species. Effective population size was determined by counting the number of flowering rosettes. Productivity was assessed by clipping three vegetation plots of 20x20 cm in or, in the case of very small populations, close to the population. The vegetation samples were dried in a stove for three days at 75°C, and dry weight was averaged for each site. Although a decrease in population size and an increase in site productivity co-occur in many populations, we took care to select populations so that size and productivity were not correlated (Fig. 2). For *S. pratensis* site productivity of two populations could only be estimated and these populations were discarded from statistical analyses of site

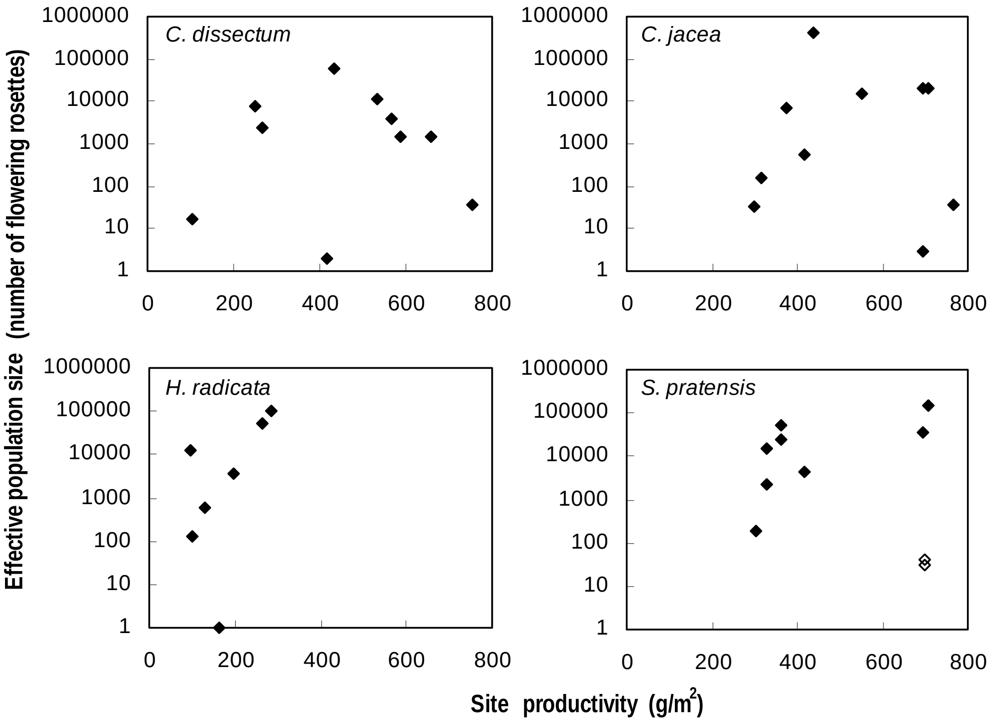

Figure 2. Population size plotted against site productivity of the selected populations. Open symbols in the graph of *S. pratensis* represent estimated, instead of measured, values of site productivity; these data points were excluded from analyses on site productivities. Pearson correlation coefficients are not significant: *C. dissectum* (0.081, p=0.823), *H. radicata* (0.519, p=0.233), *C. jacea* (-0.044, p=0.904), *S. pratensis* (-0.168, p=0.642). When the data points with estimated productivities are left out of the analysis for *S. pratensis*, Spearman's rho is however significant (0.714, p=0.047). No significant quadratic relationships were found.

productivity effects; the remaining eight populations, however, showed a correlation between size and productivity (Fig. 2). This has been taken into account during interpretation of the data on productivity effects. All selected populations have the same management regime of mowing once per year in autumn. The selected *C. dissectum* and *S. pratensis* populations have been isolated from populations of conspecifics by more than one km for over 50 and 25 years, respectively; populations of *C. jacea* and *H. radicata* have been isolated for *ca.* 25 years by more than 500 m and 100 m, respectively (Soons *et al*, unpublished data). All selected *H. radicata* populations are also isolated by forest landscape elements that act as a barrier to seed and pollen transport. As this species is still quite common in the study area however, only seven isolated populations of different sizes were found.

In each population, 10 plants with intact seed heads containing mature seeds were selected randomly for measuring seed production, H_{rel}, and v_t. In populations with less than 10 individuals, all individuals were measured. Seed production was measured by counting the number of seed heads per flowering stem and the number of viable seeds in the first produced (top) seed head. All filled seeds were assumed to be viable. In case of doubt, seed weight was used to determine viability: a previous germination experiment showed that filled seeds of all weights of *H. radicata* and *S. pratensis* could be viable, but partially filled seeds of *C. jacea* and *C. dissectum* with seed weights below 1 and 2 mg, respectively, were never viable. Seeds of these species that appeared (partially) filled but weighed less than this were discarded. The number of seed heads per stem and the number of viable seeds in the first seed head provide good estimates to compare seed production between individuals within a species. Total seed production per individual can however not be calculated from this in *H. radicata*, *C. jacea* or *S. pratensis*, because seed heads lower along the stem produce fewer seeds and stem number is also important. Stem number was not measured as it was impossible to determine non-destructively which rosettes (and thus stems) belong to one individual. H_{rel} was calculated as the height above the soil surface of the first produced seed head, minus the height at which horizontal wind speed is zero (approximately 0.74 times the vegetation height; Monteith 1973). Average vegetation height (excluding emerging flowering stalks) was estimated visually and measured with a ruler.

Determining terminal velocities

Experimental determination of v_t of many seeds is time-consuming and therefore v_t of the seeds was calculated using the mechanistic relationship (Burrows 1973):

$$v_t = \frac{\sqrt{M}}{D} \cdot \sqrt{\frac{g}{\frac{1}{8} \cdot \pi \cdot \rho_a \cdot C_d}} \qquad (1)$$

Where M is seed mass, D is seed diameter, g is the gravitational acceleration, ρ_a is the density of air, and C_d is the aerodynamic shape constant of the seed. Although seed shape within species is somewhat variable, it is assumed that under average conditions it varies relatively little. Therefore, C_d may be considered a species-specific constant (Burrows 1975), and the second term of equation 1 becomes a constant that was determined experimentally by measuring v_t, M, and D of a subset of the seeds. Values of v_t of the other seeds were calculated from their M, D, and this constant. Although beak length of the seeds of *H. radicata* is also variable, it does not affect v_t (Cody and Overton 1996).

Eight seeds per collected seed head (*i.e.* 800 per species) were selected randomly for measurements of M and D. The selected seeds were weighed using Sartorius Ultramicro scales. For the plumed seeds D was measured as the maximal diameter of the completely opened plume. For *C. jacea* the maximum diameter of the seed coat was measured, and for *S. pratensis* the maximum diameter of the seed including the calyx was measured. Sliding callipers (accuracy 0.05 mm) were used for all diameter measurements.

One hundred seeds per species (25 for *H. radicata*) were selected randomly for v_t measurements; in the case of plumed seeds, only seeds with open and intact plumes were selected. The v_t of the plumed seeds was measured by dropping the seeds over 2 m in still air inside a hardboard and Plexiglas shaft (*cf.* Andersen 1992; Cody and Overton 1996). Drop time was measured manually using a digital stopwatch (accuracy 0.01 s) and averaged over three falls per seed. Plumeless seeds were dropped down a 15.83-m shaft with mechanical drop time measurements (Jongejans and Schippers 1999). Because this shaft was made of thick plastic foil it was not entirely resistant to air movements and the air inside the shaft was not perfectly still. This reduced the high precision of the measurements, mainly because horizontal air movement caused some *S. pratensis* seeds to touch the inner side of the tower, thereby disrupting their fall. Values of v_t were calculated from drop time (T) and drop height (H) using a numerical solution of the equation describing T as a function of h and v_t, including the acceleration phase of the fall (*cf.* Burrows 1975):

$$T = \frac{v_t}{g} \cdot \operatorname{arccosh}\left(\mathrm{e}^{H \cdot g / v_t^2}\right) \tag{2}$$

v_t values of all eight seeds selected per seed head were calculated using equation 1. Both per plant and per population the variation in v_t was calculated as the coefficient of variation of v_t values, with CV=(s.d./mean)*100. The CVs calculated per plant were averaged per population, so for each population the averaged individual CV and the overall population CV are known.

The germination experiment

Four seeds per individual (*i.e.* 400 per species) were randomly selected for the greenhouse germination experiment. Seeds of *C. jacea, C. dissectum,* and *H. radicata* were air dried and stored in plastic pots in the dark at 4˚C for four months. Seeds of *S. pratensis* were stored similarly but at room temperature (ca. 18˚C), as storage at low temperatures has been found to reduce germination ability (Kotorová and Leps 1999). Seeds were put to germinate on steamed, moist sand at 21 ˚C, under a light/dark regime of 16/8 hrs and high air humidity (>90%). A seed was classified as germinated when the radicle was visible. Germination was followed for 10 weeks and scored twice per week.

Statistical analysis

All statistical analyses were conducted using SPSS 8.0. Significances of the species-specific relationships between seed v_t and M and D were tested using linear regression analysis. Log-transformed population size was used in all analyses on population size effects. The effects of population size and site productivity on the number of viable seeds, H_{rel}, v_t, the variation in v_t, and the average time to germination of the seeds were also determined by linear regression analyses. We tested whether effects were equal for both species representing the same dispersal strategy (long-distance or short-distance

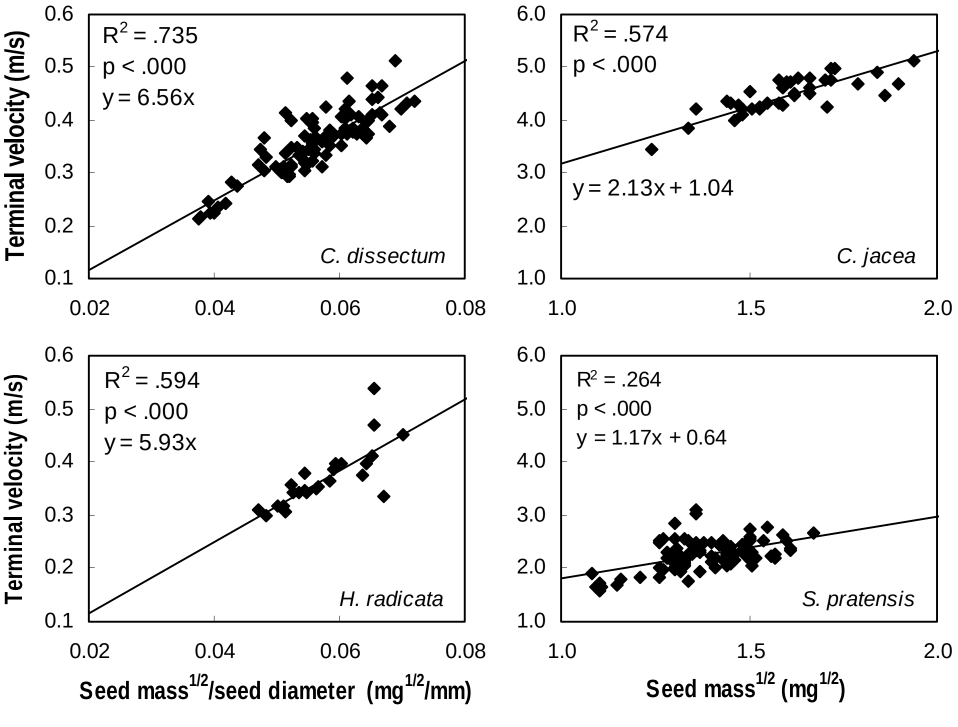

Figure 3. Relationships between terminal velocity and $\sqrt{M}/D$ (for the species with plumed seeds, *C. dissectum* and *H. radicata*) or $\sqrt{M}$ (for the species with plumeless seeds, *C. jacea* and *S. pratensis*). For the species with plumed seeds the constant in the equation is not statistically different from zero at the 0.05 significance level.

wind dispersal) by calculating the significance of a regression model that includes both species:

$$y = \beta_0 + \beta_1 * species + \beta_2 * x + \beta_3 * species * x \tag{3}$$

Where y is the dependent variable, *species* is a dummy variable, and x is the independent variable. When β_3 is not significant, the two species do not have significantly different regression coefficients. In these cases, a regression analysis excluding the last term in equation 3 was carried out to determine the regression coefficient β_2 and model statistics p and R^2. If there was no significant effect of population size or productivity for both species, but the data indicated a species-specific effect in one of the species, a linear regression analyses was carried out to test significance of that effect. Effects of log-transformed population size and site productivity on seed germination were tested for significance with a logistic regression analysis with Nagelkerke's R^2 value as indicator of the explained variation (Nagelkerke 1991).

RESULTS

Determining terminal velocities

For the plumed seeds, the relationship between v_t and $\sqrt{M/D}$ is exactly as described in equation 1, *i.e.* positive, linear and passing through the origin (Fig. 3). For the plumeless seeds, however, v_t is explained better by $\sqrt{M}$ than by $\sqrt{M/D}$ (*C. jacea* $R^2=0.574$, $p<0.001$ vs. $R^2=0.325$, $p<0.001$; *S. pratensis* $R^2=0.264$, $p<0.001$ vs. $R^2=0.247$, $p<0.001$) and $\sqrt{M}$ was therefore used to estimate v_t for these seeds. In spite of a positive intercept at the y-axis, $\sqrt{M}$ predicts v_t of the plumeless seeds adequately (Fig. 3), even for *S. pratensis*, where the relationship is much weaker due to lower accuracy of v_t measurements (see *Methods*). For all species, the relationship that predicts v_t best is linear. This shows that C_d can be considered a species-specific constant and justifies the assumption that v_t can be estimated as a linear function of $\sqrt{M/D}$ or $\sqrt{M}$.

Seed production

Average seed production statistics per species are presented in Table 1. The expected decrease in seed production with decreasing population size was found in the species with plumed seeds, due to lower numbers of viable seeds per seed head (Table 2). The species with plumeless seeds did not produce fewer seeds, and smaller populations of *S. pratensis* even had more heads per stem (Table 2).

The expected increase in seed production with increasing site productivity was significant in the species with plumeless seeds (Table 2), while the species with plumed seeds only showed a non-significant trend in this direction. Populations at more productive sites produced more seeds in all species, but due to the very slight increases

Table 1. Average values of colonization capacity parameters (species mean ± std.dev). N_{heads} = number of seed heads per stem, N_{viable} = number of viable seeds in the first seed head, H_{rel} = relative seed release height, v_t = calculated seed terminal velocity, pop CV v_t = variation in v_t per population, ind CV v_t = variation in v_t per individual.

Species	N_{heads}	N_{viable}	H_{rel} (cm)
With plumed seeds			
C. dissectum	1	24.69±16.00	9.31±21.49
H. radicata	2.88±2.31	54.59±22.42	5.20±16.23
With plumeless seeds			
C. jacea	5.69±7.57	31.72±10.91	5.98±19.26
S. pratensis	4.59±3.45	44.40±23.04	24.87±21.08

Species	v_t (m/s)	Pop. CV v_t	Ind. CV v_t	Germination (%)
With plumed seeds				
C. dissectum	0.380±0.036	7.23±1.72	5.19±1.33	52.1
H. radicata	0.335±0.039	10.08±2.65	6.97±2.90	61.4
With plumeless seeds				
C. jacea	4.33±0.44	8.38±2.07	5.47±3.25	85.1
S. pratensis	2.14±0.18	7.15±1.44	3.77±2.22	19.4

in number of seed heads per stem and number of seeds per head in *C. dissectum*, overall relationships with increasing productivity were not significant for the species with plumed seeds. In the species with plumeless seeds, plants at more productive sites produced significantly more heads per stem in *C. jacea* and significantly more seeds per head in *S. pratensis* (Table 2).

Dispersal ability

Average values of H_{rel}, v_t and the variation in v_t are presented in Table 1 (v_t values calculated using equation 1). Average seed v_t shows the greatest variation between species: almost tenfold instead of two- to fivefold for other characteristics. The averaged individual CV of v_t was always lower than its population CV.

We found no evidence for stronger selection for reduced dispersal ability in smaller populations than in larger populations. H_{rel} did not decrease with decreasing population size in any of the species (and, in *H. radicata*, H_{rel} was even significantly higher in smaller populations; Table 2), nor did v_t increase. In the species with plumeless seeds there was even a significant positive relationship between v_t and population size, due to a decrease in seed mass with decreasing population size (Table 2). The plumed seeds also decreased in seed mass with decreasing population size, but this relationship was not significant (β=5.77·10^{-2}, p=0.142, R^2=0.972) and it did not affect v_t as it was balanced by increased seed diameters. The variation in v_t decreased with decreasing population size in the species with plumed seeds, but increased in the species with plumeless seeds (Table 2). Thus, in contrast to our expectations, it appears that in the species with plumed seeds dispersal ability is lower in smaller populations, due only to a reduced variation in v_t, whereas in the species with plumeless seeds dispersal ability is higher in smaller populations, due to both a lower v_t and a higher variation in v_t.

Populations at more productive sites had a lower H_{rel}, as expected, though this was only significant in the species with plumed seeds (Table 2). In the species with plumed seeds no relationship between v_t and site productivity was found, but, in the species with plumeless seeds, $\mathrm{v_t}$ increased with increasing site productivity, mainly due to the significant increase in their seed mass (Table 2). The plumed seeds increased in seed mass as well, but this again was not significant (β=4.08A10^{-4}, p=0.182, R^2=0.971)

Table 2. Regression coefficients (β) and model statistics (p and R^2) of the regressions of plant variables on log-transformed population size and site productivity. Relationships valid for both species sharing the same dispersal strategy are shown, as well as species-specific relationships when present (denoted by *Cj* for *C. jacea*, *Hr* for *H. radicata*, *Sp* for *S. pratensis*). N_{heads} = number of seed heads per flowering stalk, N_{viable} = number of viable seeds in the first seed head, H_{rel} = relative seed release height (cm), v_t = seed terminal velocity (m/s), M = seed mass (mg). Pop CV is the coefficient of variation per population, ind CV is per individual. The regression analysis of germination percentage on population size showed no differences between the two dispersal strategies and regression statistics were calculated for all species together. [ ] Indicates a marginally significant relationship (0.050< p≤ 0.070).

Variable	β log-transformed population size	
	Plumed seeds	Plumeless seeds
N_{heads}	n.s.	*Sp*: -1.85 (p= .004; R^2=.719)
N_{viable}	6.68 (p=.007; R^2=.505)	n.s.
H_{rel}	*Hr*: -8.57 (p=.007; R^2=.794)	n.s.
v_t	n.s.	$5.96 \cdot 10^{-2}$ (p=.000; R^2=.976)
Pop. CV v_t	1.12 (p=.013; R^2=.366)	-0.804 (p=.030; R^2=.236)
Ind. CV v_t	*Hr*: 1.42 (p=.014; R^2=.811)	-1.03 (p=.007; R^2=.339)
M	n.s.	$9.56 \cdot 10^{-2}$ (p=.000; R^2=.703)
Pop. CV M	[3.46 (p=.062; R^2=.277)]	-1.44 (p=.046; R^2=.204)
Ind. CV M	[0.694 (p=.063; R^2=.226)]	-1.78 (p=.003; R^2=.497)
% Germination	4.22 (p=.000; R^2=.767)	4.22 (p=.000; R^2=.767)

Variable	β site productivity	
	Plumed seeds	Plumeless seeds
N_{heads}	n.s.	[*Cj*: $2.19 \cdot 10^{-2}$ (p=.054; R^2=.353)]
N_{viable}	n.s.	*Sp*: $8.63 \cdot 10^{-2}$ (p= .011; R^2=.690)
H_{rel}	$-8.57 \cdot 10^{-2}$ (p=.002; R^2=.583)	n.s.
v_t	n.s.	$8.29 \cdot 10^{-4}$ (p=.000; R^2=.983)
Pop. CV v_t	n.s.	n.s.
Ind. CV v_t	n.s.	n.s.
M	n.s.	$1.35 \cdot 10^{-3}$ (p=.000; R^2=.805)
Pop. CV M	n.s.	n.s.
Ind. CV M	$7.17 \cdot 10^{-3}$ (p=.030; R^2=.417)	n.s.
% Germination	$-5.42 \cdot 10^{-2}$ (p=.000; R^2=.725)	$2.34 \cdot 10^{-2}$ (p=.000; R^2=.725)

Table 3. Statistics of the logistic regression of germination status (germinated or not germinated) on the seed variable $\sqrt{M/D}$ (for the species with plumed seeds) or $\sqrt{M}$ (for the species with plumeless seeds).

Species	Nagelkerke's R^2	p	df	β	S.E.
Species with plumed seeds					
C. dissectum	.000	.883	1	3.033	20.66
H. radicata	.003	.472	1	14.65	20.35
Species with plumeless seeds					
C. jacea	.395	.000	1	7.989	1.066
S. pratensis	.039	.003	1	2.522	0.833

and did not result in an increase in v_t, as it was compensated for by increased plume diameters. Site productivity did not affect variation in v_t (Table 2). Thus, an increase in site productivity only decreased the v_t of plumeless seeds, not of plumed seeds.

Germination ability

As expected, seed germination decreased with decreasing population size in all species (Table 2). Germination of the plumeless seeds increased with increasing site productivity, as expected, but germination of the plumed seeds was lower at more productive sites (Table 2). The latter was due entirely to the strong decrease in germination in *C. dissectum*, however; *H. radicata* showed a slight increase, just like the species with plumeless seeds. Time to germination was not affected by population size or site productivity.

For the plumeless seeds a positive relationship between germination and individual seed $\sqrt{M}$, and thus v_t, was found (Table 3). No relationship between germination and $\sqrt{M/D}$, and thus v_t, was found for the plumed seeds. The hypothesis that seeds with a higher long-distance dispersal ability due to a lower v_t value have a lower germination ability, was thus supported by the data on the plumeless seeds only.

DISCUSSION

Determining terminal velocities

The mechanistic model used in this study to calculate v_t from $\sqrt{M/D}$ provides a simple and accurate method for determining v_t values of large quantities of plumed seeds of the same species. For plumeless seeds, the method is even simpler as just $\sqrt{M}$ predicts v_t accurately, though the fit between $\sqrt{M}$ and v_t is low in *S. pratensis*, which is at least partly explained by the lower precision of measurements of v_t. The model used in this study relates seed mass, diameter and terminal velocity to each other in a mechanistic

Table 4. Expected and observed relationships between colonization capacity variables and population size or site productivity. Observed relationships indicated per seed dispersal strategy. Species-specific relationships are indicated by *Hr* (*H. radicata*) or *Sp* (*S. pratensis*). O = no relationship; + = positive relationship ($p \leq 0.050$); - = negative relationship ($p \leq 0.050$).

Variable	Population size			Site productivity		
	Expected	Observed		Expected	Observed	
		Plumed	Plumeless		Plumed	Plumeless
Number of viable seeds	+	+	- (*Sp*)	+	**o**	+
Relative release height (H_{rel})	+	- (*Hr*)	**o**	-	-	**o**
Terminal velocity (v_t)	-	**o**	+	+	**o**	+
Variation in terminal velocity ($CV\ v_t$)	+	+	-	**o**	**o**	**o**
Germination	+	+	+	+	-	+

way and is therefore not only a useful tool to derive terminal velocity values of large quantities of seeds, but also explains the relationships between seed characteristics.

A decrease in population size reduces the colonization capacity

A decrease in population size affects the species with plumed seeds and the species with plumeless seeds differently. The lower values for seed production, dispersal ability (due to lower variation in v_t) and germination ability in smaller populations of species with plumed seeds are as expected from the literature (Table 4). The lower seed production may have been caused by inbreeding depression and/or pollination limitation as both have been demonstrated to occur in fragmented forb populations (Fischer and Matthies 1998b; Groom 2001; Moody-Weis and Heywood 2001). Inbreeding may likely have contributed to this, as it may also explain the lower seed germination ability of all species. For *H. radicata* and *S. pratensis* it has been demonstrated that inbreeding results in lower seed germinability (C. Mix, unpublished data). The selected species are all outcrossing and have become severely fragmented over a relatively short time period, so they may be especially susceptible to inbreeding depression (Husband and Schemske 1996; Booy *et al*. 2000). The lower variation in v_t in the species with plumed seeds may be due to genetic drift (Ellstrand and Elam 1993; Booy *et al*. 2000). This is in agreement with another study on the *S. pratensis* populations that documents lower allozyme variation in smaller populations (P. Vergeer, unpublished data). These results suggest that the isolation levels of the selected populations are sufficient to affect their genetic composition, even though low rates of pollen and seed flow may still occur.

In the species with plumeless seeds, smaller populations had a lower seed germinability but, in contrast to expectation, smaller populations of *S. pratensis* produced more seeds and smaller populations of both species had seeds with a lower average v_t and a larger variation in v_t (Table 4). The increase in variation in v_t and the decrease of average v_t values are both due to the production of increasing numbers of low quality seeds with low seed mass and, thus, low v_t. This is likely to be another effect of inbreeding depression, and may be the direct cause of the lower germinability of the seeds. Such a change in v_t is not observed in the species with plumed seeds, as plumed seeds with a lower seed mass also have a smaller plume diameter, and v_t remains constant. Thus, the long-distance dispersal ability of individual plumed seeds remains unaffected. The data suggest that plumeless seeds from smaller populations have a higher dispersal ability. However, in the species with plumeless seeds, a strong positive correlation between v_t and germinability of individual seeds was found. Because of this relationship, the decrease in v_t and the increase in variation in v_t hardly increase the dispersal ability of the seeds, as the seeds that disperse furthest are the ones least likely to germinate.

Overall, therefore, the colonization capacity of all four wind-dispersed grassland forbs is reduced by a decrease in population size, with the lower seed production and seed germinability also reducing local recruitment to the population and the (transient) seed bank.

No short-term evolution of reduced long-distance dispersal

No support for the hypothesis that selection pressure for reduced dispersal is more effective in smaller populations was found for any species (Table 4). Cody and Overton (1996) found evidence of selection for reduced dispersal in wind-dispersed species after just up to 6 generations of isolation, but in this study no indication of such selection was found at all. For *C. dissectum*, *S. pratensis* and *C. jacea* the time of isolation spanned only a few plant generations, and may be too short for such a selection pressure to have had a measurable effect, but populations of *H. radicata* have been isolated for up to 12 generations. Possibly, the isolation levels of the remnant populations may not have been high enough to prevent gene flow sufficiently, particularly in *H. radicata*. Although both seed dispersal by wind and pollen dispersal by insects over distances of more than 100 m are rare, the occurrence of low rates of gene flow may explain the lack of evidence for selection against dispersal. The isolation levels did however appear to be sufficient to affect the genetic composition of small populations.

An increase in site productivity changes the colonization capacity

The effects of an increase in site productivity were mostly as expected (Table 4). In the species with plumed seeds, however, the strong decrease in germination ability of *C. dissectum* seeds resulted in an overall significant negative relationship between site productivity and seed germination ability, despite *H. radicata* showing the expected positive relationship. Other studies on effects of maternal site productivity on germinability yielded ambiguous results. In most cases, an increase in site productivity resulted in larger plants with more reproductive output (Bazzaz *et al*. 2000) and higher seed germinability (Roach and Wulff 1987). Nevertheless, plants may also produce seeds with a lower germinability when their nutrient availability is increased (Wulff and

Bazzaz 1992; Galloway 2001). This has been attributed to a relatively larger allocation to the seed coat than to endosperm and embryo, but if this is the case, also time to germination is generally longer (Galloway 2001). This was not found in *C. dissectum*, where lower seed quality is a more likely cause for the decrease in germination.

In one important aspect the effect of an increase in site productivity is not as expected: v_t increased with increasing productivity for plumeless but not for plumed seeds (Table 4). The significant increase in v_t of the plumeless seeds is due to the increase in seed mass, which is also reflected in the increase in germination ability. The v_t of the plumed seeds is not affected, because the increase in seed mass is proportional to the increase in plume diameter.

Overall, an increase in site productivity changes the colonization capacity of all four wind-dispersed grassland forbs: more seeds are produced, and these seeds germinate better (except in *C. dissectum*). All seeds are dispersed over shorter distances, as their dispersal ability is lower. Higher site productivity thus appears to result in a higher colonization capacity at shorter distances, but a lower colonization capacity at longer distances. This may result in an overall lower recruitment, because the seedlings that emerge closer to the parent plant may suffer from increased density dependent mortality (Willson and Traveset 2000). Also, the colonization capacity over time may be reduced, as larger seeds tend to form shorter-lived seed banks (Thompson *et al*. 1998).

Dispersal ability and germination ability are negatively correlated in plumeless seeds only

In contrast to the findings of Strykstra *et al*. (1998b), no relationship between dispersal ability as determined by v_t and germination ability was found in the species with plumed seeds. In the plumeless seeds, however, lower v_t values were caused by lower seed mass and strongly correlated to lower germination ability. We found that both smaller population size and lower site productivity correlate with lower seed mass of plumed seeds, but this never affected v_t of these seeds due to compensating adjustments in plume diameter. This is in agreement with the findings of Matlack (1987), who measured a variation in seed weight by a factor of 82.3, but a variation in wing loading by only a factor 2.8 in plumed seeds of *Asteraceae* species. In species with plumed seeds, there appears to have been a strong selection for constant low v_t values, ensuring a high long-distance dispersal ability of the seeds. This is in agreement with the results of recent model analyses (Tackenberg 2003; Tackenberg *et al*. 2003) that show species v_t to be the most important plant-controlled variable in determining long-distance seed dispersal.

Conclusions

The results of this study show that a decrease in population size reduces the colonization capacity of fragmented populations of wind-dispersed grassland forbs, and that an increase in site productivity shifts their colonization capacity to a higher capacity to colonize nearby sites, but a lower capacity to colonize distant sites. Although these effects are not dependent on the wind-dispersal strategy of the species, the mechanisms that determine them are. The main difference between the dispersal strategies is that the long-distance dispersal ability of the species with plumed seeds is decreased only by a reduction in relative release height of the seeds, whereas for the species with plumeless seeds it is also reduced by an increase in their terminal velocity. This indicates a selection for constant low seed terminal velocity in the species adapted to long-distance dispersal.

Habitat fragmentation is a major cause of decreasing population size and increasing site productivity of remnant populations of wind-dispersed grassland forbs. In these populations a decrease in population size and an increase in site productivity often co-occur and their effects will reinforce each other. The resulting reduced colonization capacity, even when selection for reduced dispersal does not occur, has important consequences for species survival. Lower local recruitment contributes to a higher extinction risk of fragmented populations, while lower regional recruitment and colonization of new sites increase the regional extinction risks of species. For wind-dispersed species in increasingly fragmented landscapes, the connectivity between habitat patches not only decreases because distances between habitat patches increase, but also because the colonization capacity of the remaining populations decreases. Also, the total (re)colonization capacity of the species is reduced as even recruitment to the seed bank is reduced. Together, these factors pose yet another threat to the regional survival of wind-dispersed forbs restricted to nutrient-poor grasslands.

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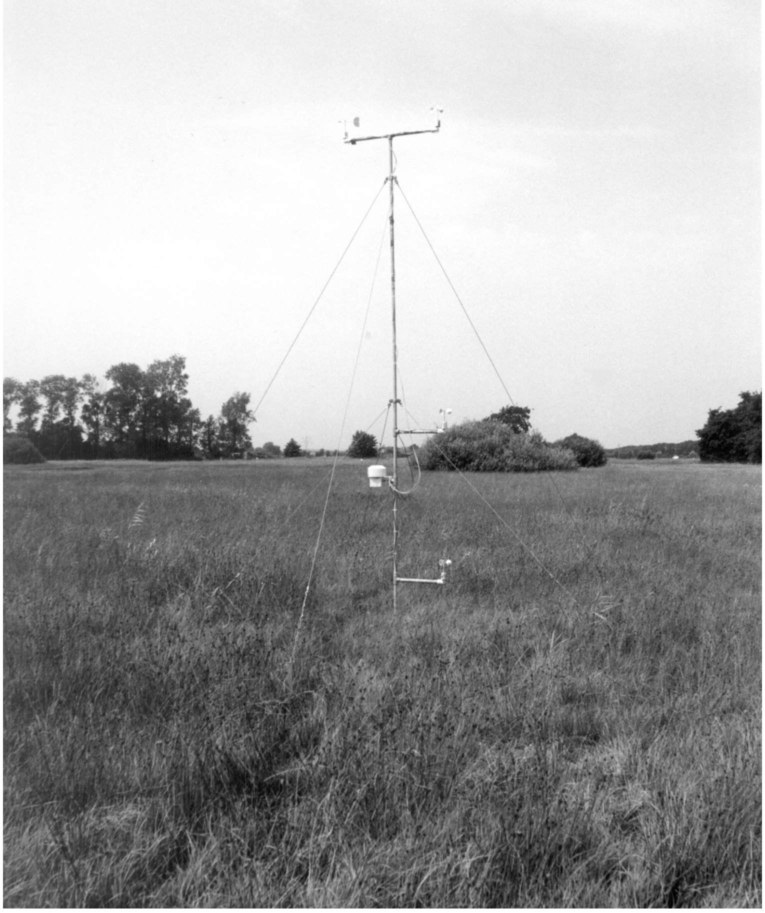


3. Determinants of long-distance seed dispersal by wind in grasslands

M.B. Soons, G.W. Heil, R. Nathan, and G.G. Katul

SUMMARY

Long-distance seed dispersal is an important topic in ecology, but notoriously difficult to quantify. Previous modeling approaches failed to simulate long-distance dispersal, and it 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 different models using data from field dispersal experiments. For relatively short wind dispersal distances (<15 m) differences between the mechanistic models were small. However, the models differed greatly in ability to simulate long-distance dispersal. Comparisons between model simulations showed that autocorrelated turbulent fluctuations in vertical wind velocity are the key mechanism determining 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 further when there is more surface heating, but under these conditions dispersal distances are still much shorter than during strong wind events. Sensitivity analyses of the models showed that mean horizontal wind velocity, seed release height, and vegetation height are crucial for dispersal potential and median dispersal distances. These are also the most important parameters determining long-distance dispersal within plant species. Between plant 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 individual plants, and that the structure of the local vegetation can greatly affect 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, mechanistic dispersal models, long-distance seed dispersal, 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 (Bakker *et al*. 1996; Poschlod and Bonn 1998; Nathan and Muller-Landau 2000) and has been the topic of many recent studies. The ecological importance of long-distance dispersal has been stressed especially (Clark 1998; Clark *et al*. 1998, 2001; Cain *et al*. 1998, 2000; Nathan 2001a), although long-distance dispersal is notoriously difficult to quantify (Bullock and Clarke 2000; Cain *et al*. 2000; Nathan 2001b; Nathan *et al*. 2003). The main mechanism of long-distance dispersal that has been studied is wind dispersal (*e.g.* Greene and Johnson 1995; Horn *et al*. 2001; Nathan *et al*. 2002b). Wind dispersal is one of the most common long-distance dispersal mechanisms (Van der Pijl 1982; Bouman *et al*. 2000), and apparently less complex than the other mechanisms of long-distance dispersal, such as zoochory.

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; Strykstra *et al*. 1998; Bullock and Clarke 2000), statistical modeling approaches (Ribbens *et al*. 1994; Clark *et al*. 1999), and various mechanistic modeling approaches (*e.g.* Okubo and Levin 1989; Andersen 1991; Greene and Johnson 1996; Nathan *et al*. 2002b; 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 long dispersal distances. 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 long-distance dispersal (Tackenberg *et al*. 2003). However, others state that wind velocity is much more important in determining long-distance dispersal 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 long-distance seed dispersal 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 long-distance dispersal (Horn *et al*. 2001; Nathan *et al*. 2002b).

Both the relative importance of plant attributes versus environmental conditions and the role of vertical wind movements in determining long-distance dispersal 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 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 consider 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:

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

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 i) random fluctuations in vertical wind velocity, ii) (auto-)correlated mechanically-produced wind turbulence, or iii) (auto-)correlated mechanically-produced and buoyant-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 long-distance seed dispersal.

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 dispersal distance (D) depends only on the falling time of a seed from its release height (H_0) to its interception height (defined below) and on the horizontal wind velocities it experiences during this time. The mean (*i.e.* time-averaged) horizontal wind velocity ($\overline{U}$) is a function of height (following Surface Layer Similarity Theory for neutral stationary and planar-homogeneous flow; Monteith 1973; Stull 1988):

$$\overline{U}(z) = \frac{u_*}{k} \ln\left(\frac{z-d}{z_o}\right) \tag{2}$$

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 ranging from 15 to 60 minutes. The seed interception height is set at (z_0+d), the height at which horizontal wind velocity is reduced to zero. Estimates of d and z_0 can be obtained from the mean canopy 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):

$$D = \frac{u_*}{k \times v_t}\left((H_0 - d) \ln\left(\frac{H_0 - d}{\mathrm{e} \times z_0}\right) + z_0 \right) \tag{3}$$

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; Nathan *et al.* 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 long-distance dispersal (Horn *et al.* 2001; Nathan *et al.* 2002b; Tackenberg 2003). Although it is possible to add upward vertical air movement to this 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 $\overline{U}$. To assess how random vertical velocity fluctuations affect seed dispersal distances, the previous model is extended by adding a vertical velocity component given by:

$$\begin{aligned} &\overline{W} = 0 \\ &w' = W - \overline{W} = \sigma_w \times \varepsilon(t) \\ &\sigma_w = \left[\overline{w'^2}\right]^{1/2} \end{aligned} \tag{4}$$

where $\overline{W}$ 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. Following Surface Layer Similarity theory, $\sigma_w = 1.25 \times u_*$ for near-neutral atmospheric conditions (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 Gaussian (Chu *et al*. 1996).

This model requires numerical calculation. The vertical wind velocity is computed from $\overline{W}$ 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 horizontal displacement, computed from $\overline{U}(z)$, and

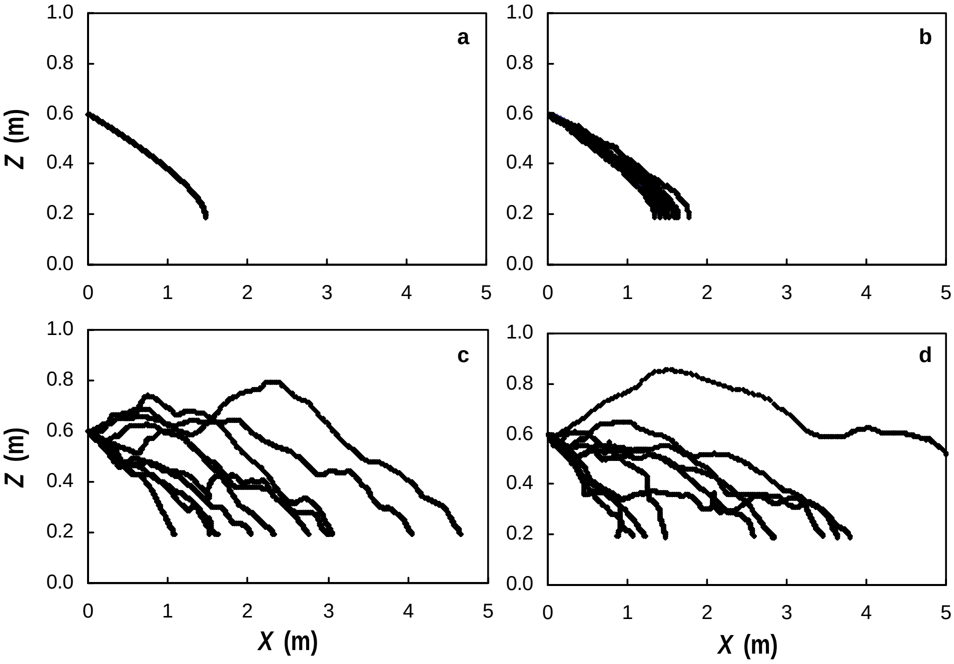


Figure 1. Ten random dispersal trajectories of a single plumed seed dispersing from a long flowering stalk in a short-grass grassland for an average wind velocity. (a) The simple deterministic model; (b) the simple stochastic model; (c) the Markov chain STG model; (d) the Markov chain ASC model. Simulated time series all based on the same parameter set: $\overline{U}_{5.2m}$ = 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 Wm^{-2}.

new horizontal position of the seed are computed for each Δt. Calculations stop when the seed is intercepted by the vegetation at $z = (z_0+d)$. Due to the fluctuations in vertical velocity this model simulates 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 used this exact same modeling approach to simulate seed dispersal. Andersen (1991) and Jongejans and Schippers (1999) used an elaborated version of this approach, which is discussed in the next section. Another approach using random vertical velocity fluctuations was proposed by Greene and Johnson (1996). They calculated the variance of seed drop times from the variance in seed v_t values and a realistic Gaussian distribution of vertical wind velocity fluctuations (with zero mean and fixed σ_w). 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 is 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 an approach otherwise closely similar to their previously discussed model (Greene and Johnson 1996, see previous section). Andersen (1991) and Jongejans and Schippers (1999) used a version of the simple stochastic model in which w' is autocorrelated. Their approach is mechanistic but highly simplified, and ignores the conservation of kinetic energy, effects of the vegetation structure, and the correlation between fluctuations in vertical and horizontal wind velocities. Therefore, we selected the mechanistic model of Nathan *et al*. (2002b) to simulate turbulence (*i.e.* the fluctuations in both vertical and horizontal wind velocity) in a realistic manner. We adjusted this model for grassland ecosystems. In this model the instantaneous wind velocities W and U are random variables that posses 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 long-distance dispersal of tree seeds in a forest ecosystem (Nathan *et al*. 2002b). Both spatial and temporal correlations 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

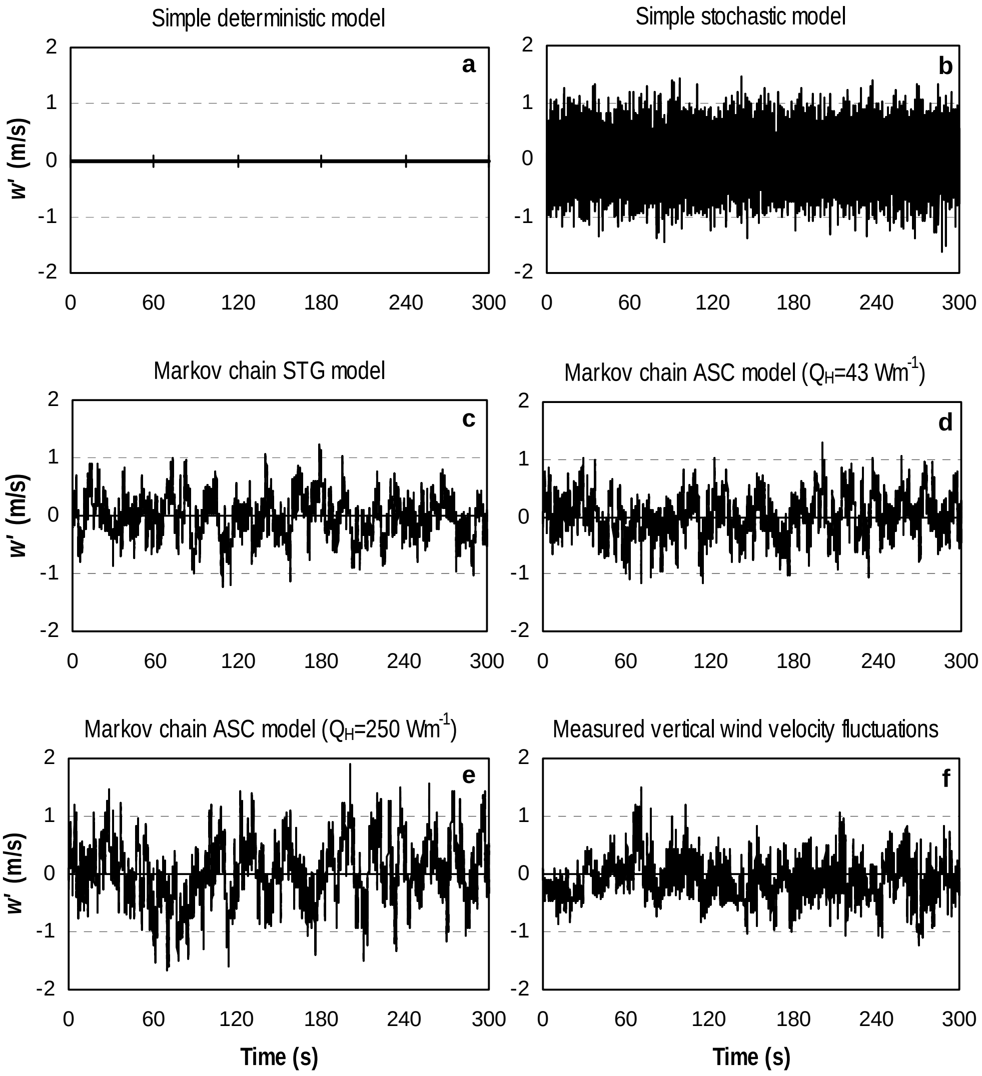


Figure 2. Randomly selected time series of simulated and measured fluctuations in vertical wind velocity (*w'*). (a) The simple deterministic model – no simulation of vertical wind velocity; (b) the simple stochastic model – simulation of random fluctuations in vertical wind velocity; (c) the Markov chain STG model – simulation of mechanically-produced autocorrelated fluctuations in vertical wind velocity; (d) the Markov chain ASC model - simulation of mechanically- and buoyant-produced autocorrelated fluctuations in vertical wind velocity; (e) the Markov chain ASC model with increased sensible heat flux (Q_H = 250 Wm^{-2}); (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 $\overline{U}_{5m}$ = 3.3 m/s, T = 32°C, Q_H = 43 Wm^{-2}), except for Q_H in (e).

given by Rodean (1996). Using the Markov process assumption, the change in u_i can be expressed by:

$$\mathrm{d}u_i = a(x_i, u_i, t)\mathrm{d}t + b(x_i, u_i, t)\, \mathrm{d}\Omega \tag{5}$$

where u_i is the instantaneous wind velocity in direction x_i, a is the drift coefficient, b is the stochastic acceleration coefficient, and dΩ is a Gaussian random variable with zero mean and variance dt, with dt dependent on the time-scale of turbulent air movements (dt = $0.005 \times T_L$ Appendix 1). For stationary and inhomogeneous near-Gaussian turbulent flows, a and b are estimated from Thomson's (1987) "simplest solution" using a procedure outlined by Rodean (1996; Appendix 1). The Markov process assumption and the incorporation of a coherent time scale ensure the (auto-)correlation of fluctuations in wind velocity. We refer to Nathan *et al*. (2002b) for a more detailed description of the model, and to Appendix 2 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 turbulence by drawing from a database of time series of w' for different values of $\overline{U}$ as measured at one study site and at one height (0.6 m above the ground; Tackenberg 2001). His method results in highly realistic vertical velocity simulations for that specific site and height. However, the simulations cannot be extrapolated to other conditions, other heights above the ground surface, or other sites than those under which w' was specifically measured. This is even more important considering that Tackenberg used measurement series with non-zero $\overline{W}$. In the general case $\overline{W} = 0$. $\overline{W} = 0$ is a necessary condition for planar-homogeneous boundary layer flow and the validity of the logarithmic wind-profile (Eq. 2), which Tackenberg also applied in his model. Through the fluid continuity equation for incompressible flows (such as airflow over canopies), a non-zero $\overline{W}$ implies that $\overline{U}$ must vary in both x and z, not just z as assumed by the logarithmic wind-profile. As such consistent spatial variation in $\overline{U}$ is not incorporated in Tackenberg's model, data series with non-zero $\overline{W}$ cannot be applied to any other site than the specific one on which it was measured. Also, w' and the autocorrelation in w' change (generally increase) with height. Data series of w' measured at 0.6 m cannot be applied at other heights. Especially for seeds uplifted to great heights above the canopy such data underestimate w' and the autocorrelation in w'. For our model study we therefore selected the mechanistic and general, though more complex, STG model instead of the simpler method used by Tackenberg.

4. The Markov chain model with Atmospheric Stability Correction (ASC model)

The STG model simulates mechanically-produced turbulence caused by frictional drag of a non-zero $\overline{U}$ flowing over 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 buoyant-produced turbulence. Buoyant-produced turbulence dominates under unstable boundary layer conditions, when solar heating of the ground causes parcels of warm air to move upwards (Stull 1988). As a final step in increasing model realism, we account for atmospheric stability and simulate both mechanically- and buoyant-produced turbulence, and any combination thereof. For this purpose we developed a new simulation model. We did this by elaborating 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 $\overline{U}$ at a reference height z_{ref}, the value of u_* is now computed by numerically solving:

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

where

$$L = -\frac{u_*^{\,3}}{k \times g \dfrac{Q_H}{\rho \times C_{pd} \times T_a}} \tag{7}$$

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 buoyant- versus mechanically-produced turbulence (Stull 1988): when Q_H is high and $\overline{U}$ is low (and hence u_* is low) buoyant-produced turbulence is dominant, whereas mechanically-produced turbulence is dominant at high $\overline{U}$ (and hence high u_*) and low Q_H. The values of Q_H and $\overline{U}$ thus determine whether the model computes turbulent wind fluctuations typical of more unstable or more neutral atmospheric conditions.

In the Markov chain 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 mowed *Lolium perenne* production grasslands with short grass to unmown 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 its release point to its landing point. Vegetation height (excluding protruding flowering stalks) was measured at each experimental site. Leaf area density profiles and LAI of the selected grassland types were estimated from literature (Fliervoet and Werger 1984; Werger *et al*. 1986). During the flight of each seed a transportable mini-meteorological station (Eijkelkamp Agrisearch Equipment) measured horizontal wind velocity with cup-anemometers at three heights (0.7, 2.7, and 5.2 m), as well as air temperature (at 2.7 m), close to the seed release point.

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 long-distance dispersal by wind (Bouman *et al*. 2000). Seeds of the two other species, *Centaurea jacea* L. (*Asteraceae*) and *Succisa pratensis* Moench (*Dipsacaceae*), are also classified as wind-dispersed (Bouman *et al*. 2000), 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 further 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 is dry and hairy and increases the surface area of the seed without adding much weight, thereby functioning as a balloon (Bouman *et al*. 2000). After collection the seeds were air-dried, weighed, and plume diameter of the plumed seeds was measured. The terminal velocity of each seed was calculated using a previously derived species-specific relationship between v_t, seed mass and plume diameter (Soons and Heil 2002). Thus, the values of model input parameters v_t, H_0, $\overline{U}_{zref}$, z_{ref}, h, and LAI and of model output D are known for each experimentally dispersed seed (Table 1). All other model parameters are computed from these measured input parameters (see *Model descriptions*).

Model comparisons

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 that were measured during the dispersal events in the field experiments. For the simple deterministic model, each set of input parameters yields one single dispersal distance. This allowed for 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 based on simulation of 5000 seed trajectories for each set of input parameters. We then compared the median values of the simulated PDFs to the measured distances. We compared simulated and measured dispersal distances using linear regression analyses. To test for significant differences between the regression coefficients and intercepts of the simulation 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. To compare the stochastic models better, we combined the individual dispersal events per species to a PDF of measured dispersal distances. We compared these PDFs to simulated PDFs (based on the same input parameters). This comparison was made for each plant species separately, because between-species variation in dispersal distance was large compared to within-species variation. We used a Kolmogorov-Smirnov test for two independent samples to compare model performance between models and species. This test does not provide a measure of absolute model performance, because the measured distances are not a fully representative subset of the true species PDFs. The set of measured distances is biased towards shorter dispersal distances, because seeds that were dispersed faster and further had a higher probability of being lost from sight and thus of being not included in the data set. We therefore also compared the ability of the two stochastic models to simulate long-distance dispersal events by comparing the ranges of the simulated PDFs.

The Markov chain 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 below). All statistical analyses were carried out in SPSS 8.

Sensitivity analyses

For the simple deterministic model and the Markov chain STG model sensitivity analyses were carried out to determine which input parameters are most important for computing seed dispersal distances. 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 gives an overview of the input parameters assessed per model. The sensitivity analyses followed the approach described by Nathan *et al*. (2001). Per model, the following analysis steps were carried out: (i) The natural range of values of each selected parameter was divided into 20 equal intervals. (ii) A random set of 20 Latin hypercubes was created so that each interval of each selected parameter was

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. Model input parameters included in the sensitivity analysis of the simple deterministic model (S.A. simple) or the STG model (S.A. STG) are indicated by '+'. 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 from Soons and Heil (2002), except *LAI* and wind velocity (see *Methods*).

Parameter	Values in dispersal experiments	Mean value under natural conditions	Range under natural conditions	S.A. simple	S.A. STG
Terminal velocity (v_t)					
- *C. dissectum*	0.30 - 0.45 m/s	0.38 m/s	0.30 - 0.51 m/s	+	+
- *H. radicata*	0.28 - 0.40 m/s	0.34 m/s	0.24 - 0.54 m/s	+	+
- *C. jacea*	3.17 - 5.17 m/s	4.33 m/s	3.17 – 5.57 m/s	+	+
- *S. pratensis*	1.72 - 2.59 m/s	2.14 m/s	1.64 – 2.60 m/s	+	+
Release height (H_0)	0.50-1.50 m	0.45 m	0.09 – 0.96 m	+	+
Vegetation height (h)	0.15 - 0.40 m	0.30 m	0.1 – 0.8 m	+	+
Leaf Area Index (*LAI*)	2.5 - 6.0	3.5	2.0 – 6.0		+
Horizontal wind velocity at ref. height ($\overline{U}_{zref}$)	0 - 6.9 m/s per 10 s interval	3.8 m/s per 1hr interval	0 - 15.2 m/s per 1 hr interval	+	+
Reference height (z_{ref})	5.2 m	10 m	10 m		

selected once in each hypercube. (iii) 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. Step (ii) and (iii) were repeated ten times, so that in total 200 parameter combinations were simulated. (iv) The resulting 200 sets of independent variables (the input parameters) and dependent variables (the calculateddistances) were rank-transformed and analyzed using stepwise multiple linear regression analysis in SPSS. 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 Markov chain ASC model, to assess the sensitivity of dispersal distances to Q_H. As the effect of Q_H changes with $\overline{U}$, we simulated seed dispersal for different combinations of Q_H and $\overline{U}$ (5000 dispersal trajectories for each parameter combination). We carried out these simulations for three types of 'seeds': plumed seeds with low terminal velocity (0.34 m/s, as in *H. radicata*), plumeless seeds with relatively high terminal velocity (4.33 m/s, as in *C. jacea*), 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 Wm^{-2} and are representative of the full range of values common to temperate grasslands in the daytime (approximately –10 to 300 Wm^{-2}; Stull 1988). Simulated values of $\overline{U}$ ranged from 0.01 to 16 m/s at a reference height of 10 m. The first value represents a very low $\overline{U}$ (almost no wind), and the second value a high $\overline{U}$ (stormy weather), for one seed dispersal season (June to October) in the inner area of The Netherlands (Wieringa and Rijkoort 1983).

RESULTS

Model predictions and field data

Figures 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 with measured dispersal distances from the field experiments. The first model test

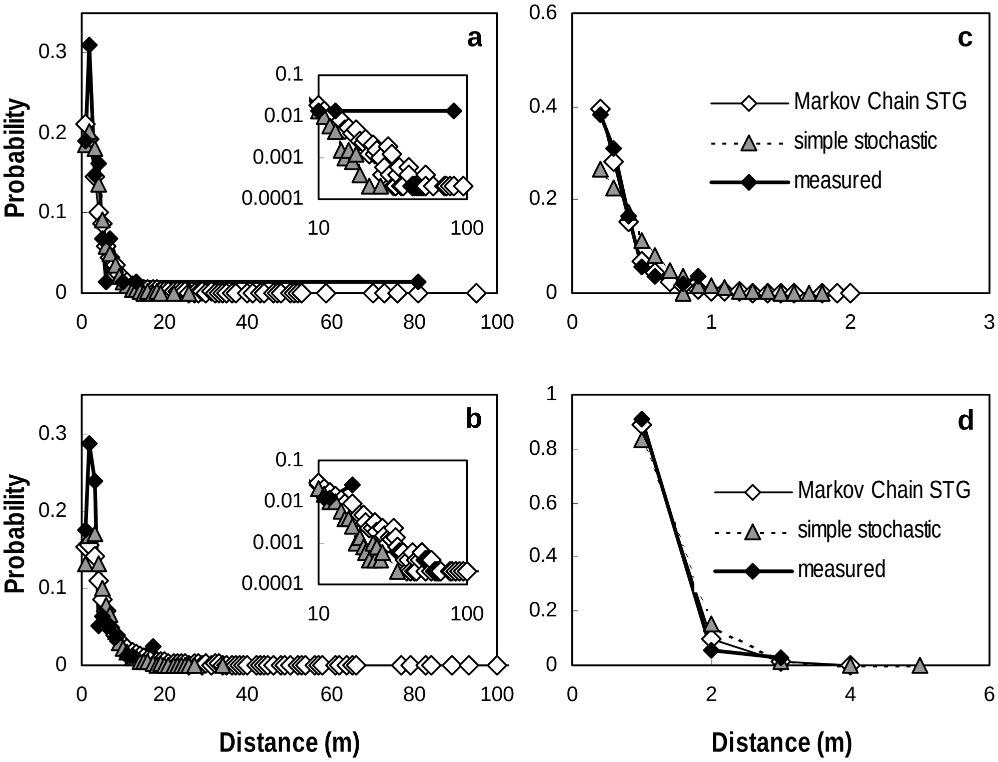


Figure 3. Simulated and measured seed dispersal Probability Density Functions. (a) *C. dissectum*; (b) *H. radicata*; (c) *C. jacea*; (d) *S. pratensis*.

Table 2. Model performance statistics. Regression statistics for the simple deterministic model are the same as for the simple stochastic model and therefore not shown separately. Z values are Kolmogorov-Smirnov Z statistics, presented per species. Abbreviations: *Cd* = *C. dissectum*, *Hr* = *H. radicata*, *Cj* = *C. jacea*, *Sp* = *S. pratensis*; ^{ns} no significant difference between measured and modeled PDFs; * p<0.05; ** p<0.01; *** p<0.001 .

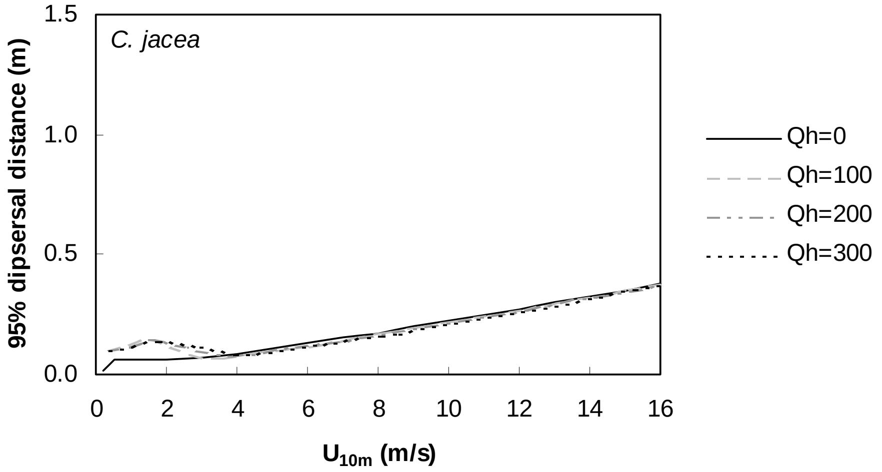
Model	Dispersal distance medians			Dispersal distance PDFs			
	Regression eqn.	R^2	p	*Cd.* Z	*Hr.* Z	*Cj.* Z	*Sp.* Z
Simple stochastic	y = 1.33x - 0.62	0.30	<0.001	1.33^{ns}	2.20 ***	2.22 ***	1.72 **
Markov chain STG	y = 0.92x – 0.36	0.29	<0.001	1.54 *	2.28 ***	1.34^{ns}	0.98^{ns}

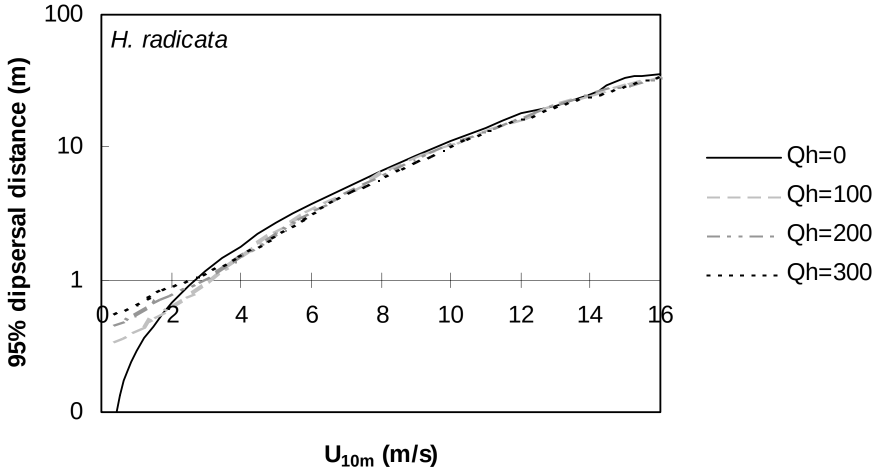
compares the simulated distances of the simple deterministic model, the median distances of the simple stochastic model, and the median distances of the Markov chain STG model to the measured distances (Table 2). Median simulated distances of the STG model are better predictors of the measured distances, as they have a regression coefficient significantly closer to 1 (p=0.008) and an intercept closer to 0 (n.s., all calculated intercepts not significantly different from 0).

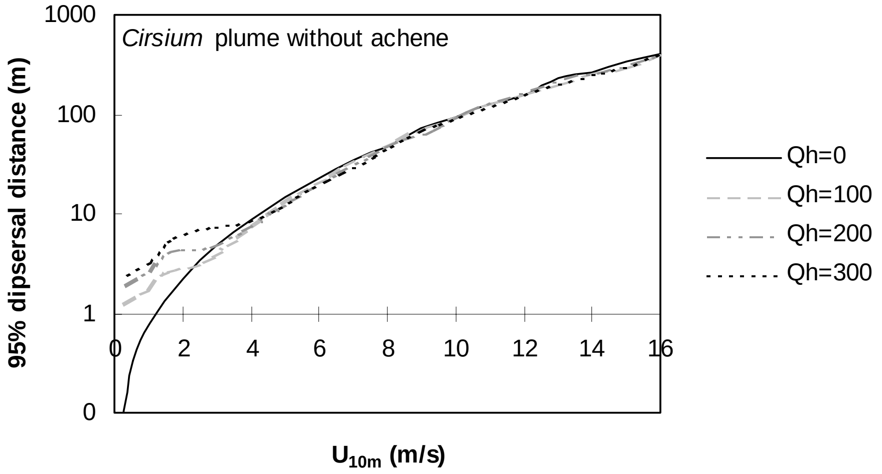
The PDFs simulated by the STG model generally resemble the measured data more closely than those of the simple stochastic model (Figure 3). For the species with short-distance seed dispersal by wind, the PDFs simulated by the STG model are not statistically different from the PDFs of measured distances (Table 2). The PDFs simulated by the simple stochastic model are statistically different from the measured PDFs for these species. For the species with plumed seeds, adapted to long-distance wind dispersal, the PDFs simulated by the STG model are significantly different from the measured PDFs. This is caused by an underestimation of relatively short-distance dispersal events (around 2 m) by the model. The simple stochastic model also underestimates dispersal over these distances, but to a lesser extent than the STG model. For these species, the STG model simulates long-distance dispersal events over >100 m (Figure 3). The simple stochastic model is not able to simulate long-distance dispersal (all simulated dispersal distances <34m), and this is an important difference between the two stochastic models (Kolmogorov-Smirnov test, p<0.001). The simple deterministic model does not simulate long-distance dispersal at all; dispersal distances simulated by this model are similar to median distances simulated by the simple stochastic model.

Following page:

Figure 4. 95-Percentile dispersal distances simulated by the Markov chain ASC model for different levels of sensible heat flux (Q_H) and mean horizontal wind velocity ($\overline{U}_{10m}$); H_0 = 0.45 m, h = 0.30 m, LAI = 3.5. Top: plumeless seeds of *C. jacea* (v_t = 4.33 m/s); center: plumed seeds of *H. radicata* (v_t = 0.34 m/s); bottom: *Cirsium arvense* plumes without achene (0.15 m/s; Tackenberg 2001). Distances of *H. radicata* seeds and *Cirsium* plumes are plotted on a log scale.


C. jacea
95% dipsersal distance (m)
1.5
1.0
0.5
0.0
0
2
4
6
8
10
12
14
16
U10m (m/s)
Qh=0
Qh=100
Qh=200
Qh=300


H. radicata
95% dipsersal distance (m)
100
10
1
0
0
2
4
6
8
10
12
14
16
U10m (m/s)
Qh=0
Qh=100
Qh=200
Qh=300


Cirsium plume without achene
95% dipsersal distance (m)
1000
100
10
1
0
0
2
4
6
8
10
12
14
16
U10m (m/s)
Qh=0
Qh=100
Qh=200
Qh=300

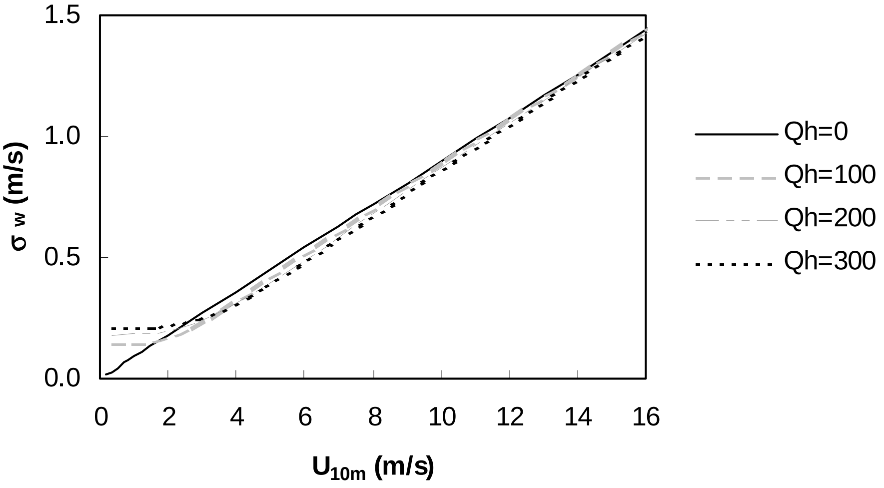


Figure 5. Standard deviation of the vertical wind velocity (σ_w) plotted against mean horizontal wind velocity ($\overline{U}_{10m}$) for different levels of sensible heat flux (Q_H); H_0 = 0.45 m, h = 0.30 m, LAI = 3.5, T = 20°C.

The difference in performance between the STG model and the two simple models is due to the more realistic simulation of fluctuations in vertical wind velocity and the simulation of fluctuations in horizontal wind velocity in the STG model. Simulation of these (auto-)correlated fluctuations in wind velocity creates more coherent dispersal trajectories. Some seeds experience coherent updrafts propelling them further and further as they experience stronger horizontal wind velocities at greater heights, while other seeds experience downdrafts until they land in the vegetation. The STG model is thus able to predict a wider and more realistic range of dispersal distances.

The effect of surface heating

To assess the importance of buoyant-produced fluctuations in wind velocity for dispersal distances, we carried out simulations with the Markov chain ASC model for a series of wind velocities ($\overline{U}$) and heat fluxes (Q_H) (Fig. 4). Seed dispersal distances are longest at high $\overline{U}$. The large-scale buoyant-produced fluctuations in wind velocity that occur under highly unstable atmospheric conditions with high Q_H and low $\overline{U}$ have the potential to lift seeds up high (relatively large *w*’ and large autocorrelation time scale T_L; Figs. 5 and 6). However, even when seeds are lifted up high, they are not transported very far in horizontal direction, because of the low $\overline{U}$. The high values of $\overline{U}$, which occur under near-neutral atmospheric conditions, have the greatest potential for transporting seeds

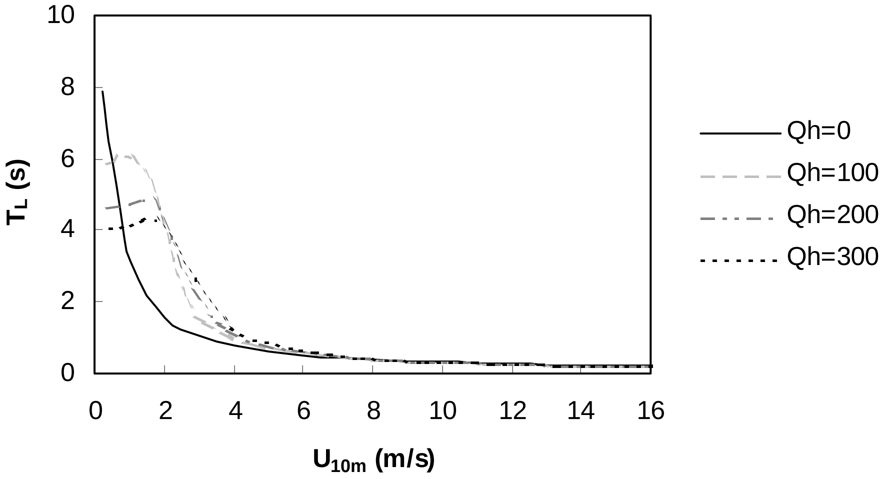


Figure 6. Autocorrelation time scale of the fluctuations in vertical wind velocity (T_L) plotted against mean horizontal wind velocity ($\overline{U}_{10m}$) for different levels of sensible heat flux (Q_H); H_0 = 0.45 m, *h* = 0.30 m, *LAI* = 3.5, *T* = 20°C.

rapidly in horizontal direction. 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 autocorrelation time scale T_L; Figs. 5 and 6), seeds are dispersed much further under stormy conditions than under unstable atmospheric conditions.

Sensitivity analyses

Results of the sensitivity analyses demonstrate that in the simple deterministic model and the Markov chain STG model the same parameters are most important in determining seed dispersal distances (Table 3). For each model, regression analyses were carried out on two groups of data. One group consists of all data and the other consists of a subset 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 combinations of input parameters resulted in conditions for which seeds did not disperse from the mother plant, because wind velocity was zero at the height at which the seeds were released. As the results of the regression analyses are dependent on the inclusion of these parameter combinations, we carried out two separate analyses.

The first regression analysis includes all simulated parameter combinations and shows that seed release height (H_0) is the most important parameter determining seed

Table 3. Results of the stepwise multiple regression in the sensitivity analyses. The dependent variable is seed dispersal distance (*D*). Independent variables significantly contributing to the variation in *D* are listed as 'Variable entered' in order of inclusion in the stepwise regression model (descriptions and value ranges in Table 1). R^2 is the fraction of variance accounted for by the regression model, β is the unstandardized regression coefficient, p-values are from the regression model incorporating all significant variables. U_{zref} in the table should read $\overline{U}_{zref}$.

Species	Simple deterministic model, all seeds				Simple deterministic model, only dispersed seeds ($H_0 > (z_0 + d)$)			
	Variable entered	R^2	β	p <	Variable entered	R^2	β	p <
All	H_0	0.455	0.667	0.000	U_{zref}	0.195	0.507	0.000
	h	0.604	-0.382	0.000	v_t	0.470	-0.433	0.000
	U_{zref}	0.691	0.333	0.000	H_0	0.655	0.627	0.000
	v_t	0.786	-0.305	0.000	h	0.844	-0.421	0.000
C. dissectum	H_0	0.558	0.727	0.000	H_0	0.320	0.699	0.000
	h	0.759	-0.416	0.000	U_{zref}	0.634	0.441	0.000
	U_{zref}	0.885	0.354	0.000	h	0.867	-0.406	0.000
					v_t	0.871	-0.049	0.033
H. radicata	H_0	0.517	0.728	0.000	H_0	0.234	0.778	0.000
	h	0.787	-0.526	0.000	h	0.610	-0.591	0.000
	U_{zref}	0.845	0.234	0.000	U_{zref}	0.791	0.305	0.000
C. jacea	H_0	0.499	0.669	0.000	U_{zref}	0.508	0.561	0.000
	U_{zref}	0.660	0.419	0.000	H_0	0.682	0.595	0.000
	h	0.804	-0.364	0.000	h	0.807	-0.333	0.000
					v_t	0.819	-0.093	0.003
S. pratensis	H_0	0.326	0.656	0.000	U_{zref}	0.298	0.469	0.000
	h	0.678	-0.619	0.000	H_0	0.453	0.647	0.000
	U_{zref}	0.840	0.393	0.000	h	0.832	-0.624	0.000
	v_t	0.845	-0.072	0.010	v_t	0.840	-0.083	0.005

dispersal distance, followed first by vegetation height (h) and then by mean horizontal wind velocity $\overline{U}_{zref}$ (Table 3; STG model results not shown but similar). Seed terminal velocity (v_t) is only significant 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 second regression analysis includes the seeds with a probability of dispersal ($H_0 > (d+z_0)$; Table 3). The results of this analysis demonstrate that $\overline{U}_{zref}$ is over all the most significant parameter, followed closely by H_0 and then by h. Also v_t is now a significant parameter for dispersal, especially when all species are lumped together. Seed v_t is more important in determining long-distance dispersal than median distance dispersal. In the STG model the *LAI* is insignificant in determining median dispersal distances, but does contribute to determining long-distance dispersal.

Table 3, continued.

Species	Markov chain STG model, only dispersed seeds ($H_0 > (z_0 + d)$) MEDIAN DISTANCES				Markov chain STG model, only dispersed seeds ($H_0 > (z_0 + d)$) 95-PERCENTILE DISTANCES			
	Variable entered	R^2	β	p <	Variable entered	R^2	β	p <
All	H_0	0.229	0.491	0.000	U_{zref}	0.387	0.549	0.000
	U_{zref}	0.424	0.402	0.000	v_t	0.626	-0.416	0.000
	v_t	0.711	-0.462	0.000	H_0	0.776	0.341	0.000
	h	0.847	-0.255	0.000	LAI	0.800	-0.112	0.000
					h	0.820	-0.100	0.000
C. dissectum	U_{zref}	0.334	0.378	0.000	U_{zref}	0.710	0.484	0.000
	H_0	0.627	0.494	0.000	H_0	0.781	0.210	0.000
	h	0.730	-0.246	0.000	v_t	0.792	-0.170	0.004
	v_t	0.738	-0.155	0.031	h	0.799	-0.056	0.032
H. radicata	U_{zref}	0.269	0.356	0.000	U_{zref}	0.753	0.479	0.000
	H_0	0.483	0.845	0.000	H_0	0.824	0.322	0.000
	h	0.717	-0.480	0.000	h	0.832	-0.084	0.008
					v_t	0.840	-0.127	0.007
					LAI	0.846	-0.047	0.028
C. jacea	U_{zref}	0.451	0.341	0.000	U_{zref}	0.611	0.485	0.000
	H_0	0.741	0.483	0.000	H_0	0.759	0.372	0.000
	h	0.904	-0.242	0.000	h	0.788	-0.123	0.000
	v_t	0.917	-0.221	0.000	v_t	0.810	-0.341	0.000
S. pratensis	U_{zref}	0.415	0.375	0.000	U_{zref}	0.758	0.634	0.000
	H_0	0.594	0.595	0.000	H_0	0.805	0.313	0.000
	h	0.905	-0.374	0.000	h	0.826	-0.135	0.000
	v_t	0.918	-0.297	0.000	LAI	0.853	-0.117	0.000

DISCUSSION

The processes that determine seed dispersal distances

The Markov chain 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 accurately. However, the difference in accuracy between the models is only small. Unfortunately we could only test model performance for relatively short dispersal distances (measured dispersal distances range from 0-16 m, and one dispersal event of 80.4 m). A test of model performance for longer dispersal distances may show a more pronounced difference between the models, but our field experiment again confirmed the difficulty in obtaining long-distance dispersal data (Bullock and Clarke 2000; Cain *et al.* 2000; Nathan 2001b; Nathan *et al.* 2003). When considering only relatively short dispersal distances (<±15m), the simple deterministic model is the most suitable wind dispersal model, because it performs almost as well as the STG model but has the lowest complexity.

However, the simple deterministic model and the simple stochastic model cannot simulate long-distance dispersal, whereas the STG model can. Results from the STG model and the simple models show that adding turbulent vertical wind flow greatly increases model realism and allows simulation of long-distance dispersal, but only when the spatial and temporal coherency of the wind flow are accounted for. Random vertical wind velocity fluctuations are able to uplift seeds, but their upward trajectories are not sustained long enough in time to achieve long-distance dispersal. The autocorrelated fluctuations in vertical wind velocity simulated by the STG and ASC models are able to uplift seeds in coherent upward dispersal trajectories, thereby greatly increasing their dispersal distance. These results are in agreement with the finding of Nathan *et al.* (2002b) and Tackenberg (2003) that seed uplifting is crucial in determining long-distance dispersal 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 long-distance dispersal

The simulations with the Markov chain STG and ASC models show that coherent upward trajectories of uplifted seeds are simulated by autocorrelated upward deviations from the mean vertical wind velocity. All models used in this study simulated a zero mean vertical wind velocity ($\overline{W} = 0$), but the model results are very different based on the differences in the way the turbulent fluctuations in vertical wind velocity (*w'*) are simulated. Tackenberg (2003) recently suggested, however, that a positive $\overline{W}$ under unstable atmospheric conditions is the most important mechanism for seed uplifting and long-distance dispersal. 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 regarding the key mechanism for seed uplifting.

First, values of $\overline{W}$ are usually very small, even under unstable atmospheric conditions. Tackenberg (2001) published values of $\overline{W}$ for unstable atmospheric conditions, ranging from ± -0.10 – 0.35 m/s. Although 0.35 m/s is an extremely high value (the range of values of $\overline{W}$ given by Stull 1988 is ± -0.2 – 0.3 m/s), it is only just enough to uplift the plumed 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, which are 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 this determines whether seeds are lifted up over significant vertical distances or not. For his measurement data set Tackenberg (2001) reports values of *w'* ranging from ± -0.25 – 1.10 m/s.

Thus, the turbulent fluctuations *w'* have a much greater potential to uplift seeds than a positive $\overline{W}$, if the positive values of *w'* are sustained long enough in space and time. We simulated realistic (auto-)correlation of the fluctuations in vertical and horizontal wind velocity. This includes the increase in the size of *w'* and the autocorrelation of w' with height. Thus, with increasing height seeds that move up are more likely to continue moving up. Tackenberg used time series of w' measured at one height. This height (0.6 m) was close to the vegetation canopy and therefore his measured series of w' contain only the relatively damped and randomized fluctuations w' at this specific height. Tackenberg's extrapolation of these values to all heights in a seed dispersal trajectory greatly underestimates the importance of w' for long-distance dispersal.

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

Third, Tackenberg's suggestion depends critically on his assumption that $\overline{U}$ and $\overline{W}$ are linearly negatively correlated. This assumption is based on measurement series from a single site and a single height, and is dependent on the local conditions (as explained above). In general this relationship is not applicable.

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

2. The importance of atmospheric stability conditions for long-distance dispersal

Due to the interrelation between horizontal wind velocity ($\overline{U}$) and sensible heat flux (Q_H), it was not possible to carry out the same kind of sensitivity analysis for the Markov chain ASC model as for the other models. However, our graphical analysis (presented in Fig. 4-6) clearly demonstrates the relative importance of Q_H and $\overline{U}$. Some authors suggested that strong buoyancy under unstable atmospheric conditions is the main mechanism for long-distance seed dispersal by wind (Sheldon and Burrows 1973; Tackenberg 2003), and others suggested that storms (which occur during near-neutral conditions) were the main mechanism (Horn *et al*. 2001; Nathan *et al*. 2002b). Our results show that in grasslands high wind velocities are the mechanism for long-distance seed dispersal. Only under low wind speed conditions ($\overline{U}_{10m} < 4$ m/s) a strong heat flux is important in determining dispersal distances, and even then the dispersal distances are much lower than during strong winds ($\overline{U}_{10m} \geq 14$ m/s).

However, it is conceivable 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 any of the models in this study. Although the probability that this happens is low, and the probability that a seed rising up very high also disperses over a long horizontal distance is also low, the ASC model thus underestimates dispersal distances under convective conditions. Quantification of this underestimation requires a dispersal model simulating the full boundary layer dynamics under convective conditions (and not simply the addition of a constant positive $\overline{W}$). Ongoing model developments address this issue.

So far, however, our results show that for realistic simulation of long-distance seed dispersal a model for only near-neutral atmospheric conditions (such as the STG model) is just as good as a more complex model for near-neutral to convective atmospheric conditions (such as the ASC model). Because of the lower complexity of the STG model, this model should be favored over the ASC model. When data on heat flux are not readily available for the simulation of seed dispersal under more unstable conditions, simulations with the STG model will give sufficiently realistic results. Qualitative deviations from these results due to different levels of sensible heat flux under low wind velocity conditions can be estimated from Figure 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. These two parameters determine whether a seed is released at a height where there is sufficient wind speed to transport it, and thus whether it is dispersed by wind or not. If seeds are released in an environment of non-zero wind velocity (*i.e.* $H_0 > (d+z_0)$) the two parameters also affect the level of turbulence, and hence the probability of uplifting, at the location of the released seed. Thus, H_0 and h also contribute to the determination of dispersal distances. This importance of plant height and vegetation height is often underestimated in seed dispersal studies. We are aware of only very few wind dispersal studies in which both parameters were investigated (McEvoy and Cox 1987; Soons and Heil 2002).

For the seeds that are released at $H_0 > (d+z_0)$, the most important parameter determining seed dispersal distances is $\overline{U}$, both for median and long distances. Augspurger and Franson (1987), Greene and Johnson (1992), Horn *et al.* (2001), and Nathan *et al.* (2001) attributed the greater importance of $\overline{U}$ for dispersal distances to its larger variation in comparison to other dispersal parameters. Our data confirm this observation, as the natural range in $\overline{U}$ at 10 m height above grasslands in The Netherlands (excluding extremes) is roughly 0-15 m/s (approximately a 150-fold difference) and much larger than the between-species ranges of H_0 (± 10-fold difference), h (± 8-fold difference), and *LAI* (± 3-fold difference; Table 1). However, the between-species range in seed terminal velocity (v_t) is 0.24-5.57 m/s (± 23-fold difference; *cf.* the ± 24-fold difference found between 17 plumed seed species by Matlack 1987) and *between* species v_t is the second most important determinant of dispersal distance. *Within* species the range of values of v_t is relatively small (1.6- to 2.3-fold differences; Table 1) and the importance of v_t in determining dispersal distances is relatively low (Table 3); this same result was found for wind-dispersed tree seeds (Greene and Johnson 1992; Nathan *et al*. 2001). The importance of v_t in determining seed dispersal distances seems overestimated in dispersal studies that focus on within-species variation in v_t (*e.g.* Augspurger 1988; Andersen 1992; Greene and Johnson 1992). However, studies on within-species differences in v_t may explain variation in dispersal ability in species with strong seed dimorphism; the difference in v_t between seed morphs of *Crepis sancta* is at least 8-fold (Imbert 1999). Seed v_t is more important for long-distance dispersal than for median dispersal distances, due to an interaction between v_t and $\overline{U}$ (a higher $\overline{U}$, and thus larger σ_w, increase the probability of long-distance dispersal more for seeds with a lower v_t).

Our results imply that within a 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 infructurescence height (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 long-distance dispersal. 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 result in a decline in seed dispersal ability by wind, especially in species that are not able to increase H_0 sufficiently. Negative genetic effects due to isolation and small population size (Ellstrand and Elam 1993; Young *et al*. 1996; Booy *et al*. 2000) of rare grassland plant species may also affect their dispersal ability. However, these effects can only alter plant attributes related to dispersal (seed terminal velocity and release height) and are therefore likely to have less impact on dispersal ability than changes in the environmental attributes related to dispersal. Whenever a seed is dispersed, the most important determinant of the dispersal distance is the horizontal wind velocity. Changes in the frequency of occurrence of extreme wind speed 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 1 - CALCULATION OF THE MARKOV CHAIN DISPERSION PROCESS

This appendix shows how *a* and *b* in equation 5 are estimated from Thomson's (1987) 'simplest solution', using the procedure outlined by Rodean (1996) to preserve the so-called well mixed condition. The well-mixed condition states that if the concentration of an element is initially uniform in a turbulent flow, it will remain uniform if there are no sources or sinks - for consistency with the second law of thermodynamics. Thomson's (1987) 'simplest solution' in three dimensions results in the following:

$$
\begin{aligned}
du_1' = \Bigg[\Bigg[& -\frac{C_o<\varepsilon>}{2}\left(\lambda_{11}u_1'+\lambda_{13}u_3'\right)+\frac{\partial<\bar{u}_1>}{\partial x_3}u_3'+\frac{1}{2}\frac{\partial<\overline{u_1'u_3'}>}{\partial x_3}\Bigg]+\Bigg[\frac{\partial<\overline{u_1'u_1'}>}{\partial x_3}\left(\lambda_{11}u_1'+\lambda_{13}u_3'\right)+ \\
& \frac{\partial<\overline{u_1'u_3'}>}{\partial x_3}\left(\lambda_{11}u_1'+\lambda_{33}u_3'\right)\Bigg]\frac{u_3'}{2}\Bigg]dt+\sqrt{C_o<\varepsilon>}\;d\Omega
\end{aligned}
$$

$$
du_2' = \left[-\left(\frac{C_o<\varepsilon>}{2}+\frac{1}{2}\frac{\partial<\overline{u_2'u_2'}>}{\partial x_3}u_3'\right)\left(\lambda_{22}u_2'\right)\right]dt+\sqrt{C_o<\varepsilon>}\;d\Omega
$$

$$
\begin{aligned}
du_3' = \Bigg[\Bigg[& -\frac{C_o<\varepsilon>}{2}\left(\lambda_{13}u_1'+\lambda_{33}u_3'\right)+\frac{1}{2}\frac{\partial<\overline{u_3'u_3'}>}{\partial x_3}\Bigg]+\Bigg[\frac{\partial<\overline{u_1'u_3'}>}{\partial x_3}\left(\lambda_{11}u_1'+\lambda_{13}u_3'\right)+ \\
& \frac{\partial<\overline{u_3'u_3'}>}{\partial x_3}\left(\lambda_{13}u_1'+\lambda_{33}u_3'\right)\Bigg]\frac{u_3'}{2}\Bigg]dt+\sqrt{C_o<\varepsilon>}\;d\Omega
\end{aligned}
$$

where u_i' are the (instantaneous) turbulent velocities at position x_i and time t, C_0 ($\approx$5.0; see Pope 2000; p.504) is a similarity constant (related to the Kolmogorov constant) and λ_{11}, λ_{13}, λ_{22}, and λ_{33} are given by:

$$
\lambda_{11} = \frac{1}{<\overline{u_1'u_1'}>-\dfrac{<\overline{u_1'u_3'}>^2}{<\overline{u_3'u_3'}>}}
$$

$$
\lambda_{22} = <\overline{u_2'u_2'}>^{-1}
$$

$$
\lambda_{33} = \frac{1}{<\overline{u_3'u_3'}>-\dfrac{<\overline{u_1'u_3'}>^2}{<\overline{u_1'u_1'}>}}
$$

$$
\lambda_{13} = \frac{1}{<\overline{u_1'u_3'}>-\dfrac{<\overline{u_1'u_1'}><\overline{u_3'u_3'}>}{<\overline{u_1'u_3'}>}}
$$

where $<\overline{u_1}>$ is the mean longitudinal velocity (defined so that $<\overline{u_2}> = 0$), $<\overline{u_1'u_1'}>$ is σ_u^2, $<\overline{u_2'u_2'}>$ is σ_v^2, $<\overline{u_3'u_3'}>$ is σ_w^2 (σ_u^2, σ_v^2, and σ_w^2 are the standard deviations of the three velocity components), $<\overline{u_1'u_3'}>$ is the Reynolds stress, and $<\varepsilon>$ is the mean turbulent kinetic energy dissipation rate. The variation of these flow statistics with height can be computed from a one-dimensional Eulerian second order closure model developed for canopy flows as is described in Appendix 2.

The $d\Omega$ is a Gaussian random variable with zero mean and variance dt, which is dependent on the integral time scale T_L given by Pope (2000; p.486):

$$T_L = \frac{\tfrac{1}{2}\left(\sigma^2{}_u + \sigma^2{}_v + \sigma_w{}^2\right)}{<\bar{\varepsilon}>}$$

For the simulations we set dt = 0.05 $T_{L.}$

APPENDIX 2 - THE MARKOV CHAIN STG MODEL

The Markov chain STG model is a version of the forest seed dispersal model of Nathan *et al*. (2002b), adapted for grassland ecosystems. The general structure is presented in the Methods section and by Katul and Albertson (1998) and Katul and Chang (1999). In this appendix the estimation of the Eulerian flow statistics needed to drive the Lagrangian dispersion is described, followed by descriptions of the computational grid, numerical scheme, boundary conditions and closure constants.

Upon temporal and spatial averaging the conservation of momentum equations, and following the closure approximations of canopy flows, the Wilson and Shaw (1977) closure model simplifies to the following set of ordinary differential equations (ODEs):

Mean Momentum:

$$0 = -\frac{d < \overline{u'w'} >}{dz} - C_d a(z) < \bar{u} >^2$$

Tangential Stress Budget:

$$0 = - < \overline{w'^2} > \frac{d < \bar{u} >}{dz} + 2\frac{d}{dz}\left(q\lambda_1 \frac{d < \overline{u'w'} >}{dz} \right) - \frac{q < \overline{u'w'} >}{3\lambda_2} + Cq^2 \frac{d < \bar{u} >}{dz}$$

Longitudinal Velocity Variance:

$$0 = -2 < \overline{u'w'} > \frac{d < \bar{u} >}{dz} + \frac{d}{dz}\left(q\lambda_1 \frac{d < \overline{u'^2} >}{dz} \right) + 2C_d a(z) < \bar{u} >^3$$
$$- \frac{q}{3\lambda_2}\left(< \overline{u'^2} > - \frac{q^2}{3} \right) - \frac{2}{3}\frac{q^3}{\lambda_3}$$

Lateral Velocity Variance:

$$0 = \frac{d}{dz}\left(q\lambda_1 \frac{d < \overline{v'^2} >}{dz} \right) - \frac{q}{3\lambda_2}\left(< \overline{v'^2} > - \frac{q^2}{3} \right) - \frac{2}{3}\frac{q^3}{\lambda_3}$$

Vertical Velocity Variance:

$$0 = \frac{d}{dz}\left(3q\lambda_1 \frac{d < \overline{w'^2} >}{dz}\right) - \frac{q}{3\lambda_2}\left(< \overline{w'^2} > - \frac{q^2}{3}\right) - \frac{2}{3}\frac{q^3}{\lambda_3}$$

Where $q = \sqrt{< \overline{u_i' u_i'} >}$ is a characteristic velocity scale, C_d is a drag coefficient, $a(z)$ is a leaf area density, $\lambda_j = a_j \times L_{ws}$, with L_{ws} a characteristic length scale specified using the formulation given by Katul and Albertson (1998) and not permitted to increase at a rate larger than k, and a_1, a_2, a_3 and C are determined so that the flow conditions well above the canopy reproduce well-established surface layer similarity relations. With estimates of the five constants (a_1, a_2, a_3, C, and α), the above five ODEs can be solved iteratively for the five flow variables $< \overline{u} >, < \overline{u'w'} >$, $< \overline{u'^2} >$, $< \overline{v'^2} >$, and $< \overline{w'^2} >$, which are used to drive the Lagrangian model.

The computational grid

The computational flow domain was set from zero to 20×h. The grid node spacing is $\Delta z = 0.005$ m. This grid density was necessary due to rapid variability in leaf area density close to the canopy top. Parameter values at the exact location of the seed are calculated by interpolation between the grid nodes, or extrapolation in the case of $x_3 > 20 \times h$. To ensure seeds do not exit the atmospheric boundary layer during the computation of dispersal trajectories, the vertical position of a seed is not allowed to increase above 800 m.

The numerical scheme

The five ODEs for the Wilson and Shaw (1977) model were first discretized by central differencing all derivatives. An implicit numerical scheme was constructed for each ODE with boundary conditions to be discussed in the following section. The tridiagonal system resulting from the implicit forms of each discretized equation was solved using the *Tridag* routine from Press *et al.* (1992; pp.42-43) to produce the turbulent statistic profile. Profiles for all variables were initially assumed, and a variant of the relaxation scheme described by Wilson (1988) was used for all computed variables. Relaxation factors as small as 5% were necessary in the iterative scheme because of the irregularity in the leaf area density profile. The measured leaf area density was interpolated at the computational grid nodes by a cubic-spline discussed in Press *et al.* (1992; pp.107-111) to insure finite second derivatives of $a(z)$. Convergence is achieved when the maximum difference between two successive iterations in $< \overline{u} >$ did not exceed 0.0001%. We checked that all solutions were independent of Δz (as described in Katul and Albertson 1998). Calculation of dt is described in Appendix 1.

Boundary conditions and closure constants

Typically, the well-established flow statistics in the atmospheric surface layer provide convenient upper-boundary conditions for closure models. The boundary conditions used are:

$$z = 0 \qquad \begin{cases} \sigma_u = & 0 \\ \sigma_v = & 0 \\ \sigma_w = & 0 \\ u_* = & 0 \\ <\overline{u}>= & 0 \end{cases}$$

$$z = 20 \times h \quad \begin{cases} \sigma_u = & A_u u_* \\ \sigma_v = & A_v u_* \\ \sigma_w = & A_w u_* \\ u_* = & 1 \\ \dfrac{d<\overline{u}>}{dz} = & \dfrac{u_*}{k_v(z-d)} \end{cases}$$

Where σ_θ is the standard deviation of any flow variable θ $(=<\overline{\theta'^2}>^{1/2})$, $A_u = 2.2$, $A_v = 2.0$, and $A_w = 1.4$ (Panofsky and Dutton 1984).

The closure constants are dependent on the choice of the boundary conditions and are determined by assuming that in the atmospheric surface layer (z>2h), the flux-transport term is negligible and that $<\overline{u'w'}>$, $<\overline{u'^2}>^{1/2}$, and $<\overline{w'^2}>^{1/2}$ become independent of z for near-neutral conditions. These simplifications result, after some algebraic manipulations (*e.g.* see Katul and Albertson 1998; Katul and Chang 1999), in the following relationships between A_u, A_v, and A_w and a_2, a_3, and C:

$$a_2 = \frac{A_q(A_u{}^2 - A_w{}^2)}{6}$$

$$a_3 = \frac{-A_q{}^3(A_u{}^2 - A_w{}^2)}{A_w{}^2 - \dfrac{A_q{}^2}{3}}$$

$$C = \left(\frac{A_w}{A_q}\right)^2 - \frac{2}{A_q{}^2(A_u{}^2 - A_w{}^2)}$$

Where $A_q = (A_u^2+A_v^2+A_w^2)^{1/2}$. The closure constant a_1 is determined by noting that the eddy-diffusivity is $k\times(z\text{-}d)\times u_*$ in the surface layer. Hence, $q\lambda_1$ becomes identical to $k\times(z\text{-}d)\times u_*$ leading to $a_1 = 1/A_q$. The above equations are the first analytic expressions relating closure constants to ASL boundary conditions for the Wilson and Shaw (1977) model as described by Katul and Albertson (1998) and Katul and Chang (1999). Table A1 summarizes the closure constants used resulting from our choice of A_u, A_v, and A_w.

Table A1. Closure constants used in the Markov chain STG model for A_u = 2.2, A_v = 2.0, and A_w = 1.4.

Closure constant (Wilson and Shaw 1977)	Value
A_1	0.30
A_2	1.58
A_3	20.8
α	0.07
C	0.12
C_d	0.20

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 north-west 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 m^2). 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/m^2). 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.

Colonization characteristic	Relationship with log transformed population size		Relationship with site productivity	
	Plumed seeds	Plumeless seeds	Plumed seeds	Plumeless seeds
Seed				
Terminal velocity	**o**	+	**o**	+
Germination ability	+	+	- (*Cd*)	+
Plant				
Seed production	+	- (*Sp*)	**o**	+
Seed release height	**o**[1]	**o**	**o**	+
Variation in terminal velocity	+	-	**o**	**o**
Vegetation				
Height	**o**	**o**	+	+
Leaf area index	Not measured		Not measured	

[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.

Table 2. Values of the model input parameters used in this study (species average and range).

Model parameter	*C. dissectum*	*H. radicata*	*C. jacea*	*S. pratensis*	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 Rijkoort 1983

(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/m^2 (except for *H. radicata*: ca. 100-450 g/m^2). 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).

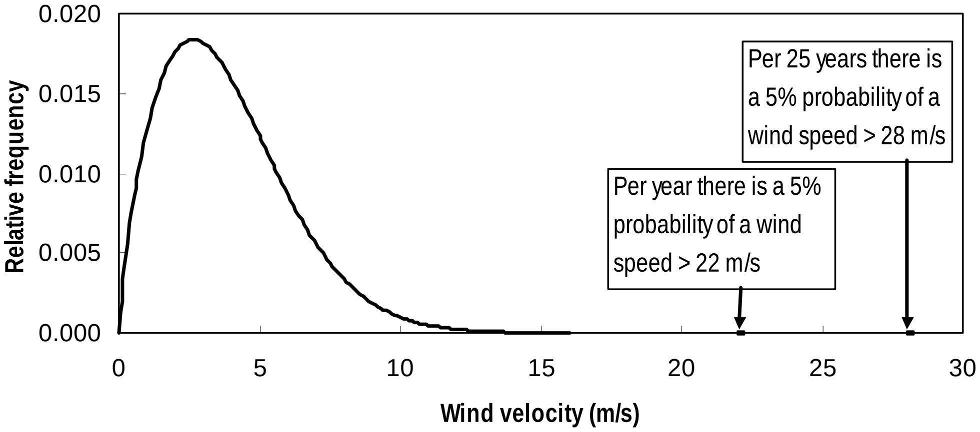

Figure 1. Relative frequencies of hourly-averaged wind velocities at 10 m height for the interior of The Netherlands (Weibull distribution $f(U) = k/a \cdot (U/a)^{k-1} \cdot \exp(-(U/a)^k)$; $k = 1.74$; $a = 4.3$). Wind velocities >16 m/s cannot be predicted reliably using the fitted Weibull distribution,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

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.

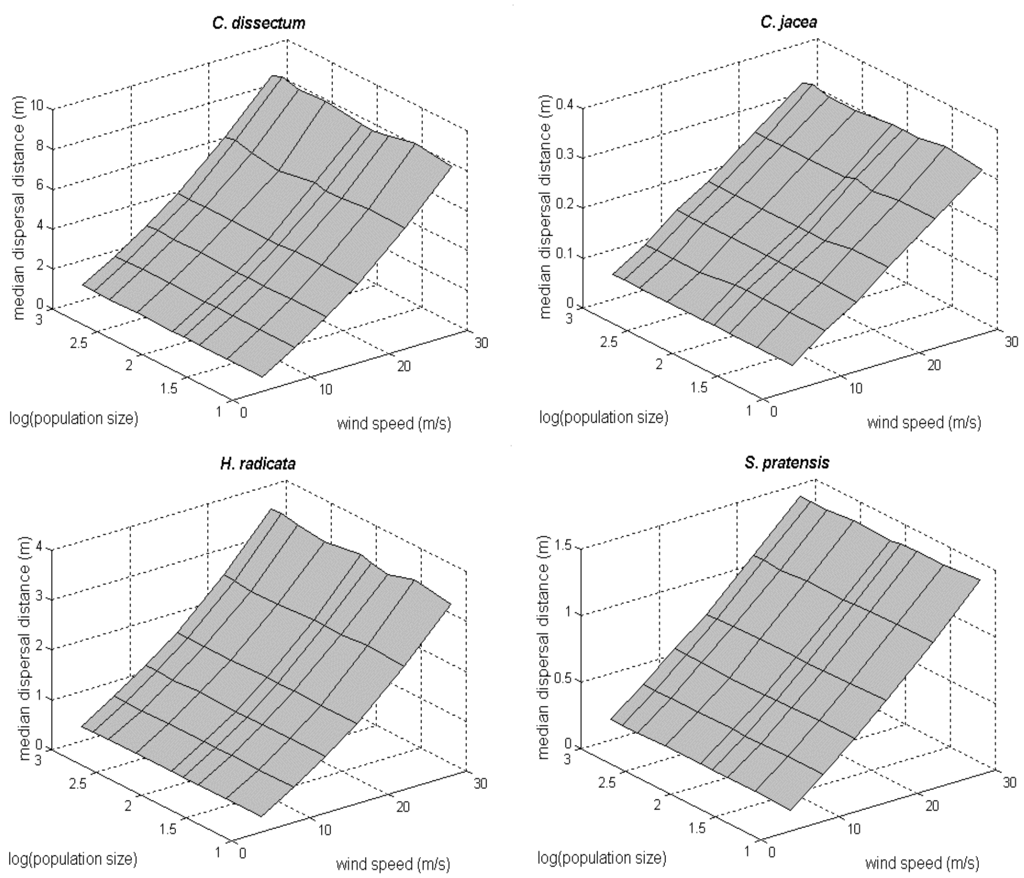

Figure 2. Median dispersal distances for different population sizes (log transformed) and wind velocities.

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

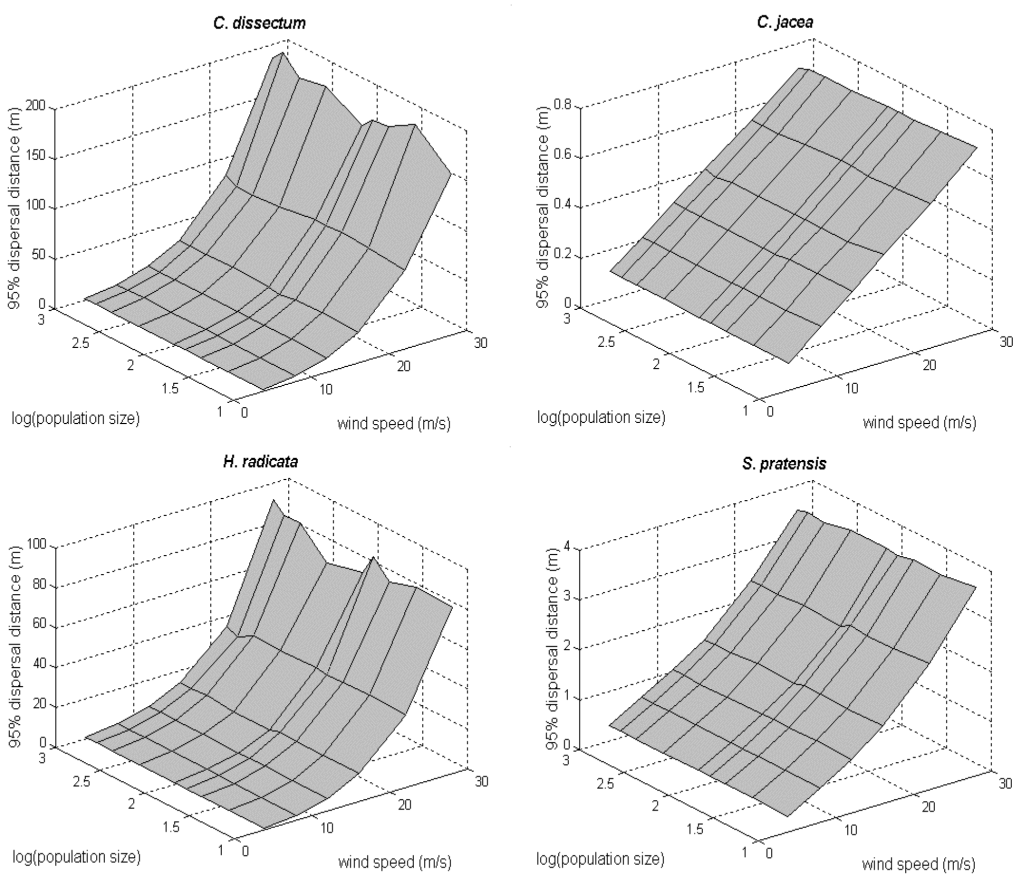

Figure 3. 95-Percentile dispersal distances for different population sizes (log transformed) and wind velocities.

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

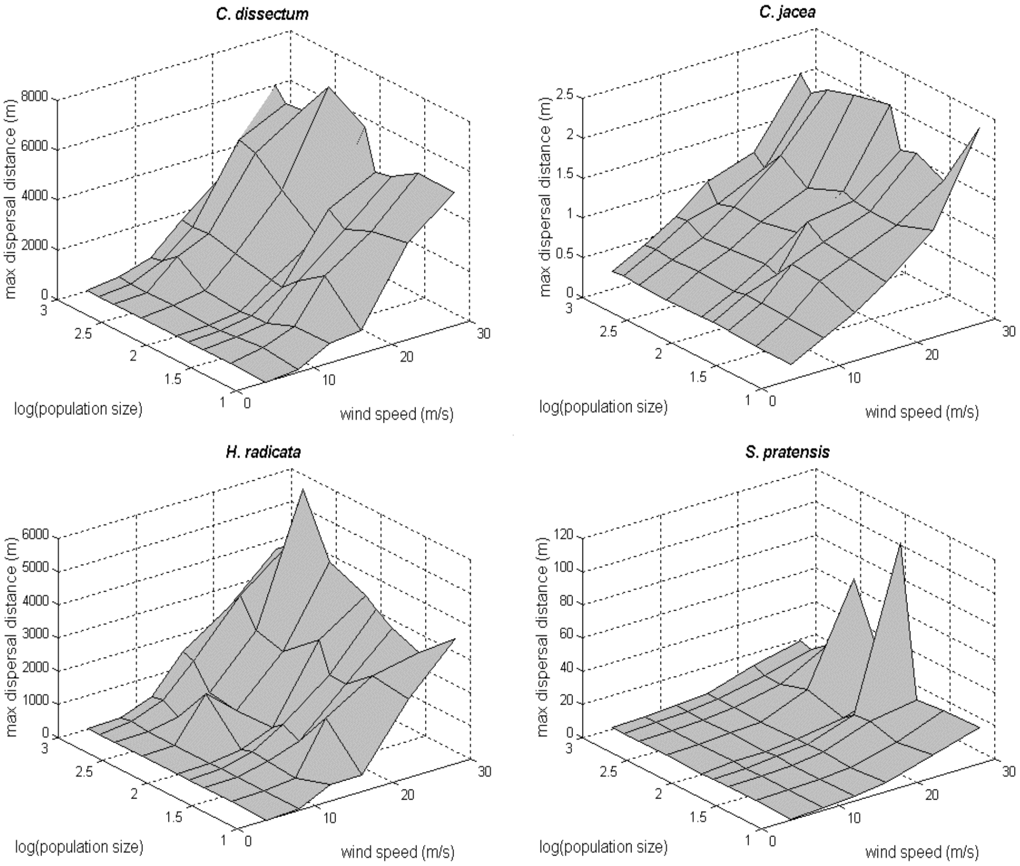

Figure 4. Maximum dispersal distances for different population sizes (log transformed) and wind velocities.

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.

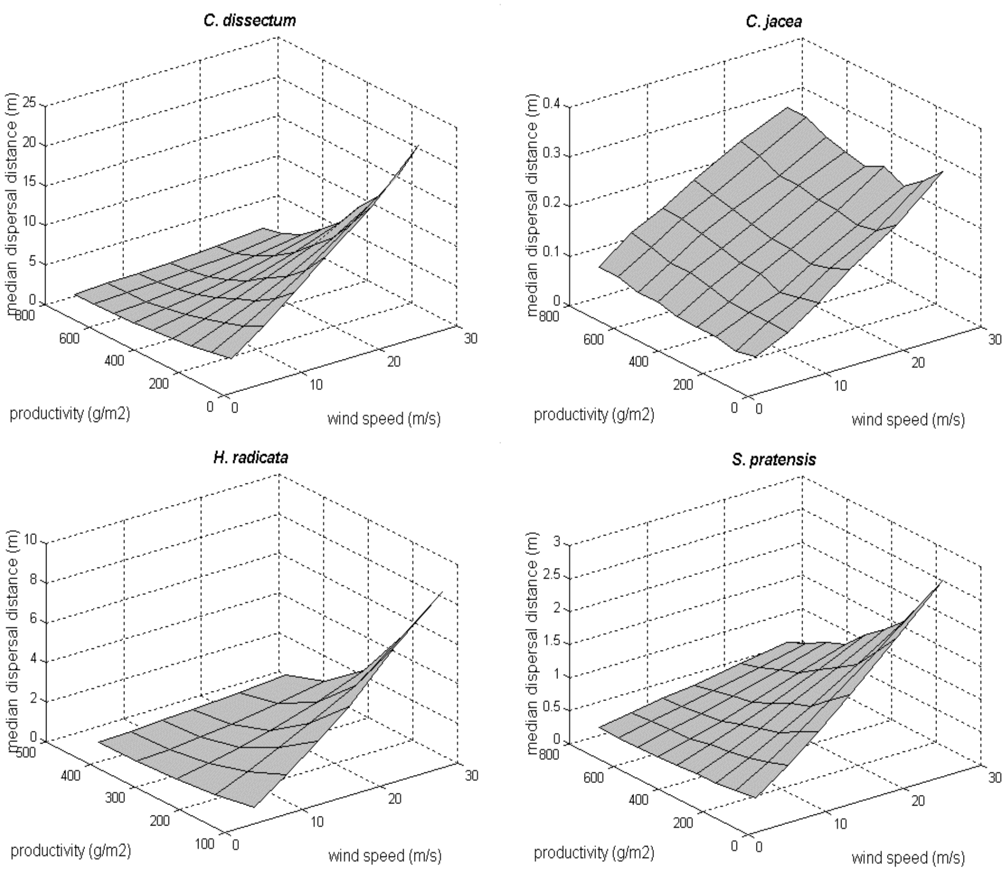

Figure 5. Median dispersal distances for different site productivities and wind velocities.

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

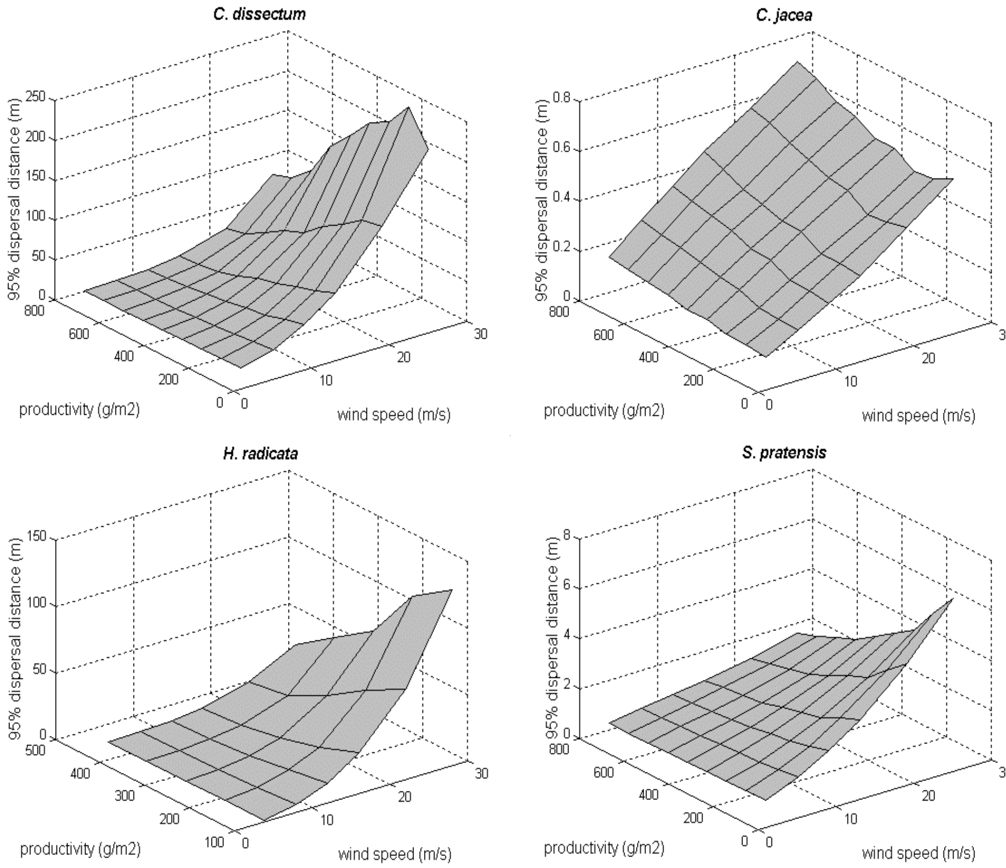

Figure 6. 95-Percentile dispersal distances for different site productivities and wind velocities.

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 infructurescence height of the studied species also increases, but less than the vegetation height (though hardly less in *C. jacea*). The increase in infructurescence 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,

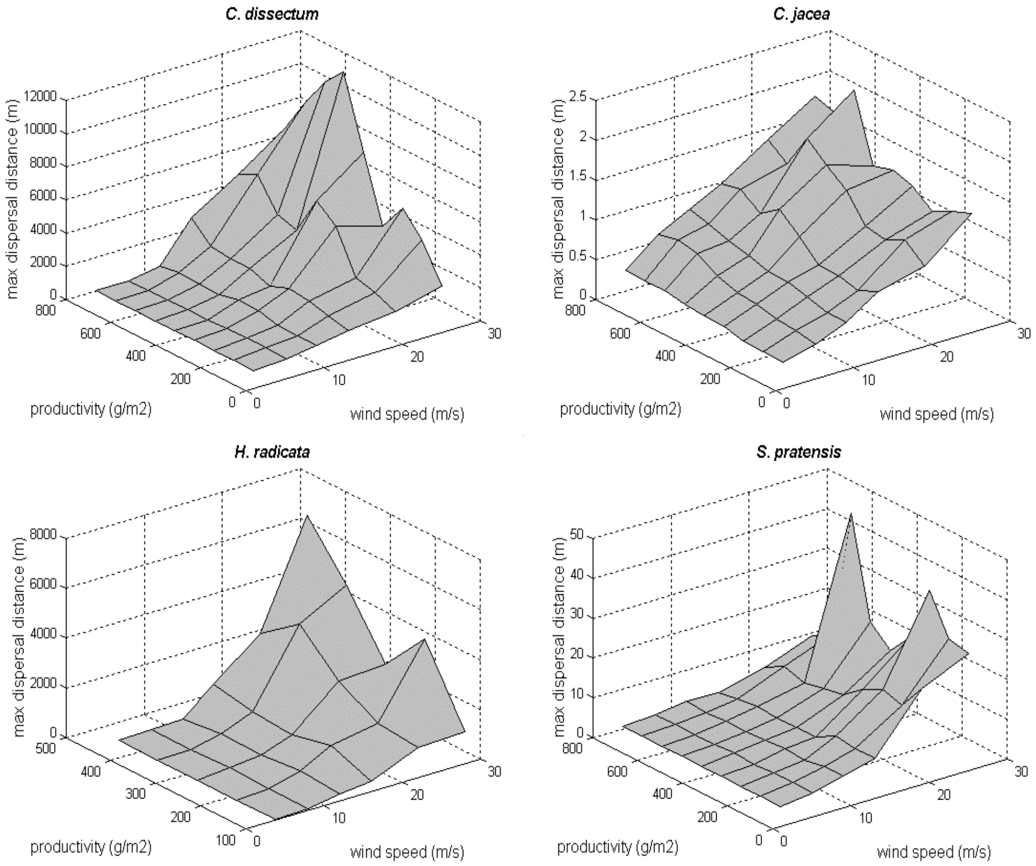

Figure 7. Maximum dispersal distances for different population sizes (log transformed) and wind velocities.

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 ρ =0.965, $p<0.001$, 2-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 (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. Over all, 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/m^2; 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/m^2, *H. radicata* 180 g/m^2, *C. jacea* 500 g/m^2, *S. pratensis* 400 g/m^2; 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/m^2, for *H. radicata* to 450 g/m^2. 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.

Species	Seed production per population (× 10^3) #				Germination percentage (%) *			
	O	HF	EU	W	**O**	HF	EU	W
C. dissectum	**30**	2.6	30	30	**52**	48	34	52
H. radicata	**160**	14	160	160	**61**	54	61	61
C. jacea	**190**	19	340	190	**85**	81	91	85
S. pratensis	**220**	32	390	220	**19**	13	30	19

Species	95-Percentile dispersal distance (m)				Germinable seeds at distance > 95-perc. (× 10^3)			
	O	HF	EU	W	**O**	HF	EU	W
C. dissectum	**81**	81	25	110	**0.8**	0.1	0.5	0.8
H. radicata	**36**	36	13	49	**4.9**	0.4	4.9	4.9
C. jacea	**0.56**	0.56	0.57	0.62	**8.1**	0.8	16	8.1
S. pratensis	**2.4**	2.4	1.2	2.8	**2.1**	0.2	5.9	2.1

[#] 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 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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5. Fragmentation and connectivity of species-rich semi-natural grasslands

M.B. Soons, J.H. Messelink, E. Jongejans, and G.W. Heil

SUMMARY

1. Detailed understanding of habitat fragmentation is essential for species conservation. However, few studies reconstructed the actual habitat fragmentation process. Also, few studies quantified the effects of habitat fragmentation on functional habitat connectivity for plant species. We reconstructed the fragmentation of nutrient-poor semi-natural moist grasslands in The Netherlands to answer the questions: When, at what rate, and by how much have habitat area and functional habitat connectivity been reduced? How connected are current habitat patches?

2. We used a vegetation-based habitat classification system to map habitat patches. This system is based on tools that recently became available, including vegetation databases with detailed historic data. We mapped habitat patches in one 10×11 km area for a time series spanning the 20th century to quantify the fragmentation process. We mapped current habitat patches in three areas to quantify current habitat connectivity. Tests of the classification framework using population maps of selected species and a seed addition experiment show its accuracy.

3. We quantified functional habitat connectivity by relating the spatial configuration of habitat patches to the colonization capacity of selected plant species. Our connectivity measure is new and more realistic than previous measures, because it includes realistic seed dispersal distributions and long-distance dispersal. We used a mechanistic simulation model to quantify long-distance seed dispersal by wind.

4. The area and functional connectivity of nutrient-poor semi-natural moist grasslands have decreased dramatically during the 20th century, especially during the first half. Currently their area is very small and their connectivity very low, even for species with plumed seeds and high wind dispersal ability. Linear landscape elements hardly contribute to the area and functional connectivity. Regional survival of plant species restricted to the studied grasslands is now completely dependent on the survival of a few large populations in nature reserves. The other remaining populations are decreasing in number and size, and have low colonization capacity. All remaining populations are practically isolated regarding seed dispersal and the probability that they colonize new or restored sites is very low (unless dispersal is assisted by man).

Key words: functional connectivity, grassland, habitat fragmentation, seed dispersal, wind dispersal

INTRODUCTION

The reallocation of land for agricultural and industrial purposes, settlements, and infrastructure has resulted in the fragmentation of (semi-)natural areas all over the world. Habitat fragmentation still occurs at an alarming rate and poses a major threat to the regional survival of many plant species (Saunders *et al*. 1991; Tilman *et al*. 1994; Vitousek *et al*. 1997; Hanski and Ovaskainen 2000). Firstly, habitat fragmentation reduces total habitat area, so that fewer individuals of a species restricted to that habitat can survive. Secondly, habitat fragmentation reduces the connectivity between habitat patches, so that colonization of unoccupied habitat patches and gene flow between occupied patches decrease. Thirdly, habitat fragmentation reduces the area of habitat patches. This decreases the size and thus the survival probability of the populations in habitat patches. It also makes the internal patch conditions more vulnerable to influences from the surroundings, which can reduce habitat patch quality. Regional species survival depends on the rate and spatial pattern of habitat fragmentation, and on the population dynamics and colonization capacity of the species (Keymer *et al*. 2000; Tischendorf and Fahrig 2000; Vos *et al*. 2001; Moilanen and Nieminen 2002).

A detailed understanding of habitat fragmentation in relation to species dynamics and colonization capacity is essential for species conservation. However, few studies have reconstructed the actual habitat fragmentation process in grasslands. This is in part due to the difficulty of habitat classification for plant species, especially at sites where the species is not present and for past time periods. Also, few studies have quantified the effects of habitat fragmentation on the functional habitat connectivity for plant species. Functional habitat connectivity (sensu Tischendorf and Fahrig 2000) reflects the probability of colonization of unoccupied habitat patches and gene flow between occupied habitat patches. Many different connectivity measures have been used (Schumaker 1996; Tischendorf and Fahrig 2000; Vos *et al*. 2001; Moilanen and Nieminen 2002), but most of them fail to quantify functional habitat connectivity in a realistic way for plant species. This is primarily because most of them do not include realistic seed dispersal distributions, and especially long-distance dispersal. Long-distance seed dispersal is a crucial component of plant colonization capacity, but notoriously difficult to quantify (Cain *et al*. 2000; Nathan 2001; Nathan *et al*. 2003). Also, many measures of functional habitat connectivity do not meet one or more of the following requirements (Tischendorf and Fahrig 2000; Moilanen and Nieminen 2002): 1) consideration of all habitat patches within species' colonization and gene flow distances, 2) consideration of relative contributions to colonization and gene flow by habitat patches at different distances and with populations of different size and/or colonization capacity, 3) consideration of the effects of the landscape matrix on dispersal, 4) consideration of both within-patch and between-patch dispersal, and 5) expression of connectivity per equal-sized unit of habitat. The longevity of seed banks should also be taken into account, because this contributes to the landscape connectivity in time (Fahrig 1992; Keymer *et al*. 2000).

We reconstructed the fragmentation of species-rich, nutrient-poor semi-natural grasslands to answer the following questions:

- When, at what rate, and by how much have the habitat area and the functional habitat connectivity been reduced?
- How connected are the current habitat patches?

Answering these questions increases our understanding of the habitat fragmentation process and its consequences for functional habitat connectivity. Also, it gives information on the current habitat connectivity for grassland species, which is essential for species conservation measures. Our approach is based on a set of tools that recently became available. Detailed historic vegetation data have been digitized and are now available (*e.g.* Hennekens *et al*. 2001). A mechanistic dispersal model is available for the quantification of long-distance seed dispersal by wind in grasslands (this thesis, Chapter 3). The colonization characteristics of wind-dispersed grassland plants have been measured (Soons and Heil 2002). Advanced GIS tools are available to combine spatial data from many sources to create and analyze habitat maps, and to calculate connectivity measures that involve spatial map operations. In this study we show how these tools can be combined to provide quantitative data on habitat fragmentation and a new, realistic, measure of functional habitat connectivity.

METHODS

To quantify the rate and spatial pattern of the fragmentation of nutrient-poor semi-natural grasslands we created maps of the distribution of these grasslands. We mapped the grassland habitat for a time series to quantify the habitat fragmentation process in one study area (De Achterhoek). The time series spans the 20th century, with analyses carried out for the years 1900, 1950, and 2000. We mapped the current grassland habitat in three different study areas to assess the current habitat connectivity. We combined the habitat fragmentation data with data on the colonization capacities of four wind-dispersed grassland forbs to quantify the functional habitat connectivity for wind-dispersed grassland species. Species nomenclature follows Van der Meijden (1990). Syntaxa nomenclature follows Schaminée *et al*. (1999).

The study system

We carried out this study in The Netherlands, one of the world’s most densely populated countries. Human population growth, increasing industrialization and intensification of agriculture have resulted in large-scale, well-documented landscape changes in The Netherlands during the 20th century. The nutrient-poor semi-natural grasslands that were once widespread have become highly fragmented. The negative consequences of habitat fragmentation are affecting many once-common grassland species (Ouborg 1993; Willems 2001; Soons and Heil 2002).

Figure 1. Location of the three study areas in the Pleistocene soil areas (darker shade) of The Netherlands. Location of Pleistocene soil and flora areas adapted from Weeda (1990).

Different types of nutrient-poor semi-natural grasslands occur throughout The Netherlands (Schaminée *et al*. 1999). For an accurate and practical definition of the studied habitat we restricted this study to the floristically similar Pleistocene soil areas of The Netherlands (Fig. 1). The nutrient-poor grassland fragments that still occur in these areas belong for a large part to the *Molinietalia, Nardetalia*, and *Caricetalia*. This study focuses on these grassland types. They contain several floristically closely related communities that we used to define the studied habitat (Table 1; see *Habitat maps* section).

Habitat was mapped in three study areas that represent different land use histories. The Achterhoek (AH) area is 11x10 km (Fig. 1; lower-left coordinate

51°59’20” N, 6°25’15” E). Until the end of the 19th century, wet parts of the AH area contained large bogs and fens. Small settlements were located in the driest areas. In between, nutrient-poor moist grasslands were abundant. Most of these grasslands were used for cattle grazing. Around 1900 land drainage and peat cutting had already started to reduce the area of the wetlands and moist grasslands. This process accelerated during the first half of the 20th century, when artificial fertilizers became available. However, land use remained relatively extensive and small-scale until the 1970’s, when a major land reallotment procedure resulted in the loss of small-scale patchiness and the disappearance of almost all remaining wet or moist (semi-)natural areas.

The Gelderse Vallei (GV) area is 10x10 km (Fig. 1; lower-left coordinate 51°58’31” N, 5°31’58” E). This area was intensively cultivated much earlier than the AH area. Although originally also a fen-filled area, large parts of the GV area were drained and turned into arable land before 1900. The wettest areas, around brooks and rivers, remained in use as grazing lands until the early decades of the 20th century. From the first half of the 20th century onwards the area has been a highly productive agricultural area.

The Veluwe (VE) area is 10x10 km (Fig. 1; lower-left coordinate 52°13’36” N, 5°39’02” E). This is the driest of the three study areas. Most of the area was in use as common grazing ground for sheep during the Middle Ages. This resulted in the formation of extensive heathlands. Overgrazing resulted in the formation of drifting sands in the driest areas, and before 1900 people started planting pine trees to stabilize the sand. Large-scale sheep grazing was abandoned in the early decades of the 20th century. Since then more land has been planted with trees, and the moist and fertile areas were drained and reclaimed for agriculture.

Selected plant species

For our study we selected four wind-dispersed grassland forbs that co-occur in nutrient-poor semi-natural grasslands. Like their habitat, the species all were common in the Pleistocene soil areas of The Netherlands, but are now relatively rare. The species are representative of two common seed dispersal strategies in grasslands. *Cirsium dissectum* (L.) Hill and *Hypochaeris radicata* L. (both *Asteraceae*) have plumed seeds that are adapted to long-distance dispersal by wind. Seeds of *Centaurea jacea* L. (*Asteraceae*) and *Succisa pratensis* Moench (*Dipsacaceae*) are also dispersed by wind, but only over short distances. *C. jacea* has plumeless, smooth-surfaced seeds that are ejected from the seed head, and transported further by wind, when wind gusts fling the seed head back and forth (Bouman *et al*. 2000). *S. pratensis* has seeds with a persistent calyx, which is dry and hairy and increases the surface area of the seed without adding much weight (Bouman *et al*. 2000). All four species are hemicryptophytes and overwinter as leaf rosettes (Van der Meijden 1990; Grime *et al*. 1988). They all propagate sexually via seeds and asexually by side-rosettes and clonal extension (Hartemink *et al*. submitted), and have transient seed banks (Thompson *et al*. 1997). More details on the species are given by Soons and Heil (2002).

Table 1. The vegetation communities that define the grassland habitat studied in this paper. These communities often occur adjacent to each other and may show floristic gradients in contact zones. A few closely related communities that are very rare or not present in the study areas are not listed. For detailed information on the communities we refer to Schaminée et al. (1999).

Vegetation community	Description	Habitat class
Cirsio dissecti–Molinietum	Semi-natural, relatively nutrient-poor grassland communities at moist sites (commonly inundated during winter)	1
Gentiano pneumonanthes-Nardetum	Extensively managed, nutrient-poor grassland communities at moist sites, often adjacent to moist heathland	1
Campylio-Caricetum dioicae	Nutrient-poor wetland communities, commonly inundated during winter	1
Carici curtae-Agrostietum caninae	Extensively managed, (relatively) nutrient-poor wetland communities, e.g. in the lagg zone of bogs	1
Ericetum tetralicis (esp. *orchietosum*)	Semi-natural, nutrient-poor heathland communities at moist to wet sites	2
Basal/derivative communities	Communities that resemble the communities listed above but lack (several of) the characteristic species	2

Habitat maps

Mapping the habitat of plant species is a difficult task. For most plant species the exact biotic and abiotic conditions that define its habitat are unknown. Even if these conditions are known, the effort required to test for these conditions at every site in a landscape is enormous. On the other extreme, the use of simple species presence/absence data to define its habitat is a too simple approach. There are habitat patches in which the species is not present because it has not dispersed to those patches. Also, there are patches with a transient status, in which some individuals of the species are present as relicts of a former situation, but where the population is now declining and no rejuvenation occurs. We therefore made a set of basic assumptions and designed an objective habitat classification system to make the mapping of habitat feasible.

1) We defined patches using borders of land parcels and of legend categories on topographical survey maps (1:25000, Topografische Dienst, Emmen, NL). For the habitat maps of the years 2000, 1950, and 1900 we used topographic maps dating from 1995-1999, 1947-1957, and 1886-1912, respectively. We assumed that the interior of every patch is homogeneous.

2) We assumed that all patches classified on topographic maps as built-up, paved, forested, or arable land, open water, or sand contain no grassland habitat. Thus, only dry to wet grasslands and heathlands remained to be classified.

3) We based our habitat classification on vegetation communities, for several practical reasons. Firstly, a detailed description of past and present vegetation communities in The Netherlands is available and provides an accessible reference system (Schaminée *et al*. 1999). Secondly, the use of vegetation communities rather than only

the selected species allows more accurate classification of patches in which the selected species are not present. Thirdly, this approach requires no detailed studies on the biotic and abiotic habitat conditions of the selected species. For the current situation visual inspection of field sites suffices. For historic situations detailed vegetation data are available for many sites and species. And in this way, the accuracy of the habitat classification is best comparable between past and present situations.

4) We used a set of floristically closely related grassland communities, in which *C. jacea*, *C. dissectum*, and *S. pratensis* co-occur, to define the studied habitat (Table 1). Within the study areas the three species co-occur almost exclusively in these grassland communities, although with different probability of occurrence for each community. Therefore, we assigned the communities to two habitat classes. Class 1 indicates a very high probability of occurrence of *C. jacea*, *C. dissectum*, and *S. pratensis.* Class 2 indicates a lower probability of occurrence of all three species (Table 1). *H. radicata* co-occurs with the other three species in the grassland communities, but is also common in drier grassland communities and road verges.

5) If the vegetation community of a patch could not be determined we assessed the presence of 18 indicator species (Table 2). These species were selected based on their indicative value for, and commonness in, the grassland communities listed in Table 1. When six or more indicator species were present we classified a habitat patch as class 1. When three to five indicator species were present we classified a habitat patch as class 2.

Table 2. Indicator species for the habitat classification. All indicator species are representative of the grassland communities listed in Table 1. Some species are also representative of other vegetation types, but the species co-occur almost exclusively in the defined habitat in the study areas.

Indicator species	
Carex dioica L.	Red list species
Carex hostiana DC.	Red list species
Carex panicea L.	
Carex pulicaris L.	Red list species
Centaurea jacea L., *s.l.*	
Cirsium dissectum (L.) Hill	Red list species
Dactylorhiza maculata (L.) Soó	Red list species
Danthonia decumbens (L.) DC.	
Equisetum palustre L.	
Erica tetralix L.	
Gentiana pneumonanthe L.	
Juncus squarrosus L.	
Molinia caerulea (L.) Moench	
Pedicularis sylvatica L.	Red list species
Pinguicula vulgaris L.	Red list species
Platanthera bifolia (L.) Rich.	Red list species
Polygala serpyllifolia Hose	Red list species
Succisa pratensis Moench	

6) For the habitat maps of the year 2000 we visited all nature reserves in each study area. We recorded the vegetation community or presence of indicator species to classify them as habitat class 1, 2, or non-habitat. For the current Dutch agricultural landscapes, it is safe to assume that all patches that are not nature reserves are intensively used by man for other purposes (*e.g.* agriculture, sports). Still, we checked all grasslands of odd size or shape to see if they might be classified as habitat. We also searched linear landscape elements (see next section) for the presence of indicator species and classified them accordingly.

7) For the habitat maps of 1950 we used historic vegetation and species distribution data from floristic databases: the ALTERRA Dutch Vegetation Database (Hennekens *et al*. 2001), the database of the Province of Gelderland, and FLORBASE, the floristic database containing spatial information on the occurrence of plant species in The Netherlands. The data are provided by nature conservation organizations, individual biologists, and (regional) government. We also used historic descriptions of the nature reserves (archives of Staatsbosbeheer, Arnhem) and interviews with farmers and other local people (Messelink 2001). For the nature reserves and other floristically rich sites adequate data were available to classify patches. However, there were several potential

Table 3. Habitat classification criteria. Habitat class 1 comprises grassland patches that almost certainly contain the grassland communities defined as class 1 in Table 1. Habitat class 2 comprises grassland patches that highly likely contain the grassland communities defined as class 2 in Table 1. Habitat class 3 consists of grassland patches that are relatively moist and nutrient-poor, but which cannot be assigned a class value of 1 or 2 because too little information on the patch is available. If a patch meets the criteria of multiple classes, it is assigned the numerically lowest class value.

Habitat class	2000	1950	1900
1	All patches with - vegetation communities listed as class 1 in Table 1, or - six or more indicator species	As class 1, 2000	As class 1, 2000, and moist meadows and moist heathlands in the wet areas (‘Velden’, ‘Broeken’), but not in bogs, on the topographic map
2	All patches with - vegetation communities listed as class 2 in Table 1, or - three to five indicator species	As class 2, 2000	As class 2, 2000, and heathlands in the wet areas (‘Velden’, ‘Broeken’), but not in bogs, on the topographic map
3		All patches indicated as moist heathlands on the topographic map of 1950, and patches indicated by literature or in interviews	Heathlands and meadows in the border zone of bogs on the topographic map

habitat patches (especially sites that were marked as moist grassland or heathland on the topographic maps) for which no data were available. These sites could not be classified as habitat class 1or 2, but there was still a probability that they were habitat patches. We therefore classified them as habitat class 3.

8) For the habitat maps of 1900 only few vegetation and species data were available from the sources listed above. We therefore also used detailed historic landscape and vegetation descriptions (Messelink 2001) and information from the historic topographic maps. The maps from 1886-1912 contain more detail on land use and soil moisture than the later maps. They also show the old names of fields, which often reflect their purpose or vegetation composition. We combined all these sources of information to create objective and generally applicable criteria for the mapping of habitat for the year 1900. Table 3 gives an overview of the habitat mapping criteria.

Species distribution maps

The selected species may also occur at sites that do not meet the habitat criteria, *e.g.* in linear landscape elements such as road verges. To assess the accuracy of our habitat classification system and to quantify the presence of the selected species, we made distribution maps for the selected species in the study areas for the year 2000. To make these maps we searched all semi-natural areas in the study areas for the selected species. It was not feasible to also search all linear landscape elements. Therefore, we searched these in the AH area only. This area was selected, because road verge populations of the selected species in the AH area are natural, while in the GV and VE areas *C. jacea* has been sown in road verges. We searched the linear landscape elements on a random basis and when there was information suggesting that *C. jacea*, *C. dissectum*, or *S. pratensis* may previously have been present in the surroundings. This information was obtained from the habitat maps and the data sources listed under (7) in the previous section. In total ±50% of all linear landscape elements were investigated.

The seed addition experiment

To further assess the accuracy of our habitat classification system we carried out a seed addition experiment. This experiment allows comparison of seedling establishment between sites classified as habitat and non-habitat. We selected 10 nature reserves and 10 road verges in the AH area for the experiment. Nature reserves were selected so that each habitat class was represented, and also included three recently restored sites. At the restored sites the topsoil was removed to remove nutrients and unwanted species and to create an opportunity for establishment of rare species. Hydrological conditions were also restored. The restoration measures were carried out in winter 1999/2000, so that at the time of the experiment hardly any vegetation was present at the restored sites. Road verges were selected to represent the full range in productivity and vegetation openness present in the AH area. Only road verges along unpaved roads were selected, because these are the least disturbed.

At each site, seeds of the selected species were sown in 8 plots (5×50 cm) per species. These plots were randomly located along a 20 m long transect and intermixed with 8 plots per species in which no seeds were sown (the control plots). We measured vegetation productivity and openness to quantify site conditions. We clipped aboveground biomass (excluding moss layer) in three vegetation plots (20×20 cm) per site in July 2001. Biomass samples were dried 70 hrs in a stove at 75°C, weighed stove-dry and averaged per site. We estimated vegetation height and percentage cover at peak standing crop.

Seeds were added after the vegetation was mown, October-November 2000. Per plot 100 seeds were sown for *H. radicata, C. jacea,* and *S. pratensis* (800 seeds per site). For *C. dissectum* 70 seeds were sown per plot (560 per site), because we could not collect more seeds. All seeds were collected from several large populations in July-September 2000, mixed, counted, and stored in the dark at room temperature until the start of the experiment. Before seeds were sown, all rosettes of the selected species already present in the plots were recorded. The number of rosettes of the selected species was recorded again for all plots one year after sowing, in October-November 2001. The number of individuals established from seed in each plot in 2001 was calculated as the number of rosettes in 2001 minus the number of rosettes in 2000. In case of doubt whether a rosette was a seedling or clonal offspring, the rosette was dug out. If a rhizome was present, the rosette was left out of the analysis. Seedling establishment of the added seeds was calculated per species as the total number of individuals established in 2001 in the seed addition plots of each transect minus the total number of individuals established in 2001 in the control plots of that transect. All seedlings of the selected species in the plots were removed at the end of the experiment.

Quantification of habitat fragmentation and connectivity

Quantitative analyses of habitat fragmentation and functional habitat connectivity for the three habitat classes were carried out as scenario analyses. The analysis of habitat class 1 is the ‘worst-case’ scenario, where only patches assigned class 1 are really habitat for the selected species. The analysis of habitat class 1 and 2 together is the ‘intermediate’ scenario, where patches assigned class 1 or 2 are habitat. The analysis of habitat class 1, 2, and 3 together is the ‘best-case’ scenario, where all patches assigned class 1, 2, or 3 are habitat.

We used several measures to quantify habitat area and configuration. We calculated four general and easily interpreted quantitative habitat descriptors: total habitat area, number of patches, average (and range in) patch size, and average (and range in) distance of patches to their nearest neighbors. As a measure of functional habitat connectivity we calculated the species-specific probability that seeds dispersing from a habitat patch over a distance r reach another habitat patch ($C_{ij}(r)$, see below). This measure is the result of 1) the probability that a seed that disperses over distance r lands at a habitat site ($O_{ij}(r)$, *cf.* Wiegand *et al.* 1999), and 2) the probability that a seed disperses over a distance r ($D_i(r)$, the distribution of seed dispersal distances).

$O_{ij}(r)$ is the probability that a seed that disperses over distance r from a habitat unit of class i lands at a habitat unit of class j. For each i:

$$O_{ij}(r) = \frac{1}{n} \sum_{h=1}^{h=n} \frac{N_{hj}(r)}{N_h(r)}$$

where $h = 1, ..., n$ are the habitat units of class i, $N_{hj}(r)$ is the number of units of habitat class j at distance r from habitat unit h, and $N_h(r)$ is the total number of landscape units at distance r from a habitat unit i. We calculated $N_{hj}(r)$ using a raster GIS (PCRaster) and digitized habitat maps with a resolution of 4×4 m (thus, unit size 4×4 m).

$D_i(r)$ is the probability that a seed that disperses from a habitat unit of class i disperses over a distance r. We calculated $D_i(r)$ for each species by simulating seed dispersal trajectories of 10,000 seeds using a mechanistic wind-dispersal model that is able to simulate long-distance seed dispersal (the Markov chain Synthetic Turbulence Generation model in this thesis, Chapter 3). For the simulations we used average values (incl. standard deviations) of the dispersal parameters (seed terminal velocity, release height, and vegetation height) measured for each of the selected species under natural conditions (Soons and Heil 2002). We simulated dispersal for the average vegetation conditions and the average wind velocity distribution during a dispersal season (June-October) in the interior of The Netherlands (Royal Netherlands Meteorological Institute, www.knmi.nl). For simplicity we assumed $D_i(r)$ to be equal for i= 1, 2, 3.

For each species $C_{ij}(r)$ of the study areas was calculated by multiplying $O_{ij}(r)$ by $D_i(r)$. The resulting probability distribution $C_{ij}(r)$ is a species-specific measure of functional habitat connectivity: it is the probability that a seed dispersing from a habitat unit of class i disperses to a habitat unit of class j at dispersal distance r. The probability of patch colonization can be assessed for each population by multiplying $C_{ij}(r)$ by the number of germinable seeds produced. Seed production and germination ability were determined in a previous study (Soons and Heil 2002).

RESULTS

The habitat maps

The habitat maps are presented in Fig. 2-6. In the GV area, only three patches in nature reserves matched the habitat criteria in 2000. In the VE area only one nature reserve contained an area that matched the habitat criteria of class 1 in 2000. In addition, one species-rich road verge matched the habitat criteria of class 2. In the AH area eight small nature reserves that lie scattered throughout the landscape matched the habitat criteria. One species-rich road verge in the AH area was classified as habitat class 2. The recently restored nature reserves in the AH area mentioned in *The seed addition experiment* section were not mapped as habitat. This was because there was hardly any vegetation at

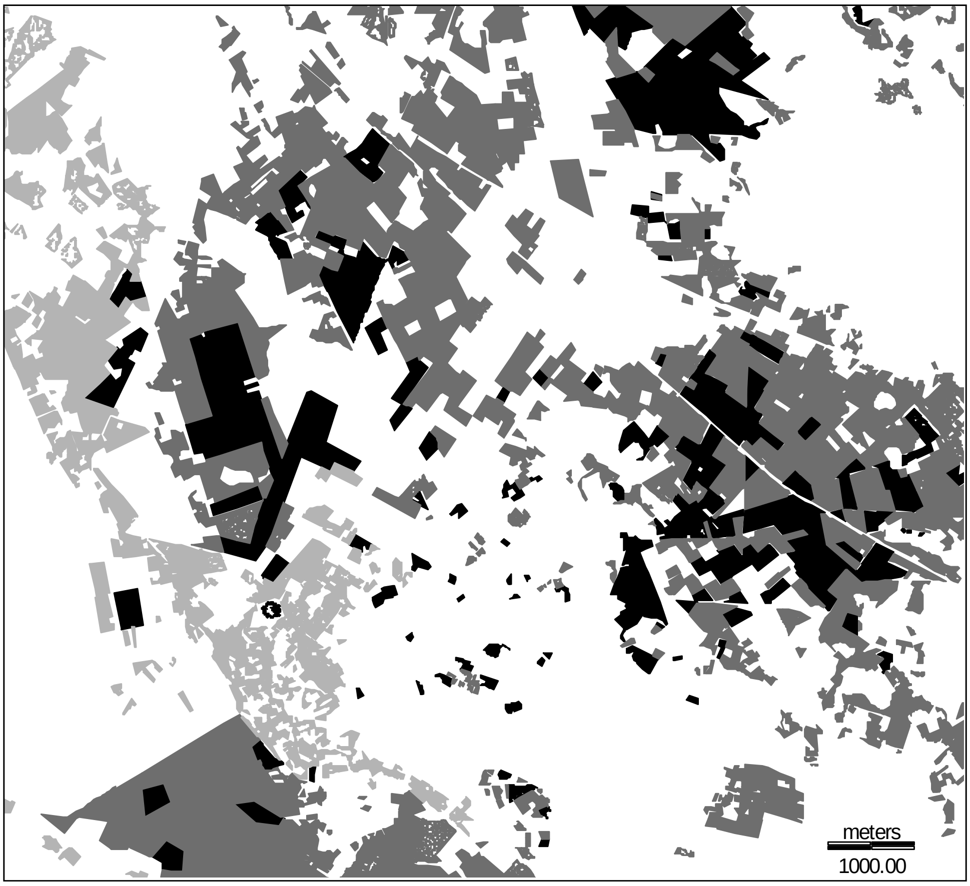

Figure 2. Habitat map of the AH area in 1900 (black: habitat class 1, dark gray: habitat class 2, light gray: habitat class 3).

these sites in 2000 and 2001, so that the sites did not meet the habitat criteria. The historic maps of the AH area in 1950 and 1900 demonstrate how fragmented the grassland habitat has become.

The species distributions

Six out of the eight habitat patches classified as class 1 in 2000 contained all four selected species. *C. dissectum* is the rarest of these species, and the only one that occurs exclusively in patches classified as habitat (Table 4). Populations of *H. radicata*, *C. jacea*, and *S. pratensis* are larger and more numerous (Table 4). There are more populations of these species in linear landscape elements than in patches classified as habitat. However, for *C. jacea* and *S. pratensis* the populations in linear landscape

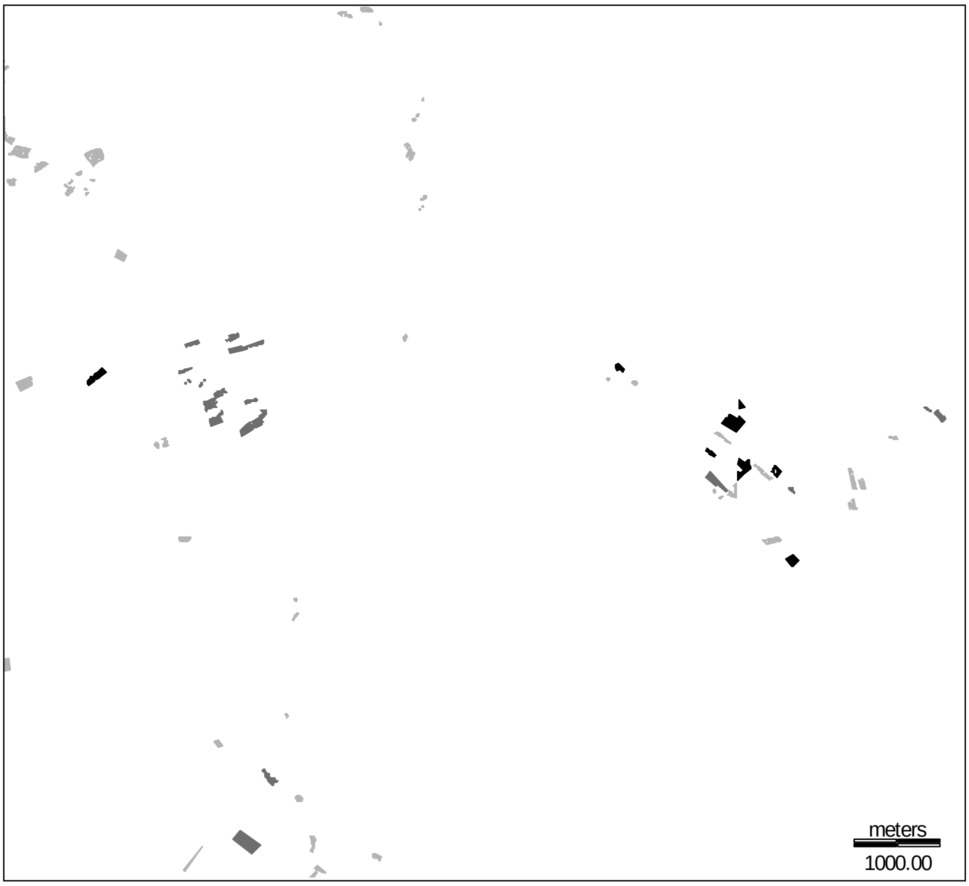

Figure 3. Habitat map of the AH area in 1950 (black: habitat class 1, dark gray: habitat class 2, light gray: habitat class 3).

elements are generally much smaller than those in patches classified as habitat. Six of the *C. jacea* populations and four of the *S. pratensis* populations in linear landscape elements even consist of two or fewer rosettes. *H. radicata* occurs widespread, though in low densities, in linear landscape elements with an open, mown or naturally low, vegetation in all study areas. The population occurs more or less as a continuum of individuals in the study areas, with only few clearly separated populations.

The seed addition experiment

Seedling establishment from the added seeds was higher in patches classified as habitat than in patches classified as non-habitat (Fig. 7). Establishment was higher in habitat class 1 than in class 2, but this difference was not significant. The highest establishment

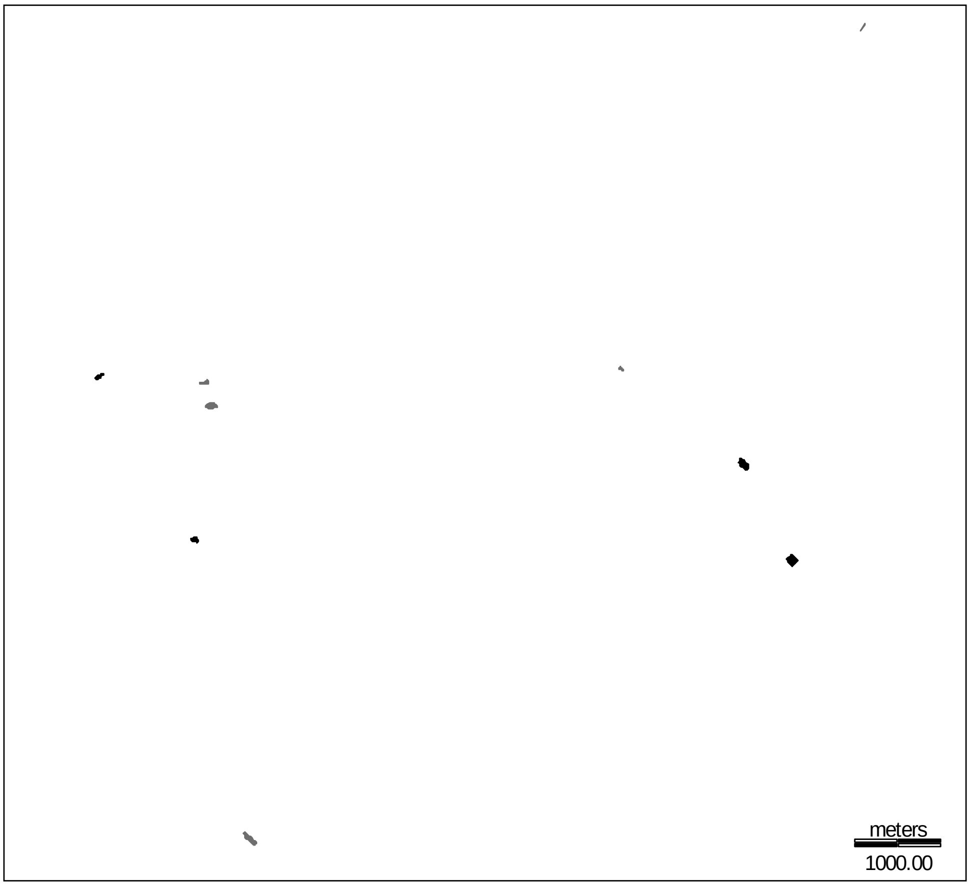

Figure 4. Habitat map of the AH area in 2000 (black: habitat class 1, dark gray: habitat class 2).

was found at the recently restored nature reserves. At these sites the topsoil had been removed and biotic and abiotic conditions were optimized for germination and establishment of species of nutrient-poor moist grasslands. Because of the openness of the restored sites, many of the experimentally added seeds were dispersed by wind or water over short distances outside the plots and germinated and established seedlings there. At one site we counted all established seedlings in a radius of 1 m outside the plots to give an impression of the total numbers of established seedlings. This increased the establishment percentages to 10% for *C. dissectum*, 18% for *H. radicata*, 15% for *C. jacea*, and 13% for *S. pratensis*. Low productivity and high vegetation openness increased seedling establishment significantly in the habitat and non-habitat sites (logistic regression, $p<0.001$ and $p<0.004$, respectively). This partly explains the low suitability of road verges for the establishment of *C. dissectum*, *C. jacea*, and *S. pratensis* (Fig. 8). However, other factors also played a role, because establishment was higher in

Figure 5. Habitat map of the GV area in 2000 (black: habitat class 1).

nature reserves than in road verges even when these had similar productivity and vegetation openness. Seedlings in the road verges were often very small and etiolated, especially in *S. pratensis*, and will likely have a low probability of survival. *H. radicata* was the only species that established relatively well in the road verges.

Habitat fragmentation and connectivity

The habitat fragmentation process in the AH area (Fig. 2-4) drastically reduced the total habitat area and the number and size of habitat patches since 1900 (Table 5). The distance between habitat patches increased (Table 5). The reductions in total habitat area and patch size, and the increase in inter-patch distances, all decreased the habitat connectivity since 1900 (Fig. 9). Seed dispersal distributions of the selected species are shown in Fig. 10. For the species with plumed seeds, *C. dissectum* and *H. radicata*,

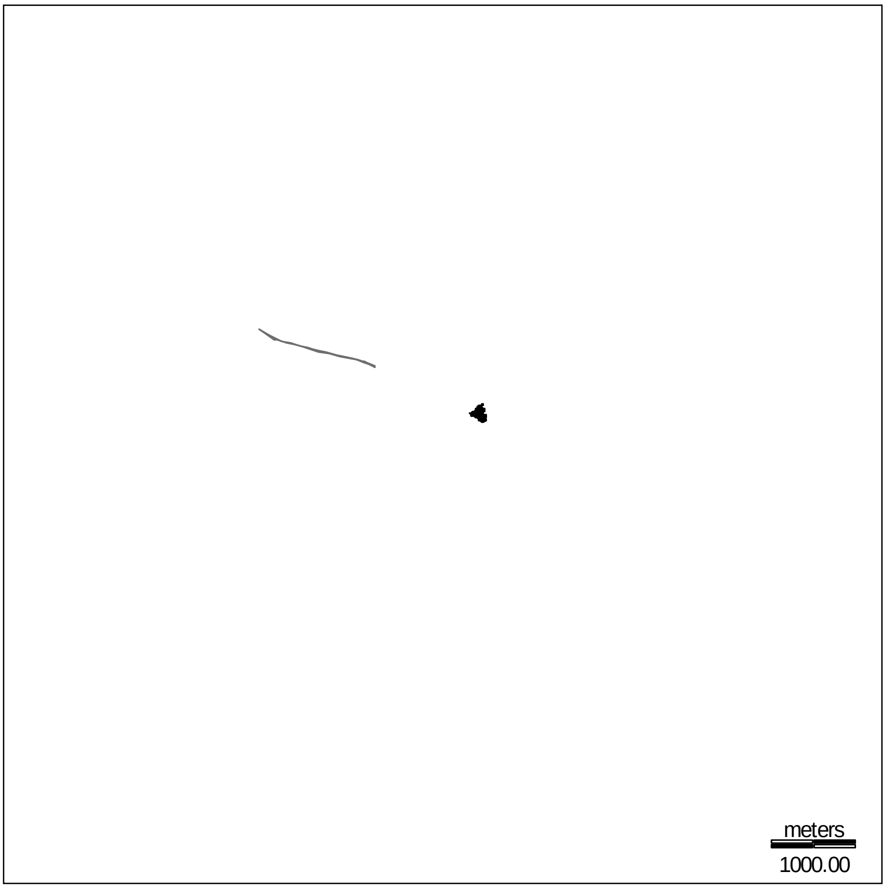

Figure 6. Habitat map of the VE area in 2000 (black: habitat class 1, dark gray: habitat class 2).

functional habitat connectivity was reduced drastically by habitat fragmentation (Fig. 11). Especially the probability of seed dispersal to habitat sites at a distance >50 m was greatly reduced (by >90%). For *C. jacea* and *S. pratensis* functional habitat connectivity was hardly reduced. These species disperse their seeds generally over such short distances (<4 m) that almost all seeds land in the habitat patch in which they are released, in 1900 as well as 2000.

The largest reductions in habitat area and connectivity mostly took place between 1900 and 1950. The rate of habitat fragmentation was very high in that period: 922 ha (worst-case scenario: only habitat class 1 is habitat) – 3658 ha (best-case scenario: class 1, 2, and 3 are all habitat) of habitat was lost. This is equivalent to 18–73 ha/yr. The average patch size was reduced by 10 ha (0.2 ha/yr). These rates were much lower during the second half of the 20th century: a reduction in habitat area of 6-42 ha (0.1-0.8 ha/yr), a reduction in average patch area of 0.5-0.2 ha (0.01-0.004 ha/yr). Only the increase in average inter-patch distances was similar for both time periods: by 1.2-0.3 km (24-6 m/yr) for 1900-1950, and by 0.2-1.4 km (4-28 m/yr) for 1950-2000. In total, 929-3700 ha of habitat was lost during the 20th century. Total habitat area decreased by 99.7-99.9%. The number of patches decreased by 95-97%.

The habitat maps for 2000 clearly demonstrate how little grassland habitat area is left (Fig. 4-6). Most habitat area is left in the GV area. In the AH area the largest number of habitat patches are left, but their sizes are smaller than in the other areas. In all areas the few remaining habitat patches are very small (Table 6). The distances between the remaining patches are large, especially in the AH area, as patches occur scattered throughout the landscape (Table 6). The values of $O_{ij}(r)$ show that habitat connectivity currently is highest in the GV area, and lowest in the AH area (Fig. 9). Large patches at short distances from each other provide the highest connectivity. Smaller and more distant patches, and especially habitat patches in linear landscape elements, decrease connectivity (Fig. 9).

The functional habitat connectivity $C_{ij}(r)$ in the study areas is very low for *C. jacea* and *S. pratensis* (Fig. 11). This is due to the low seed dispersal ability of these two species (<4 m) relative to inter-patch distances (minimum 220 m). For *C. dissectum* and *H. radicata* the functional habitat connectivity in the study areas is higher (Fig. 11), because these species have seeds that can be dispersed over much greater distances by wind (Fig. 10). However, also for these species the functional habitat connectivity is very low. This is due to the low availability of habitat, small size of habitat patches, and large distance between habitat patches relative to the species' seed dispersal distances. The minimum distance between habitat patches is 220 m. The probability that seeds disperse over 220 m and land at a habitat site is <0.0001 for *C. dissectum* and *H. radicata* (and 0

Table 4. The species distributions. Number of populations and range in population sizes (measured as number of flowering rosettes) for the habitat classes and the linear landscape elements (LLE). The two habitat patches in LLE are listed with the habitat patches (class 2). All populations found at sites that were classified as non-habitat, were in LLE.

Populations in the year 2000	Class 1 (total: 8 patches)	Class 2 (total: 6 patches)	LLE (AH only)
C. dissectum			
- Number of pops.	6	0	0
- Pop. size range	4–11,000	-	-
H. radicata			
- Number of pops.	8	5	Continuum
- Pop. size range	1–50,000	1- >100,000	-
C. jacea			
- Number of pops.	8	1	23
- Pop. size range	10–20,000	2	1-350
S. pratensis			
- Number of pops.	8	3	15
- Pop. size range	150- >100,000	75–2200	1-100

for *C. jacea* and *S. pratensis*). The largest populations of *C. dissectum* and *H. radicata* in the study areas (Table 4) produce ca. 14×10^4 and 500×10^4 germinable seeds. Thus, ca. 14 and 500 seeds per year of *C. dissectum* and *H. radicata* (and 0 of *C. jacea* and *S. pratensis*) could travel from one patch to the other over 220 m. However, the two patches that are separated by 220 m are both unoccupied by the selected species. The minimum distance between an occupied habitat patch and another patch is 670 m. The probability that seeds of the selected species travel between these patches is almost 0.

DISCUSSION

Accuracy of the habitat maps

Our habitat classification system served its purpose well. Classification of patches was objective and practical. Results from the species distribution maps and the seed addition experiment demonstrate the accuracy of the habitat maps for 2000. All large populations of *C. dissectum*, *C. jacea*, and *S. pratensis* occur in patches classified as habitat. More and larger populations occur in patches classified as habitat class 1 than in class 2.

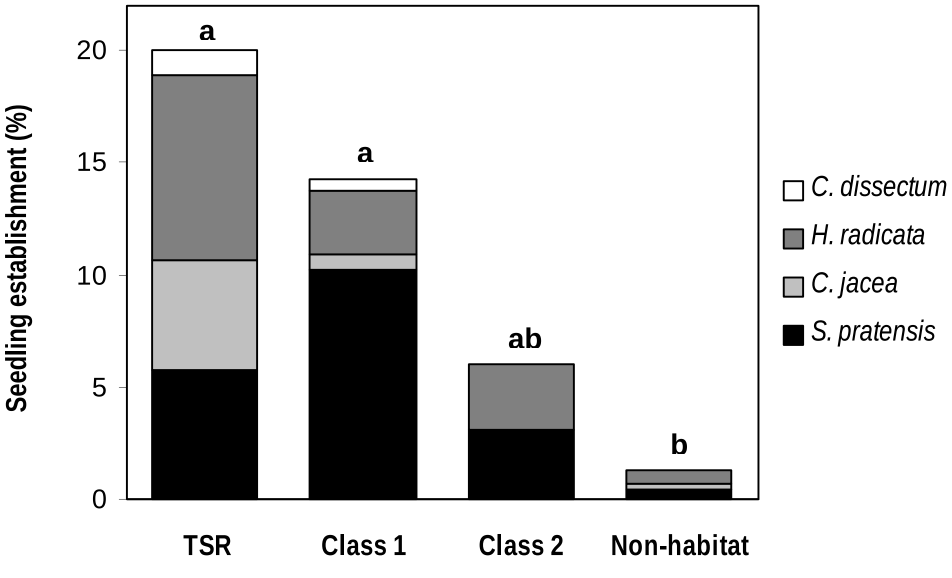

Figure 7. Seedling establishment at sites of different habitat classes one year after sowing. TSR = topsoil removed site (no habitat class assigned; n=3), habitat class 1 (n=2), habitat class 2 (n=2), non-habitat (includes all road verges; n=13). Different letters indicate statistically significant differences (Kruskall-Wallis test with Dunn post-hoc test, α=0.05).

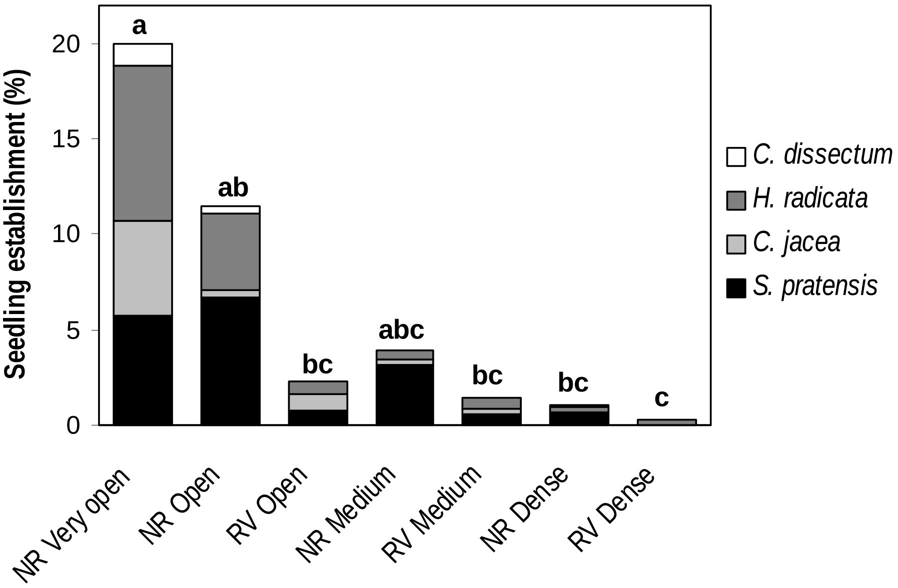

Figure 8. Seedling establishment at sites with different vegetation openness one year after sowing. NR = nature reserve (n=10), RV = road verge (n=10). Very open: average aboveground biomass 77 g/m^2, average vegetation height 0.05 m, average vegetation cover 35% (n=3). Open: 198 g/m^2, 0.18 m, 55% (n=6). Medium: 346 g/m^2, 0.31 m, 83% (n=6). Dense: 672 g/m^2, 0.43 m, 96% (n=5). Different letters indicate statistically significant differences (Kruskall-Wallis test with Dunn post-hoc test, α=0.05).

Seedling establishment from experimentally added seeds was higher in patches classified as habitat than in patches classified as non-habitat. Seedling establishment was higher in habitat class 1 than in class 2. The habitat of *H. radicata* was not included in the habitat definition for this study, because *H. radicata* has a wider ecological range than the other selected species. *H. radicata* populations were found in almost all patches classified as habitat but also in patches classified as non-habitat (especially road verges). In spite of this, we included *H. radicata* in our analysis to demonstrate the effects of habitat fragmentation on functional habitat connectivity for a species with such high wind-dispersal ability and seed production.

C. jacea and *S. pratensis* also occur in linear landscape elements that were not classified as habitat, but these populations are predominantly relict populations reflecting past site suitability. In the AH area in 2000, most rosettes in road verge populations of *C. jacea* and *S. pratensis* were large and relatively old. Rosette leaves of *S. pratensis* were often overshaded by higher growing grasses and ruderal species. We found no naturally established seedlings of these species in the road verge populations, and only few clonally produced offspring. Seedling establishment from the experimentally added seeds was very low. This was likely caused by the high productivity and vegetation cover in most road verges. In the AH area the populations of *C. jacea* and *S. pratensis* in linear landscape elements are declining in number and size. During previous vegetation surveys in the area in 1988-1995, 102 populations of *C. jacea* and 38 of *S. pratensis* were recorded in linear landscape elements (Messelink 2001). From then till 2000 the numbers of populations of *C. jacea* and *S. pratensis* in linear landscape elements thus decreased by 77% and 61%, respectively. We did not discover any new populations in the AH area during our mapping survey. *H. radicata* also declined in road verges since the 1980's (Van Ast *et al*. 1987), but this species is currently still relatively abundant.

The only patches for which our habitat classification system for 2000 did not work were recently restored (or created) nature reserves. Insufficient vegetation had established at these sites to classify them as habitat following our system. The high seedling establishment from experimentally added seeds however suggests that the restoration measures at these sites were successful and the sites are suitable habitat for the selected species. The low productivity and vegetation cover at these sites have likely contributed to the successful seedling establishment. If we add the recently restored sites in the AH area to the habitat patches of class 1, the total area of habitat class 1 in 2000 would increase by ca. 16 ha.

The habitat classification for 1950 and 1900 involved much more uncertainty than for 2000. Detailed information was available on species-rich sites and sites that are currently nature reserves. However, we may have missed out some habitat patches for which there was no indication that they may have been habitat. In 1950 and 1900 linear landscape elements were more nutrient-poor and species-rich than they are currently, and may have contained habitat patches. However, very little information was available on these elements for 1950 and 1900. The most likely error in our habitat maps for 1950 and 1900 is therefore an underestimation of habitat patches in linear landscape elements. The main uncertainties in the classification of patches for 1950 and 1900 are demonstrated by our scenario analyses, which show the estimated extremes of the habitat fragmentation process. The absolute differences between the scenarios are large, but the relative changes in habitat area and configuration are similar for all scenarios.

Fragmentation and connectivity measures

We used simple and straightforward measures to quantify habitat fragmentation and connectivity, so that our results can be interpreted easily. For a realistic quantification of functional habitat connectivity it is important to relate habitat area and configuration measures to species-specific dispersal ability and colonization capacity. Our measure of functional habitat connectivity ($C_{ij}(r)$) is a realistic and straightforward measure, provided that long-distance seed dispersal is quantified accurately. This measure improves on previous measures of functional habitat connectivity (Tischendorf and Fahrig 2000; Moilanen and Nieminen 2002) because 1) it considers all patches within the seed dispersal range of a species, 2) contributions to colonization and gene flow are weighed by inter-patch distances, and can easily be weighed also by the population size,

Table 5. Habitat area and configuration at different times in the AH area. Total area of the AH area is 11,000 ha.

Habitat in the AH area	AH 2000		AH 1950		
Habitat class	1	1&2	1	1&2	1&2&3
Total habitat area (ha)	2.40	4.11	8.74	24.4	45.9
Number of patches	4	9	8	22	74
Average patch size (ha)	0.60	0.46	1.09	1.11	0.62
Range in patch sizes (ha)	0.25-0.95	0.03-0.95	0.31-2.93	0.03-4.69	0.01-4.69
Average inter-patch distance (km)	1.6	1.8	1.4	0.27	0.40
Range in inter-patch distances (km)	1.1-2.1	0.22-4.7	0.09-5.9	0.01-1.3	0.01-2.4

Habitat in the AH area	AH 1900		
Habitat class	1	1&2	1&2&3
Total habitat area (ha)	931	3132	3704
Number of patches	87	263	335
Average patch size (ha)	10.7	11.91	11.1
Range in patch sizes (ha)	0.11-179	0.08-384	0.03-384
Average inter-patch distance (km)	0.24	0.14	0.11
Range in inter-patch distances (km)	0.01-1.2	0.01-0.81	0.01-0.32

Table 6. Habitat area and configuration in the three study areas in 2000. Total area of the GV and VE areas is 10,000 ha, total area of the AH area is 11,000 ha.

Habitat in the year 2000	GV 2000	VE 2000		AH 2000	
Habitat class	1	1	1&2	1	1&2
Total area (ha)	19.1	2.06	2.99	2.40	4.11
Number of patches	3	1	2	4	9
Average patch size (ha)	6.35	2.06	1.49	0.60	0.46
Range in patch sizes (ha)	1.62-12.9	-	0.92-2.06	0.25-0.95	0.03-0.95
Average inter-patch distance (km)	2.2	-	1.2	1.6	1.8
Range in inter-patch distances (km)	0.67-5.3	-	-	1.1-2.1	0.22-4.7

seed production, and seed germinability in habitat patches, 3) it uses a pixel-based approach to express both within-patch and inter-patch seed dispersal, and 4) it expresses connectivity per equal-sized unit of habitat. We did not take into account connectivity through time, because the selected species have only short-lived seed banks. Also, we did not consider the presence of dispersal barriers in the landscape matrix. Inclusion of this additional information would reduce the estimates of functional landscape connectivity further. The qualitative results of our analyses would however not be affected much by inclusion of this, because the results indicate that the habitat patches in 2000 are already practically isolated regarding seed dispersal (see next section).

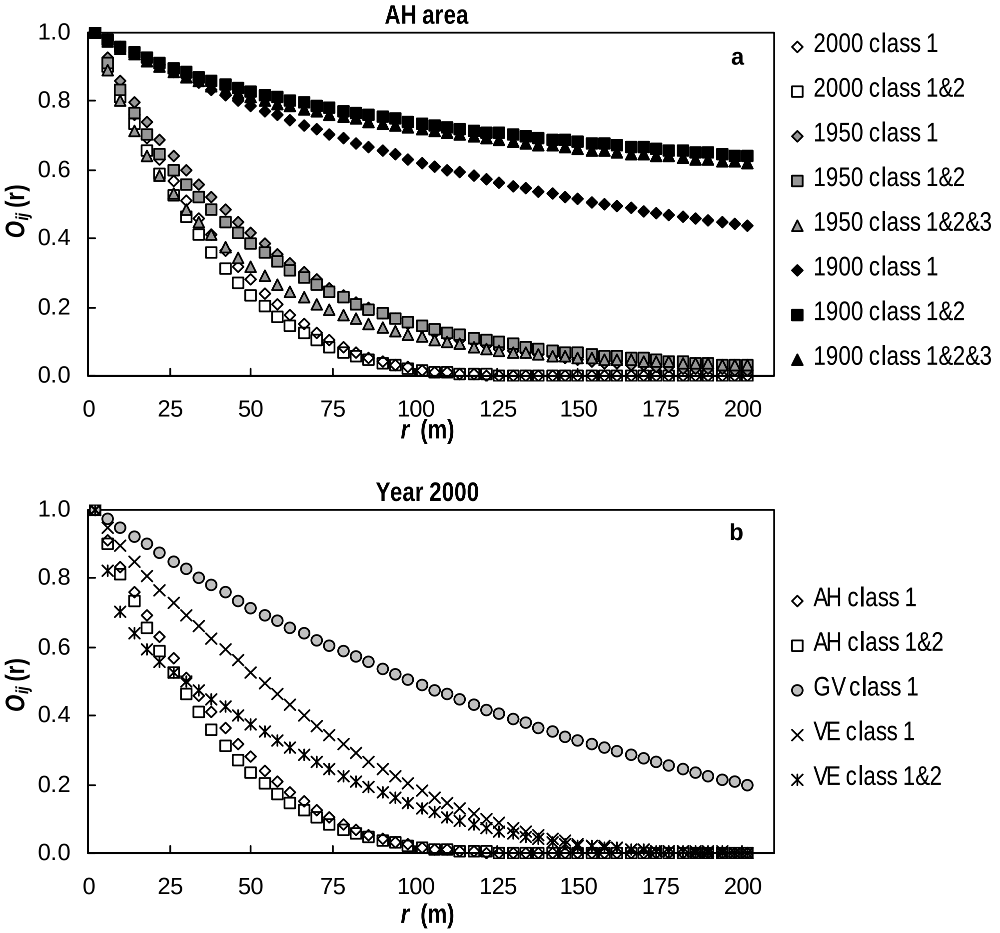

Figure 9. $O_{ij}(r)$, the probability that seeds that disperse over distance *r* from a habitat unit *i* end up at another habitat unit *j*. (a) The time series in the AH area; (b) the three study areas in 2000.

Habitat fragmentation and connectivity

We quantified the rate and spatial pattern of the fragmentation of nutrient-poor semi-natural moist grasslands in the AH area. Fragmentation occurred predominantly during the first half of the 20th century. Most of the remaining habitat patches have been small and isolated for at least 50 years. All but two of the remaining habitat patches in the three study areas are located in nature reserves. The two habitat patches not located in nature reserves are two road verges classified as habitat class 2. Both are low productive, species-rich road verges that are likely remnants of former nutrient-poor, species-rich

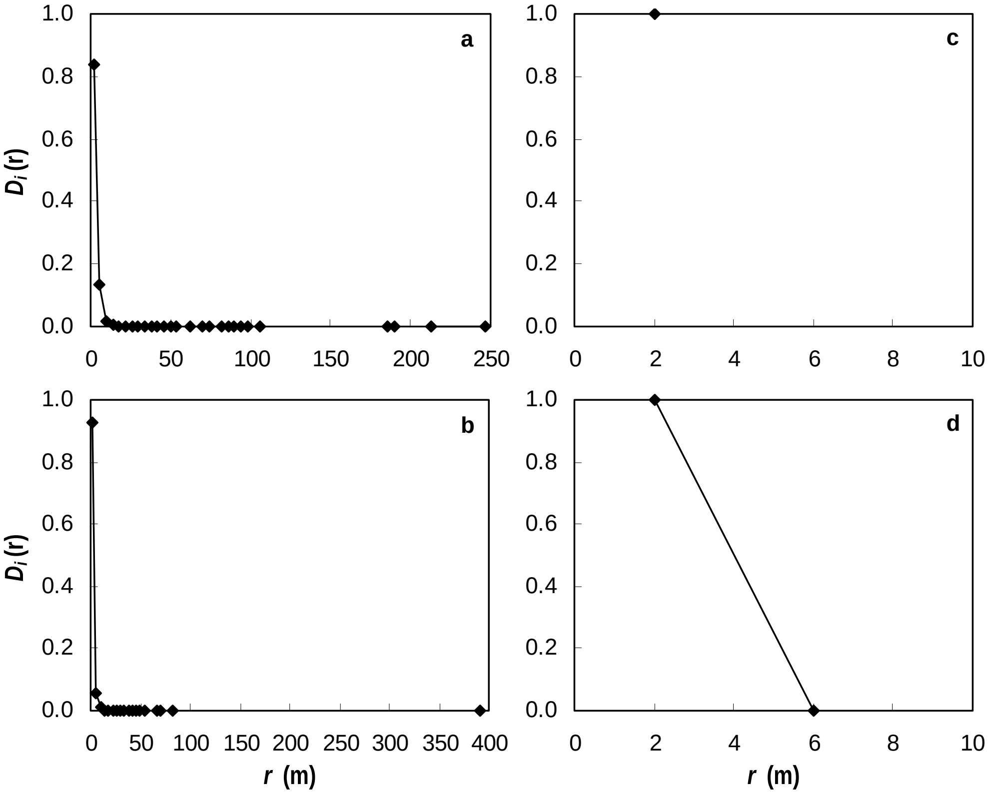

Figure 10. $D_i(r)$, the probability that seeds disperse over distance r from their release point. (a) *C. dissectum* (seed terminal velocity 0.38 ± 0.03 m/s, seed release height 0.50 ± 0.14 m, vegetation height 0.35 m); (b) *H. radicata* (0.34 ± 0.01 m/s, 0.28 ± 0.12 m, 0.23 m); (c) *C. jacea* (4.32 ± 0.45 m/s, 0.45 ± 0.15 m, 0.35 m); (d) *S. pratensis* (2.14 ± 0.20 m/s, 0.56 ± 0.14 m, 0.35 m). The resolution of r is 4 m to match $O_{ij}(r)$, which is calculated from the 4×4m-resolution habitat maps. Zero values not shown.

grasslands. The road verge in the AH area is located at a site that was mapped partially as habitat class 1 and partially as class 2 for 1900.

Not only the remaining habitat patches are small. The remaining populations of the selected species are also small, especially at sites classified as non-habitat or habitat class 2. Also some of the populations in class 1 habitat patches in nature reserves are small. Two of the six *C. dissectum* populations consist of 4 and 17 flowering rosettes. Four of the nine *C. jacea* populations in habitat patches consist of <200 flowering rosettes (range 2-161). Four of the 11 *S. pratensis* populations in habitat patches consist of <200 flowering rosettes (range 75-182). Such small populations have an increased probability of extinction and a reduced colonization capacity, especially because they produce few seeds and the produced seeds may have low germination ability (Fischer and Matthies 1998; Kery *et al.* 2000; Soons and Heil 2002; Vergeer *et al.* 2003). The

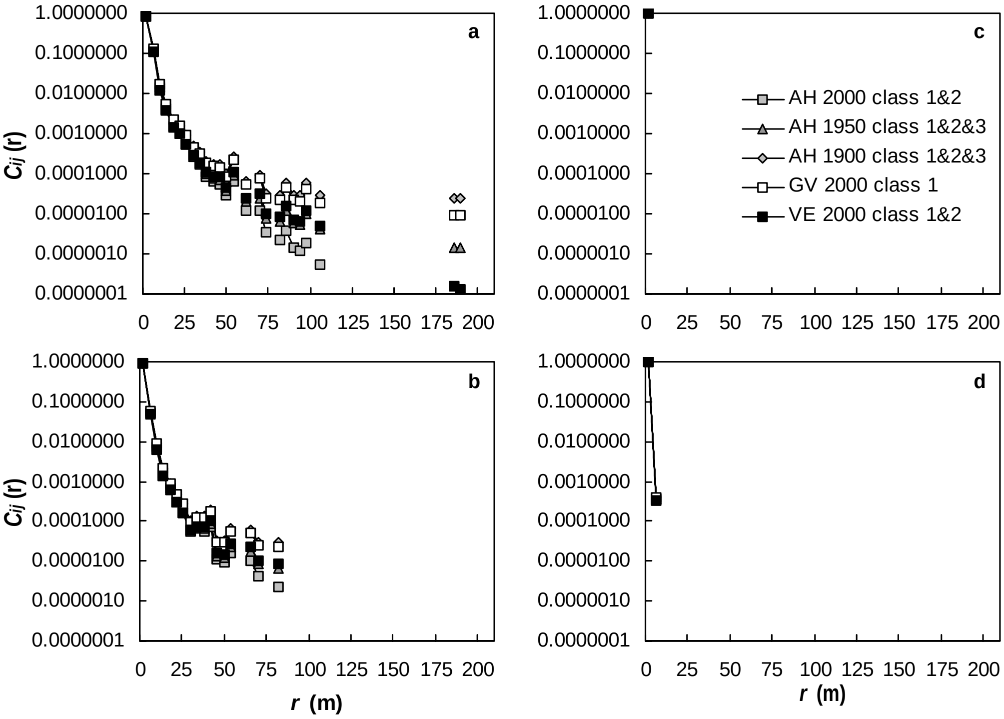

Figure 11. $C_{ij}(r)$, the probability that seeds that disperse from a habitat unit *i* end up at another habitat unit *j* at distance *r* from their release point (the functional habitat connectivity). (a) *C. dissectum*; (b) *H. radicata*; (c) *C. jacea*; (d) *S. pratensis* (all parameters as in Figure 10). Y-axis is log-scale. Zero values not shown. Legends of (a), (b), and (d) same as in (c).

survival till the present time of the (small) populations of *C. dissectum*, *C. jacea*, and *S. pratensis* in small habitat patches is probably due to the high longevity of individuals of these species.

The functional habitat connectivity is now very low in the three study areas. Linear landscape elements such as road verges do not increase functional habitat connectivity for *C. dissectum*, *C. jacea*, and *S. pratensis*. Firstly, most linear landscape elements are currently unsuitable for seedling establishment, probably due to their high productivity and vegetation cover. Secondly, the area and shape of habitat patches in linear landscape elements are such that seeds dispersing from them have an extremely low probability of ending up at another habitat site. This result is in agreement with the low functionality of linear landscape elements as corridors for migration of wind-dispersed plants (Van Dorp *et al*. 1997). Thirdly, the populations in linear landscape elements have a low colonization capacity because they produce only few seeds and their wind dispersal ability is low due to the high and dense vegetation (Soons and Heil 2002; Chapter 3). Currently, the remaining habitat patches and populations of the selected species (except *H. radicata*) are practically isolated regarding seed dispersal by wind.

Seed dispersal between the remaining habitat patches and populations by other seed dispersal mechanisms is also unlikely. The changes in land use that accompanied the habitat fragmentation have interrupted most previously existing seed dispersal mechanisms (Poschlod and Bonn 1998). The only mammals left in the study areas that are large enough to disperse seeds between the grassland habitat patches are roe deer. Roe deer have home ranges of ca. 2-24 ha (Pakeman 2001), which is generally not large enough to include more than one of the habitat patches. Flooding nowadays occurs only locally within nature reserves. Even dispersal of seeds by mowing machinery (Strykstra *et al*. 1997) is unlikely, because most habitat patches are too distant to be mown by the same farmer/machinery (pers.comm. Johan Wensink). Spreading out of mown material from species-rich reserves in nearby restored sites is currently the only management tool applied to increase seed dispersal between habitat patches (pers.comm. Johan Wensink).

As a consequence of the very low functional habitat connectivity in the study areas, there is a very low probability of natural colonization of many of the recently restored (or created) patches. This is the case even for the species that are adapted to long-distance seed dispersal by wind. In the case of the selected species re-colonization from the seed bank is also unlikely, because the species have transient seed banks (Thompson *et al*. 1997). The regional survival of the selected species in the study areas is now completely dependent on the survival of the few remaining large populations in habitat patches in nature reserves. For their conservation it is therefore of utmost importance that 1) management of the remaining habitat patches is aimed at the conservation of the remaining populations, 2) new habitat patches are restored or created, and 3) these new patches are located in close proximity to the remaining large populations in habitat patches, or that seed dispersal to the new patches is actively assisted by man.

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6. Summary and perspectives

SUMMARY

Habitat fragmentation (including habitat loss) poses a major threat to regional species survival. It is currently the most important cause of species extinction. To ameliorate the negative consequences of habitat fragmentation it is essential to understand the process of habitat fragmentation and the mechanisms by which it affects regional species survival. The effects of habitat fragmentation on regional species survival depend for an important part on the effects on functional habitat connectivity (hereafter ‘connectivity’). Connectivity reflects the probability that unoccupied habitat patches are colonized by populations in other patches, and that gene flow occurs between populations in different habitat patches. This study was carried out to increase our understanding of the process of habitat fragmentation and its effects on connectivity. To achieve this aim, the main determinants of connectivity were quantified: the spatial and temporal distribution of habitat area, the colonization capacity of plant species, and the interaction between these two. Gene flow by pollen dispersal also contributes to connectivity, but is not considered in this study.

This study focused on the consequences of the fragmentation of nutrient-poor semi-natural moist grasslands for wind-dispersed grassland plants. Nutrient-poor semi-natural grasslands have become highly fragmented in north-west Europe and many other areas in the world. The continuation of their fragmentation, and the concomitant loss of species and biodiversity, are reason for concern and advocated the selection of such grasslands as study system. Four wind-dispersed grassland plant species were selected as study species. These species represent two of the most common dispersal strategies in grasslands. *Cirsium dissectum* and *Hypochaeris radicata* have plumed seeds that are adapted to long-distance dispersal by wind. *Centaurea jacea* and *Succisa pratensis* have plumeless seeds that are adapted to only short-distance dispersal by wind. Field research was carried out in The Netherlands.

In Chapter 2 the effects of habitat fragmentation on the colonization capacity of the selected plant species are quantified. The colonization capacity was quantified by measurements on seed production, seed germination ability, and seed dispersal characteristics of the seeds, plants, and vegetation. Habitat fragmentation was found to affect the colonization capacity when it reduces the size of plant populations and/or increases the site productivity of habitat patches. A reduction in population size decreases seed production (in some species even per individual), seed germination ability, and, in the species with plumed seeds, the estimated range of seed dispersal distances. Inbreeding depression is the most likely cause of these effects. An increase in site productivity decreases the probability of colonization of distant sites, because it decreases estimated seed dispersal ability. The probability of colonization of nearby sites however increases, because increased site productivity increases seed production and seed germination ability in most species. No evidence was found for selection for reduced dispersal ability in small and isolated fragmented populations.

In Chapter 3 the key mechanisms for long-distance seed dispersal by wind are determined. Quantification of long-distance seed dispersal is required for an accurate quantification of plant colonization capacity. However, long-distance seed dispersal is extremely difficult to measure and previous model studies gave conflicting results regarding the processes and parameters that determine long-distance dispersal. Therefore, a combination of different mechanistic models and field data was here used to assess which processes, and which wind, plant, and vegetation characteristics determine long-distance seed dispersal. Model results show that autocorrelated turbulent fluctuations in vertical wind velocity are the key mechanism for long-distance dispersal. Seed dispersal distances are longest during storms, because then wind velocity and turbulent wind fluctuations are highest. Under very low wind velocity conditions seed dispersal distances increase when there is more surface heating, because then buoyant-produced turbulence increases. Mean horizontal wind velocity, seed release height, vegetation height, and seed terminal velocity are the most important determinants of long-distance seed dispersal. Seed terminal velocity is only important, however, when considering differences between species. The great importance of seed release height and vegetation height indicates that changes in the vegetation in habitat patches (e.g. due to eutrophication) will significantly affect long-distance seed dispersal ability.

In Chapter 4 the current and future colonization capacity of wind-dispersed plant species in fragmented landscapes are estimated. The most important future disturbances that may affect wind dispersal in semi-natural grasslands include habitat fragmentation, eutrophication, and an increase in extreme wind velocity events due to climate change. It was previously impossible to quantify the effects of these disturbances on plant colonization capacity, because long-distance seed dispersal could not be quantified. Here, the effects on (long-distance) seed dispersal were simulated using a mechanistic dispersal model presented in Chapter 3. The dispersal characteristics that are quantified in Chapter 2 served as model input data. Simulated dispersal distances were combined with data on seed production and germination ability from Chapter 2 to estimate colonization capacity. The results show that the decrease in population sizes caused by habitat fragmentation does not affect seed dispersal ability, but reduces seed production and germinability. It thus reduces colonization capacity. 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. An increase in extreme winds increases long-distance dispersal and long-distance colonization capacity, but not sufficiently to compensate the reductions caused by habitat fragmentation or eutrophication.

In Chapter 5 the effects of habitat fragmentation on the connectivity of the studied grasslands are quantified. This was done by combining the data on plant colonization capacity from the previous chapters with data on habitat fragmentation. This approach is new because it provides quantitative data on the process and pattern of habitat fragmentation, and relates these data to the actual colonization capacity of plant species to determine connectivity in a realistic way. Habitat fragmentation was determined from a time-series of habitat maps. Habitat was mapped using an objective vegetation-based habitat classification framework and vegetation data from digital databases and other (historic) sources. Results from this study show that the availability and connectivity of nutrient-poor semi-natural moist grasslands decreased dramatically during the 20th century and are now both very low. The remaining populations of the studied plant species are decreasing in number and size and have a reduced colonization capacity. The grassland connectivity is now so low that most habitat patches are effectively isolated, even for species with adaptations to long-distance dispersal by wind. The probability that new or restored habitat patches are colonized is also very low, except when these patches are adjacent to occupied patches (or seed dispersal is assisted by man). Regional species survival is now completely dependent on the survival of the few large populations in nature reserves. The regional survival of wind-dispersed species restricted to nutrient-poor semi-natural moist grasslands is severely threatened.

PERSPECTIVES

Perspectives for nature conservation

"With an increasing number of habitats becoming fragmented, we are faced with the task of conserving a patchy world" (Roslin 2002). This study shows just how patchy the nutrient-poor semi-natural moist grassland habitat has become, even in the less densely populated areas in The Netherlands. In the fragmented grasslands, but also in many other (semi-)natural systems all over the world, the long-term regional survival of plant species has become totally dependent on the survival of a few remaining populations in habitat patches that are located in nature reserves. Continuation of habitat fragmentation will reduce the number and connectivity of surviving populations further and reduce the probability of regional species survival. But even when habitat fragmentation stops, the consequences of the past fragmentation continue to threaten regional species survival. Almost all of the remnant patches are effectively isolated and many of them are small. This increases the probability of extinction of the populations in these patches due to reduced fecundity, inbreeding depression, loss of genetic variation, or environmental, demographic, or genetic stochasticity (Ellstrand and Elam 1993; Husband and Schemske 1996; Booy *et al*. 2000). Small habitat patches are also more exposed to external influences (Saunders *et al*. 1991). Eutrophication of habitat patches further reduces the capacity of the remaining populations to colonize distant sites and eventually results in the loss of habitat. In the future, climate change may pose an additional threat to the survival of the remaining populations. Climate change may alter local conditions so that they become unsuitable for the species, while the low level of habitat connectivity prevents migration to sites with suitable conditions (Pitelka *et al*. 1997; Walther *et al*. 2002). To secure species survival, measures need to be taken.

Results of this study show that for the long-term regional survival of wind-dispersed plant species restricted to nutrient-poor semi-natural moist grasslands the following points are essential:

- Firstly, it is of crucial importance to adjust the management of the nature reserves in which remaining populations occur to optimize local survival of these remaining populations. Regional species survival is totally dependent on the survival of these populations.

- Secondly, the connectivity between the remaining habitat patches needs to be increased. To achieve this, barriers to seed dispersal between habitat patches need to be removed. Also, measures need to be taken to increase the colonization capacity of the remaining populations. This involves measures aimed at increasing the size of the remaining populations, so that more seeds are produced, and at reducing site productivity, so that wind-dispersed seeds of species adapted to nutrient-poor systems are dispersed further. Finally, the connectivity between existing habitat patches needs to be increased by creating new habitat patches at strategic locations. Results of this study suggest the following guidelines for the latter:

- For plant species with seeds adapted to long-distance dispersal by wind, 95% of the dispersed seeds disperse over less than ca. 100 m (even during storms). To ensure connectivity for such species, new habitat patches should be created at less than 100 m from other habitat patches.

- Many other species have lower dispersal abilities. Plant species with seeds adapted to dispersal by wind over only short distances, such as *C. jacea* and *S. pratensis*, disperse 95-100% of their seeds over less than 4 m. To increase the connectivity for such species new habitat patches should be created at less than 4 m from other habitat patches. Practically, this means creation of new habitat patches adjacent to existing habitat patches.

- Newly created habitat should preferably consist of strategically located fields and not of linear landscape elements such as road verges. The latter hardly increase the habitat connectivity for wind-dispersed species.

For many plant species it may not be feasible to restore the functional habitat connectivity to a level that ensures natural seed dispersal between habitat patches. For species with seeds adapted to dispersal over short distances by wind, or species with seeds adapted to dispersal by other mechanisms that generally disperse seeds over comparable short distances (*e.g.* dispersal by ants), it will be very difficult to create new habitat patches that connect occupied habitat patches. In such cases, colonization of new patches and re-colonization of extinct patches needs to be assisted by man. This can be done by spreading of mown material from occupied habitat patches on new or restored patches. This method is useful when management of the occupied patches requires mowing at the time when seeds of many plant species are ripe (and still attached to the plant). If this is not the case, assisted (re-)colonization requires the direct (re-) introduction of seeds or plants (Van Groenendael *et al*. 1998; Smulders *et al*. 2000).

Perspectives for further research

Our understanding of the effects of habitat fragmentation on connectivity will increase further especially by further increasing our knowledge of the seed dispersal process. Firstly, mechanistic wind dispersal models (such as the Markov Chain STG model presented in this study) should be extended to simulate seed dispersal by convective plumes and thermals. This will allow more thorough assessment of the relative importance of these weather phenomena for long-distance dispersal by wind. Secondly, the consequences of the presence of dispersal barriers and landscape heterogeneity for wind dispersal should be studied using mechanistic models and field experiments. This will increase the realism of wind dispersal estimates. When barriers and landscape heterogeneity are simulated, wind direction should also be included in the simulations. Thirdly, other seed dispersal mechanisms should be studied. This is of importance especially for accurate estimation of the transport of seeds along linear landscape elements. It has been suggested that in road verges seeds are dispersed by traffic, wind movements caused by traffic, and passing pedestrians and dogs. It also has been suggested that seed dispersal by birds and roe deer still plays an important role in connecting habitat patches. The relative importance of these dispersal mechanisms needs to be assessed. Finally, mechanistic dispersal models that predict long-distance dispersal need to be tested against long-distance dispersal data to better assess their accuracy. This requires measurement of long-distance seed dispersal by the different long-distance dispersal mechanisms. Genetic analyses provide a promising tool for estimation of (long-distance) gene flow by seed dispersal, but cannot distinguish between different seed dispersal mechanisms. Thus, further effort in dispersal experiments and field measurements is also required.

Our understanding of the effects of habitat fragmentation on connectivity will also increase further by more insight into the habitat fragmentation process. For many habitat types the rate and spatial pattern of the fragmentation process are not known in detail, or known only for short time periods relative to the life span of long-lived plant species. A vegetation-based framework for the mapping of habitat, such as used in this study, provides a tool to quantify the rate and spatial pattern of habitat fragmentation. Future analyses of habitat fragmentation and connectivity will greatly improve in detail and accuracy if detailed species distribution data are collected. These data should include at least the exact locations of populations (instead of only the km^2 in which the population is located) and information on the population size, preferably in number of rosettes and/or number of flowering rosettes (instead of only stating presence of a population).

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Samenvatting in het Nederlands

SAMENVATTING

Dit proefschrift gaat over de versnippering van de habitat van plantensoorten en over de gevolgen hiervan voor die plantensoorten. De habitat van een plantensoort is de verzameling van alle plaatsen die voor die soort geschikt zijn om zich te vestigen, te groeien en voort te planten. Voor veel plantensoorten bevindt de habitat zich in natuurlijke en halfnatuurlijke gebieden. Over de hele wereld verdwijnen steeds meer (delen van) natuurlijke en halfnatuurlijke gebieden, doordat mensen steeds meer ruimte in beslag nemen voor landbouw en industrie, wonen, recrëeren en vervoer. Hierdoor blijft er steeds minder habitat over en bestaat de habitat die over blijft uit steeds kleinere gebieden, die op steeds grotere afstanden van elkaar liggen (in plaats van de oorspronkelijke grote en aaneengesloten gebieden). Dit proces wordt habitat-versnippering genoemd.

Habitatversnippering heeft grote gevolgen voor plantensoorten. Ten eerste is het zo dat het aantal individuen van een soort afneemt als het oppervlak aan habitat afneemt. Als de habitat helemaal verdwijnt, sterft een soort uit. Maar ook als er wel habitatgebieden over blijven, maar deze erg klein zijn en geïsoleerd liggen, kan een soort uitsterven. In een paar kleine en geïsoleerde gebieden kunnen maar een paar kleine en geïsoleerde populaties van een plantensoort over blijven. Kleine populaties lopen een groter risico om lokaal (d.w.z. in het door hen bezette habitatgebied) uit te sterven dan grotere populaties. Dit kan gebeuren door toeval (er rijdt een trekker precies door de hele populatie), of bijvoorbeeld doordat de insecten die de planten moeten bestuiven kleine populaties niet opmerken. Bovendien lopen kleine en geïsoleerde populaties een groter risico om lokaal uit te sterven als gevolg van inteelt of het verlies van genetische variatie. Naarmate de habitatgebieden verder van elkaar af liggen neemt ook de kans af dat een populatie andere habitatgebieden koloniseert, omdat zaadverspreiding dan over een langere afstand moet plaatsvinden. Dit betekent dat, wanneer een populatie in een habitatgebied lokaal uitsterft, of wanneer er nieuwe natuur wordt aangelegd die een nieuw habitatgebied oplevert, zo'n gebied een kleinere kans heeft om door de soort bezet te worden. Als de kolonisatie van onbezette habitatgebieden afneemt door isolatie, terwijl in bezette habitatgebieden het risico dat populaties lokaal uitsterven toeneemt door isolatie en klein oppervlak, dan zal een plantensoort uiteindelijk regionaal (in een heel landschap of in een heel land) uitsterven. Op dit moment is habitatversnippering wereldwijd de belangrijkste oorzaak van het uitsterven van plantensoorten en verlies van biodiversiteit.

Om de negatieve gevolgen van habitatversnippering te kunnen verminderen, of zelfs tegen te gaan, is gedetailleerde kennis nodig van dit proces en van de mechanismen waarlangs dit proces de lokale overleving van populaties en de kolonisatie van habitatgebieden beïnvloedt. Het in dit proefschrift beschreven onderzoek is gericht op het verkrijgen van gedetailleerde kennis van het proces van habitatversnippering en de effecten hiervan op de isolatie of connectiviteit van habitatgebieden. Connectiviteit is het omgekeerde van isolatie. Het beschrijft de kans dat een habitatgebied gekoloniseerd wordt en/of dat er uitwisseling van genetisch materiaal optreedt tussen populaties in bezette habitatgebieden. Dit laatste kan door zaadverspreiding en door pollenverspreiding gebeuren. In het hier beschreven onderzoek is alleen naar zaadverspreiding gekeken. Dit onderzoek maakt deel uit van het door NWO-ALW gesubsidieerde Nederlandse onderzoeksprogramma ‘Overleving van plantensoorten in gefragmenteerde landschappen’. Binnen dit onderzoeksprogramma is ook onderzoek verricht naar de effecten van habitatversnippering op de lokale overleving en de genetische samenstelling van populaties. De resultaten hiervan zullen in de proefschriften van Eelke Jongejans (WUR) en Carolin Mix (KUN) worden beschreven.

Om gedetailleerde kennis van het proces van habitatversnippering en de effecten hiervan op de connectiviteit van habitatgebieden te verkrijgen, zijn in dit onderzoek de bepalende factoren van connectiviteit bestudeerd, namelijk: de ruimtelijke en temporele verdeling van habitatoppervlak in het landschap, de kolonisatiecapaciteit van plantensoorten (zie volgende alinea) en de interactie tussen deze twee. Het onderzoek is specifiek gericht op de versnippering van voedselarme, soortenrijke, vochtige graslanden (blauwgraslanden, *Cirsio dissecti-Molinietum*, en verwante graslandtypen) en de gevolgen hiervan voor vier windverspreide plantensoorten. Voor de bestudeerde graslandtypen is gekozen, omdat deze in West-Europa sterk versnipperd zijn geraakt, hun versnippering nog steeds doorgaat en deze met een zorgwekkend verlies aan soorten en biodiversiteit gepaard gaat. De geselecteerde plantensoorten zijn representatief voor twee veel voorkomende zaadverspreidingsstrategiëen in graslanden. *Cirsium dissectum* (Spaanse ruiter) en *Hypochaeris radicata* (Gewoon biggekruid) hebben zaden met een pluisje, die zijn aangepast aan lange-afstandsverspreiding door de wind. *Centaurea jacea* (Knoopkruid) en *Succisa pratensis* (Blauwe knoop) hebben zaden zonder pluisjes, die over korte afstanden door de wind worden verspreid. Het veldonderzoek vond plaats in Nederland.

Hoofdstuk 2

Het in Hoofdstuk 2 van dit proefschrift beschreven onderzoek toont aan, dat habitatversnippering de intrinsieke kolonisatiecapaciteit van windverspreide plantensoorten verandert. Onder die kolonisatiecapaciteit wordt in dit onderzoek verstaan: de capaciteit van een plantensoort om geschikte vestigingsplaatsen te koloniseren. De kolonisatiecapaciteit wordt bepaald door de hoeveelheid zaden die geproduceerd wordt, de verspreidingsafstand van die zaden en hun kiemkracht. Door habitatversnippering neemt de grootte van lokale plantenpopulaties af. Dit onderzoek toont aan dat de populaties hierdoor minder zaden produceren en dat die zaden bovendien een lager kiemingspercentage hebben (waarschijnlijk wordt dit veroorzaakt door inteelt). Een afname in populatiegrootte leidt dus tot een afname van kolonisatiecapaciteit. Habitatversnippering heeft ook tot gevolg dat habitatgebieden meer invloeden van buitenaf ondervinden, omdat hun omtrek-oppervlak-ratio is vergroot. Hierdoor kunnen de interne milieu-omstandigheden in die gebieden veranderen. Een van de belangrijkste veranderingen in de bestudeerde graslanden is dat in meer of mindere mate eutrofiëring (vermesting) optreedt. In dit onderzoek is dat gemeten als een toenemende productie van bovengrondse biomassa. Dit onderzoek toont aan dat een toenemende productie gepaard gaat met een afnemende kolonisatiecapaciteit voor verder weg gelegen habitatgebieden. Dit komt omdat de planten zaden produceren met eigenschappen die erop wijzen dat zij minder ver door de wind worden verspreid. In tegenstelling daarmee neemt de kolonisatiecapaciteit voor dichtbij gelegen gebieden toe, omdat de planten meer zaden produceren en die zaden een hoger kiemingspercentage hebben.

Hoofdstuk 3

Het in Hoofdstuk 3 beschreven onderzoek toont aan welke eigenschappen van planten en hun omgeving het meest bepalend zijn voor de afstanden waarover zaden door de wind worden verspreid, en dus over welke afstanden mogelijk nog kolonisatie kan optreden. Dit werd onderzocht aan de hand van modelsimulaties en zaadverspreidings-experimenten. Door steeds verschillende processen toe te voegen in de simulatie van windverspreiding werd vastgesteld welke processen bepalend zijn voor zaadverspreiding (en met name lange-afstandsverspreiding) door de wind. De simulaties werden op hun realisme en nauwkeurigheid getoetst door hun resultaten te vergelijken met resultaten van zaadverspreidingsexperimenten in het veld. Tijdens deze experimenten werd de verspreiding van individuele zaden door de wind gevolgd en opgemeten. Tot slot werd een gevoeligheidsanalyse van de modellen gebruikt om vast te stellen welke eigenschappen van planten en hun omgeving het meest bepalend zijn voor verspreidingsafstanden.

Uit dit onderzoek blijkt dat turbulente windbewegingen (gesimuleerd als in tijd en ruimte gecorreleerde fluctuaties in verticale en horizontale windsnelheid) het belangrijkste mechanisme voor lange-afstandsverspreiding door de wind zijn. Zaden worden tijdens stormen het verst door de wind verspreid. Bij lage windsnelheden worden zaden verder verspreid wanneer er meer thermiek is. De horizontale windsnelheid, de hoogte vanwaar het zaad wordt verspreid, de vegetatiehoogte en de terminal velocity (valsnelheid) van het zaad zijn, in die volgorde, de meest bepalende factoren voor windverspreidingsafstanden. Een zaad wordt verder door de wind verspreid bij een hogere windsnelheid en verspreidingshoogte, en bij een lagere vegetatiehoogte en terminal velocity. De terminal velocity van een zaad is de constante valsnelheid die een zaad in stilstaande lucht bereikt (deze kan in een valtoren gemeten worden). De terminal velocity van een zaad is echter alleen van belang wanneer men verschillende soorten met elkaar vergelijkt; binnen een soort is de variatie te klein om verschillen in verspreidingsafstand te verklaren.

Hoofdstuk 4

Het in Hoofdstuk 4 beschreven onderzoek geeft een schatting van de veranderingen in de kolonisatiecapaciteit van windverspreide plantensoorten als gevolg van (toekomstige) menselijke effecten op natuur en milieu. De belangrijkste menselijke effecten die gevolgen hebben voor kolonisatie door windverspreide graslandplanten zijn: habitatversnippering, eutrofiëring (al dan niet als gevolg van habitatversnippering) en klimaatsveranderingen die kunnen leiden tot een toename in het aantal stormen en de intensiteit van stormen in West-Europa. Voorheen was het onmogelijk om de gevolgen hiervan voor kolonisatie door windverspreide plantensoorten in te schatten, omdat het onmogelijk was om één essentieel onderdeel van kolonistie, namelijk lange-afstandsverspreiding, te schatten. In dit onderzoek is hiervoor gebruik gemaakt van een nieuw, realistisch en nauwkeurig zaadverspreidingsmodel dat in Hoofdstuk 3 is beschreven. Hierdoor is het voor het eerst wel mogelijk lange-afstandsverspreiding te schatten. Analyses werden voor verschillende scenario’s uitgevoerd, gebaseerd op literatuurgegevens over stormen en de metingen aan kolonisatieparameters die in Hoofdtsuk 2 beschreven zijn.

De scenario-analyses tonen aan, dat de afname in populatiegroottes als gevolg van habitatversnippering niet tot kortere zaadverspreidingsafstanden leidt. Toch neemt de kolonisatiecapaciteit wel af, omdat er minder zaden geproduceerd worden en deze een lager kiemingspercentage hebben. De scenario-analyses tonen aan dat eutrofiëring de zaadverspreidingsafstanden sterk verkort, omdat het leidt tot een grotere vegetatiehoogte (m.n. ten opzichte van de verspreidingshoogte van de zaden). Eutrofiëring doet in veel plantensoorten echter het aantal geproduceerde zaden en de kiemkracht van de zaden toenemen. In totaal leidt eutrofiëring daarom tot een lagere capaciteit voor kolonisatie over lange afstanden en tot een hogere capaciteit voor kolonisatie over korte afstanden. Tot slot tonen de scenario-analyses aan dat een toename in (extreem) hoge windsnelheden de capaciteit voor kolonisatie over lange afstanden verhoogt, omdat zaden verder door de wind worden verspreid. Deze verhoging van kolonisatiecapaciteit compenseert de afname in zaadverspreiding en kolonisatie over lange afstanden als gevolg van habitatversnippering en eutrofiëring echter slechts in zeer geringe mate.

Hoofdstuk 5

Het in Hoofdstuk 5 beschreven onderzoek laat zien hoe het proces van habitatversnippering in een deel van Nederland gedurende de 20^e eeuw is verlopen en kwantificeert de habitatversnippering en connectiviteit. Voor dit laatste zijn de gegevens over de kolonisatiecapaciteit van windverspreide plantensoorten (beschreven in de voorgaande hoofdstukken) gecombineerd met de kwantitatieve gegevens over het proces van habitatversnippering. Het was voorheen niet mogelijk om deze combinatie te maken, omdat er geen realistische schattingen van de (toekomstige) kolonisatiecapaciteit van windverspreide plantensoorten waren en omdat het proces van habitatversnippering nog niet eerder was gekwantificeerd op een manier die directe vergelijking met kolonisatiegegevens mogelijk maakte. In dit onderzoek werden verschillende aspecten van habitatversnippering voor een 11×10 km regio in De Achterhoek gekwantificeerd door een tijdserie van habitatkaarten (1900, 1950 en 2000) met elkaar te vergelijken. De habitat werd in kaart gebracht volgens een classificatiemethode die op (historische) vegetatiegegevens is gebaseerd.

De resultaten van dit onderzoek laten zien dat de afname in het oppervlak en de connectiviteit van de graslanden gedurende de 20^e eeuw enorm is geweest. Zowel het oppervlak als de connectiviteit zijn nu zeer gering. De resterende habitatgebieden zijn voor het grootste deel wel door populaties van de bestudeerde plantensoorten bezet, maar deze populaties nemen nog steeds in aantal en grootte af en hebben een verminderde kolonisatiecapacitieit. Zowel hierdoor als door de grote afstanden tussen de habitatgebieden is de connectiviteit zo laag geworden, dat vrijwel alle gebieden compleet geïsoleerd zijn voor wat betreft zaadverspreiding door de wind. Dit geldt zelfs voor de plantensoorten met zaden met pluisjes, die door de wind over lange afstanden verspreid kunnen worden. De kans dat nieuwe of gerestaureerde habitatgebieden door de windverspreide graslandsoorten gekoloniseerd zullen worden is vrijwel nihil, tenzij deze gebieden zeer dicht bij bezette gebieden liggen (zie volgende paragraaf) of de zaadverspreiding door gericht ingrijpen van de mens wordt geholpen. De regionale overleving van de plantensoorten is nu volledig afhankelijk van de overleving van de paar grote populaties die nog in beschermde natuurgebieden aanwezig zijn. Dit betekent dat het voor de regionale overleving van de plantensoorten momenteel noodzakelijk is om de grootste zorg te besteden aan de lokale overleving van de resterende populaties en het verbeteren van de connectiviteit tussen habitatgebieden.

RICHTLIJNEN VOOR NATUURBEHEER

De resultaten van dit onderzoek laten zien hoe versnipperd voedselarme, soortenrijke, vochtige graslanden in Nederland zijn geraakt. In deze graslanden, maar ook in vele andere (half-)natuurlijke ecosystemen over de hele wereld, is de regionale overleving van plantensoorten volledig afhankelijk geworden van de lokale overleving van de laatste grote populaties die nog over zijn gebleven in beschermde natuurgebieden. Als de versnippering van de graslanden verder gaat zullen het aantal overlevende populaties en de connectiviteit nog verder afnemen. Uiteindelijk zullen de soorten van deze graslanden dan in Nederland uitsterven. Maar ook als de versnippering nu stopt, zullen de gevolgen van de versnippering die in het verleden plaatsvond doorgaan een bedreiging voor de regionale overleving van plantensoorten te vormen. Vrijwel alle resterende graslandgebieden en (dus) de daarin voorkomende plantenpopulaties zijn klein en geïsoleerd. Dit vergroot het risico op uitsterven van de resterende populaties vanwege toevalsprocessen, een verminderde voortplanting, negatieve gevolgen van inteelt en verlies van genetische variatie. Kleinere habitatgebieden zijn bovendien gevoeliger voor invloeden van buitenaf, die kunnen leiden tot eutrofiëring (vermesting), verdroging en verzuring. Eutrofiëring van habitatgebieden leidt tot een verlies van kolonisatiecapaciteit van de daarin voorkomende populaties van windverspreide plantensoorten. Voortgaande eutrofiëring, verdroging en verzuring leiden uiteindelijk tot het uitsterven van de populaties en verlies van de habitat.

De resultaten van dit onderzoek geven aan, dat de volgende maatregelen cruciaal zijn voor een langdurige regionale overleving van windverspreide plantensoorten die alleen voorkomen in voedselarme, vochtige graslanden:

- Ten eerste is het van groot belang dat het beheer van alle resterende voedselarme, vochtige graslanden wordt gericht op het maximaliseren van de lokale overlevingskans van de resterende plantenpopulaties. De regionale overleving van windverspreide plantensoorten die in dit habitattype voorkomen is volledig afhankelijk van de overleving van die resterende populaties. Elk habitatgebied dat nu nog verloren gaat, en elke plantenpopulatie die nu nog uitsterft, verkleint de kans dat de soort regionaal zal overleven. Bij het beheer van deze populaties is het van belang dat men zich realiseert dat de meeste resterende populaties voor wat betreft zaadverspreiding door de wind vrijwel volledig geïsoleerd zijn.

- Ten tweede is het van groot belang, dat de connectiviteit van de resterende voedselarme, vochtige graslanden wordt vergroot. Om dit te bereiken moeten de volgende maatregelen genomen worden: 1. Barrières tussen habitatgebieden moeten (gedeeltelijk) worden verwijderd, als dit zonder schade of verlies aan biodiversiteit kan gebeuren. 2. Management van de resterende plantenpopulaties moet er op gericht zijn de kolonisatiecapaciteit van die populaties te vergroten. Dit wordt bereikt door beheer dat is gericht op het vergroten van de populaties, zodat er meer zaden en zaden met een hoger kiemingspercentage geproduceerd worden, en door het tegengaan of terugdraaien van eutrofiëring, zodat windverspreide zaden verder verspreid kunnen worden. 3. De connectiviteit moet vergroot worden door nieuwe habitatgebieden te creëeren op strategische locaties. Dit onderzoek geeft aan dat hiervoor de volgende vuistregels kunnen worden gebruikt:

- Voor graslandsoorten met zaden met pluisjes (zoals Biggekruid en Spaanse ruiter), die aan lange-afstandsverspreiding door de wind zijn aangepast, geldt dat 95% van de verspreide zaden binnen een straal van 100 m van de ouderplant terecht komt (zelfs tijdens hevige stormen). Connectiviteit wordt gewaarborgd indien nieuwe habitatgebieden op een afstand van minder dan 100 m van bezette habitatgebieden gecreëerd worden.

- Veel andere graslandsoorten hebben kortere zaadverspreidingsafstanden. Plantensoorten met zaden die zijn aangepast aan korte-afstandsverspreiding door de wind (zoals Blauwe knoop en Knoopkruid) verspreiden 95-100% van hun zaden over minder dan 4 m. Om de connectiviteit voor zulke soorten te vergroten, zouden nieuwe habitatgebieden op minder dan 4 m van bezette habitatgebieden gecreëerd moeten worden. In praktijk betekent dit dat nieuwe habitatgebieden aan de bezette habitatgebieden moeten aansluiten.

- Nieuw te creëeren habitatgebieden moeten bij voorkeur bestaan uit velden en niet uit lineaire landschapselementen zoals wegbermen. Deze verhogen de connectiviteit voor windverspreide plantensoorten van voedselarme graslanden nauwlijks.

Voor veel plantensoorten zal het waarschijnlijk niet mogelijk zijn om de connectiviteit zo te vergroten, dat zaadverspreiding tussen verschillende habitatgebieden (weer) mogelijk wordt. Voor plantensoorten met zaden die zijn aangepast aan korte-afstandsverspreiding door wind of aan andere verspreidingsmechanismen die zaden gewoonlijk maar over korte afstanden verspreiden (zoals verspreiding door mieren), zal het erg moeilijk zijn om voldoende nieuwe habitatgebieden te creëeren om de bestaande gebieden met elkaar te verbinden. In zulke gevallen zal de kolonisatie van nieuwe habitatgebieden actief door de mens moeten worden geholpen. Dit kan door het maaisel van bezette gebieden in onbezette gebieden uit te spreiden, mits er gemaaid wordt op een tijdstip dat de zaden rijp zijn en deze nog aan de planten vast zitten. Als dit niet het geval is, zal directe introductie of re-introductie van zaden of planten door de mens (ook al is dit een controversiële methode) noodzakelijk zijn voor de regionale overleving van deze plantensoorten.

Curriculum vitae

Merel Barbara Soons was born in Zeist, The Netherlands, on 20 December 1975. She received her secondary education in The Hague at the Gymnasium Haganum. In 1993 she started to study Biology at Utrecht University. During her studies she carried out two 9-month research projects. The first project involved development of a mechanistic simulation model for predicting effects of management regimes on the dominance of *Brachypodium pinnatum* in Dutch chalk grasslands (supervised by Dr. Gerrit Heil). During the second project she assessed potential threats of dehydration, acidification, and eutrophication in a wetland nature reserve (supervised by Dr. Boudewijn Beltman). Research for this project was carried out in Sheheree Bog, County Kerry, Ireland. She was an active member of the Utrechtse Biologen Vereniging (UBV, the Biology Students Association of Utrecht University) and contributed to the UBV's research project on the feasibility of using sustainable energy sources at the University campus, organization of a scientific symposium, and organization of the Utrechtse Bèta-Bedrijvendagen. She was a teaching assistant in Plant Physiology, Field Ecology, and Theoretical Ecology. In 1998 she obtained her M.Sc. degree in Plant Ecology and Landscape Ecology *cum laude*. Subsequently, she started a Ph.D. research project at Utrecht University, funded by the Netherlands Organization for Scientific Research (NWO). Part of the research was carried out at the Nicholas School of the Environment and Earth Sciences, Duke University, North Carolina, USA. In Utrecht she supervised six M.Sc. students, who carried out research projects of varying duration. She was also a tutor for first-year Biology students, initiated a series of national discussion meetings for Ph.D. students working on spatial vegetation processes, and initiated and organized a Ph.D. course on General Laws in Ecology. In 2003 she completed her NWO Ph.D. research appointment with the publication of this thesis. She currently pursues her interest in spatial ecology, including seed dispersal and colonization, gene flow, migration, and biodiversity patterns, being involved in several research projects on these issues.