promotoren: dr. F. Berendse
hoogleraar in het natuurbeheer

dr. J.M. van Groenendael
hoogleraar in de aquatische oecologie
Katholieke Universiteit Nijmegen

SEED DISPERSAL IN AGRICULTURAL HABITATS AND THE RESTORATION OF SPECIES-RICH MEADOWS

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Dispersie van zaden in cultuurlandschappen en het herstel van soortenrijke graslanden

Proefschrift
ter verkrijging van de graad van doctor
in de landbouw- en milieuwetenschappen,
op gezag van de rector magnificus,
dr. C.M. Karssen,
in het openbaar te verdedigen
op woensdag 24 april 1996
des namiddags om vier uur in de aula
van de Landbouwuniversiteit te Wageningen

SEED DISPERSAL IN AGRICULTURAL HABITATS AND THE RESTORATION OF SPECIES-RICH MEADOWS

D. van Dorp

voor Alice
voor mijn ouders

This study was supported by the former Foundation for Social and Spatial Scientific Research (SRO) which was subsidized by the Netherlands Organization for Scientific Research (NWO).
The study was carried out at the Department of Terrestrial Ecology and Nature Conservation, Bornsesteeg 69, 6708 PD Wageningen, Agricultural University at Wageningen, the Netherlands.

Most parts of this thesis have been submitted for publication in scientific journals.

CIP-GEGEVENS KONINKLIJKE BIBLIOTHEEK, DEN HAAG

van Dorp, Dirk

Seed dispersal in agricultural habitats and the restoration of species-rich meadows / Dirk van Dorp. - Wageningen: Landbouwuniversiteit Wageningen.
Thesis Wageningen.- With ref. - With a summary in English and Dutch.
ISBN 90-5485-531-2
Subject headings: seed dispersal / restoration ecology / meadows

Grafisch Service Centrum Van Gils b.v. Wageningen
Cover: aerail view of the set-aside object Veenkampen (Photo AB-DLO)

STELLINGEN

1. Slootkanten vormen een zaadbron van zeldzame plantesoorten die belangrijker is dan vaak wordt verondersteld. Bij het dempen en opnieuw dimensioneren van watergangen wordt onvoldoende beseft wat daarmee aan genetische variatie verloren gaat
(dit proefschrift)

2. Lijnvormige elementen in cultuurlandschappen functioneren niet als corridors voor lokaal en regionaal uitgestorven plantesoorten
(dit proefschrift)

3. Het dispersievermogen van planten wordt sterk onderschat
(dit proefschrift)

4. Verbreiding van besdragende planten in cultuurlandschappen verloopt succesvoller door transversale dan door longitudinale zaadverbreiders
(dit proefschrift)

5. Herstel van dispersie-vectoren is zinvoller dan herintroductie van plantesoorten

6. Plantesoorten die alleen als zaden in de bodem aanwezig zijn dienen ook tot de flora van een plek te worden gerekend

7. Voor de karakterisering van natuurdoeltypen heeft men de verkeerde soorten geselecteerd
(D. Bal e.a. 1995. Handboek Natuurdoeltypen in Nederland)

8. Steeds vaker zal bij natuurontwikkeling ten gevolge van een slechte milieukwaliteit "natuurlijkheid" een belangrijker criterium zijn dan "verscheidenheid"
(J. van Rijen, Landschap 12(5):45-49)

9. Het ontwikkelen van natuurwaarden door middel van particulier natuurbeheer dient krachtig te worden gestimuleerd

10. Er dient meer aandacht te worden besteed aan de culturele en maatschappelijke vorming van studenten die in een verenigd Europa werkzaam willen zijn

Dick van Dorp
24 april 1996

Voorwoord

Dit proefschrift vormt de neerslag van een tamelijk lange periode van interesse naar de verbreiding van zaden in cultuurlandschappen. Deze belangstelling werd in eerste instantie gewekt door het lezen van Kropotkin's "Wederkeerig Dienstbetoon, een factor der Evolutie". Later zag ik in de Duinen van Oostvoorne waartoe het verbreiden van zaden van besdragende struiken door vogels kan leiden. Na een verblijf in een Mexicaans regenbos en een hardwood forest in New York lag het voor de hand in Nederland de betrekkingen tussen vogels en planten verder te bestuderen. Maar mijn weg volgde een andere route.

De in dit proefschrift vermelde bevindingen zijn het resultaat van een onderzoek naar het herstel van soortenrijke graslanden op voormalige landbouwgronden, in het bijzonder de rol van dispersie van plantezaden. Aan dit onderzoek heeft een aantal personen enthousiast meegewerkt. Mijn dank gaat in de eerste plaats uit naar de twee initiatiefnemers en begeleiders van dit onderzoek, Frank Berendse en Jan van Groenendael. Ik dank hen voor het vertrouwen dat ze in mij hebben gesteld. Hun kritische commentaar vormde telkens een stimulans om verder te gaan. Ik beschouw het als een voorrecht dat beiden bereid zijn als promotor op te treden.

Het personeel van de voormalige vakgroep Vegetatiekunde, Onkruidkunde en Plantenoecologie (VPO), thans vakgroep Terrestrische Oecologie en Natuurbeheer (TON), verrichtte belangrijk werk. Pieter Ketner, Herman Klees en Herman van Oeveren karteerden in menig uur de plantesoorten van het Binnenveld. Peter Schippers was onmisbaar bij het ontwikkelen van het simulatiemodel. Een aantal studenten heeft als onderdeel van hun studie ook een belangrijke bijdrage geleverd: Tineke Alons, Frank van den Berg, Hans van Dalen, Marjolijn Dannenburg, Joep Frissel, Martin de Groot, Willeke van den Hoek, Ruben Keestra, Ivo Raemakers en Henk Rap. Verder zorgden Jaap Blijenberg en Jan Koekkoek voor technische assistentie. Cees Daleboudt hielp met de statistische verwerking van een deel van de gegevens. Fia Brussen verschafte mij nuttige referenties. Ali Ormel was een baken in woelige tijden.

Daarnaast toonden andere collega's van VPO en leden van de Adviesgroep Vegetatiebeheer van het Ministerie van LNV hun belangstelling. Ook de contacten met het voormalige CABO, thans AB-DLO, en in het bijzonder met Ties Oomes, waren altijd plezierig en ondersteunend van aard. Joy Burrough-Boenisch corrigeerde prompt alle aangeleverde teksten op het Engels.

Er komt geen proefschrift tot stand zonder een meelevend thuisfront. Mijn ouders en schoonouders toonden altijd een warme belangstelling voor mijn vorderingen en zorgden ervoor dat ik mij op gezette tijden aan mijn ouderlijke verplichtingen kon onttrekken. Ook onze vrienden, leden van de redactie van Landschap en collega's van Hogeschool Larenstein gaven regelmatig blijk van hun betrokkenheid.

Ik draag dit proefschrift op aan Alice die als geen ander het wel en wee van de afronding van het proefschrift heeft meegemaakt. Door haar begrip en ondersteuning kon het karwei worden voltooid. Met het gereedkomen ervan komt er weer kostbare tijd vrij voor andere, evenzeer belangrijke zaken.

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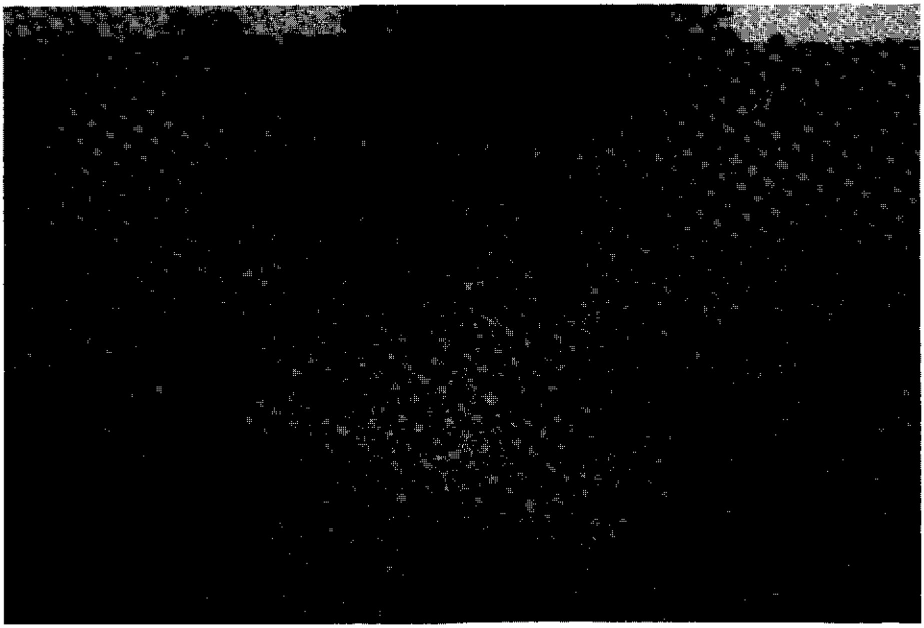

Restoration of species-rich meadows on the set-aside area Veenkampen

INTRODUCTION

The appearance of agricultural landscapes in Western Europe will gradually change as the various reforms to the global economy become effective. One of the serious consequences will be that farmland has to be taken out of agricultural production. De Wit (1988) estimated that about twenty million hectares would have to be withdrawn from agricultural production by the year 2000 in order to stabilize the agricultural production in the European Community. This scenario implies that there will be great opportunities for assigning the set-aside land to other functions, including nature. Especially for the restoration of nature in Western Europe, great challenges lie ahead for nature conservationists and physical planners to construct the ecological networks which are necessary to stem the loss of biodiversity (Arts et al. 1995).

In the Netherlands, the loss of biodiversity has been especially dramatic during this century. Between 1930 and 1990, 70 of the 1450 species of flowering plants recorded in the Netherlands disappeared and a further 500 declined seriously (Bink et al. 1994). The factors responsible for this decline include the eutrophication and acidification of ecosystems, the falling water tables and the fragmentation of natural and semi-natural habitats. In the late 1980s, the Dutch parliament endorsed several policy plans which aim to counteract the deterioration of nature. One of these, the Nature Policy Plan (Ministerie LNV 1990) specifically tries to preserve national biodiversity by developing a National Ecological Network or NEN (van Zadelhoff and Lammers 1995).

This NEN is intended to become a robust and coherent network consisting of core areas, nature restoration areas and ecological corridors. The *core areas* are large (>500 ha) areas with an ecological value of national or international significance. They function as *hot spots* which provide the propagules and juveniles for the (re)colonization of the surrounding smaller areas. The *nature restoration areas* offer good prospects for being developed into new areas of ecological value of national or international significance that are situated between already established core areas. For example, former intensively farmed areas, such as those on sandy soils with upwelling base-rich groundwater, are potentially suitable for the development of nutrient-poor wet ecosystems such as species-rich meadows, marshes and marshy woodlands. The *ecological corridors* are designated to enhance the migration between core areas, in particular for animal species such as otter, badger, red deer and certain species of fish (sea trout, river trout, salmon). They comprise linear landscape elements such as wooded banks, dikes, ditch banks, small streams and rivers.

The ecological rationale underlying the NEN rests on the island biogeographical principles of area-dependent extinction and area and distance-dependent immigration (MacArthur and Wilson 1967). According to this theory and later derivatives (Gilpin and Hanski 1991), enlarging existing favourable areas through nature development will lead to larger populations and hence lower rates of extinction (Verboom et al. 1993). Increasing the connectivity between isolated areas and decreasing the resistance to dispersing propagules and juveniles mean higher rates of (re)colonization as a result of increasing numbers of immigrants. The application of island biogeographical principles at several scales (i.e. national, regional and local) seems warranted for several medium to large vertebrate species (particularly birds and mammals), but their applicability to plant species is not clear (Opdam et al. 1993).

Aim of the study

This thesis is a feasibility study of restoring endangered species-rich plant communities on formerly farmed land that has been taken out of agricultural production and the importance of seed dispersal to achieve this goal. Restoration in this context generally refers to the efforts to reassemble a community or ecosystem and to allow it to function properly (Jordan et al. 1987).

Restoration of biodiversity has become a major policy goal in the Netherlands (Bal et al. 1995). One of the ecosystems that has a high priority in the Netherlands to become reassembled on sites with good prospects are nutrient-poor wet meadows, because these ecosystems have been disappearing rapidly due to eutrophication, acidification and desiccation because of falling water tables. In order to be able to restore such ecosystems, it is vital to analyse two sets of related problems. The first set of problems is related to restoring the growing conditions appropriate for the plant species selected, the second set is to do with the availability of propagules (seeds, fruits, vegetative parts etc.). Both sets of problems will be briefly described below.

Firstly, ecological restoration depends on the *suitability* ("*toegankelijkheid*") of a target site. In the Netherlands, the starting point for the restoration of species-rich meadows frequently is a soil with a history of agriculture that has been drained and enriched with fertilizers for decades. Restoration then involves ameliorating the habitat quality for the selected plant species by applying the correct counter measures, e.g. by rewetting the soil with base-rich groundwater that reaches the root zone (Grootjans et al. 1993). Another important measure is to reduce the availability of nutrients to plants through cutting and grazing (Bakker 1989) or by removing the complete enriched topsoil. These measures are necessary to reset the ecosystem variables such as the pH, moisture content of the soil and the availability of macro-nutrients (NPK) to levels that favour the growth of the selected plant species.

The probability of *recruitment* depends on factors such as the nature (e.g. size) and frequency of appearance of gaps in the vegetation which allow new individuals to germinate and establish. The soil fertility is an important determinant of future success as it controls which plant species are able to outcompete other species.

Secondly, ecological restoration involves the *accessibility* ("*bereikbaarheid*") of a target site. It is generally assumed that sufficient numbers of propagules are still available or will soon become available. This need not always be the case. There are two alternative strategies by which plants may (re)colonize a target site; either through the germination of seeds that have survived unfavourable periods dormant in the soil or through the dispersal of seeds produced by populations in neighbouring sites (Howe and Smallwood 1982).

The probability of *seed survival* in soil seed banks depends on factors such as the capacity of seeds to remain dormant at various depths in soil, the duration of burial and the frequency and nature of soil disturbances. The larger the size of the initial seed stocks, the greater the number of buried seeds in the soil seed bank that is available at the time restoration starts.

The probability of *seed arrival* in a target area depends on factors such as the number of seed sources in the landscape and their position relative to a target site (distance), the production of seeds and the presence and efficacy of dispersal vectors (single or multiple) such as water, wind, animals and humans (the latter includes machinery, cars, soil redistribution etc.).

In situations where soil seed banks have been depleted because of the rapid decay of buried seeds in the soil seed bank or the removal of the topsoil, dispersal of seeds is the only natural option to restock a target site with seeds. Since most grassland species have a limited dispersal capacity (Fenner 1985), the distances between seed sources and a target site are assumed to be of vital importance. Ecological corridors could facilitate the dispersal of species under the assumption that they satisfy the requirements that desirable species on the target site demand (Verkaar 1990).

Study site

The site for the restoration of species-rich meadows is a complex of long and narrow fields of grass (*Veenkampen*, 13.4 ha) that lies in an intensively exploited agricultural landscape near Wageningen, the Netherlands. It is a typical Dutch landscape in which the site undergoing restoration is surrounded by farmed fields that are criss-crossed by drainage ditches. The banks of these ditches are mostly long (up to 0.8 km), narrow (up to 5 m wide) and sloping (angle between 30° and 50°) strips of not cultivated land that are heavily influenced by agricultural activities on adjacent fields such as the application of fertilizers, herbicides and (over)grazing. Due to these high pressures of modern land use, the biological diversity of such linear elements has declined considerably. Nevertheless, in a number of cases they still function as refugia for a large number of characteristic meadow species (Melman 1991; van Strien 1991). On the study site, restoration of species-rich meadows has been the primary management goal since 1978, when the application of fertilizers was ceased.

Outline of the thesis

This thesis deals with a number of aspects of the regeneration ecology of several meadow plant species (Chapters 1-5). Two questions are raised in particular: (i) is it possible to restore species-rich meadows on previously farmed fields that have experienced several decades of intensive agricultural exploitation and (ii) do landscape elements such as ditch banks between core areas and nature restoration areas function as ecological corridors for species that are absent from a restoration site? To provide a contrast with typical grassland species, fleshy-fruited plant species and their specific dispersal characteristics have been studied as well (Chapter 6).

Chapter 1 compares (i) the recent species list of the study site (*Veenkampen*) with (ii) historical data on the former (i.e. pre-1945) species-rich meadows and with (iii) recent data on the ditch banks in the surrounding farmed landscape. These species lists are combined to yield seven categories of plant species (i.e. present in only one out of three, in two out of three or in all three lists), from which desirable species are identified. The main questions in this part of the study are which desirable plant species have indeed recolonized the study site since restoration started in 1978 and which species have failed to do so, and whether success or failure can be related to dispersal and regeneration characteristics of the species involved.

Chapter 2 examines the dynamic distribution patterns of ten such desirable plant species over a three-year period (1990/1992). The selection of these species is based on the findings of Chapter 1 and includes perennial plant species that are typical of moist to wet and moderately fertile meadows in the Netherlands. They have contrasting regenerative strategies which are based primarily on the dispersal of seeds, vegetative spread, recruitment from a seed bank in the soil or on a combination of processes.

The aim of this part of the study was to relate distribution patterns and frequencies of extinction and colonization events to the management of ditch banks and to the population size and dispersal and regeneration characteristics of the selected species. The findings are used to discuss the feasibility of restoring species-rich meadows on former agricultural land given the regenerative strategies of the selected species and the way ditch banks in the surrounding landscape are managed.

Chapter 3 deals with the question how far seeds of grassland species are dispersed by wind in relation to wind speed and release height. The vector wind was considered to be the most important natural dispersal mechanism in agricultural landscapes. An experimental approach in a wind tunnel allowed a detailed description of the distribution of dispersal distances of seeds in relation to wind speed and release height. Seeds of six of the selected plant species of Chapter 2 have been used in these experiments. As wind dispersal of most perennial grassland seeds is generally insufficient to bridge the large distances between sources and target sites in agricultural landscapes, the findings can be used to discuss the importance of rare stochastic events such as wind storms for the restoration of species-rich plant communities.

Chapter 4 reports on the results of a field trial in which the probability of establishment in a grassland undergoing restoration was determined. Restoration practices generally produce a habitat suitable for colonization, but often the appropriate plant species are still missing.

Adding the seeds of these missing species distinguishes between dispersal and habitat-related factors. In a field experiment, seeds of the ten plant species selected in Chapter 2 were added to a sward that was mown, clipped or from which the sod had been stripped. Established plants were allowed to grow (but not reproduce) for two years and were then harvested. At the same time, some seeds were buried in the soil in order to assess their survival.

Chapter 5 explores the importance of linear landscape elements as ecological corridors for plant species migrating across agricultural landscapes. The reasonable assumption that a direct input of seeds of missing desirable plant species into suitable but unoccupied habitat patches from distant seed sources is an extremely rare event, leaves stepwise migration along corridors as an important possible alternative route. A cellular automaton model was built in order to determine the relative importance of the seed dispersal capacity of plants, the quality and density of habitat patches and the width of corridors on the migration rate of plants.

Chapter 6 deals with the dispersal interactions between fruit-eating birds and fleshy-fruited plants (mainly shrubs) that grow on wooded banks in a Dutch agricultural landscape. The study site is located in the north-east of Twenthe, Overijssel province. Wooded banks are a characteristic feature of the landscape, but the density of such linear landscape elements in the landscape (*connectivity*) is changing, i.e. in some areas wooded banks have been removed to increase field size whereas new banks are being planted for aesthetic and ecological reasons elsewhere. The density of wooded landscape elements in this landscape varied more than an order of magnitude.

Fruit-eating birds play a fundamental role in dispersing the seeds of the tree and shrub species recorded on wooded banks to new sites. They favour the fleshy fruits that are abundant in the landscape. The aim of this part of the study was to compare the distribution of fruit-eating birds and fleshy-fruited plant species and the dispersal of seeds in landscapes that vary in the density of landscape elements.

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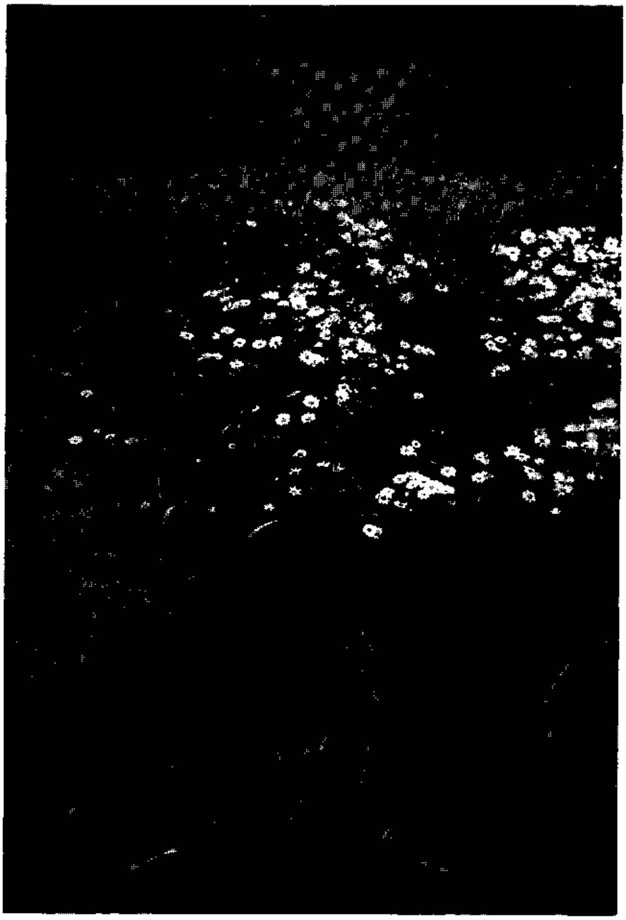

Ditch bank providing a habitat for Cirsium palustre, Leucanthemum vulgare and Lychnis flos-cuculi

CHAPTER 1

Restoration of species-rich meadows: limitations due to seed dispersal and recruitment from the soil seed bank

with M.J.M. Oomes
submitted to Biological Conservation

Abstract

The first phase of the restoration of species-rich meadows on former agricultural land in an intensively exploited farmed landscape in the centre of the Netherlands was studied. A comparison was made between the species pools of (i) the former species-rich meadows (145 species), (ii) a set-aside site or target site undergoing restoration (142 species) and (iii) the ditch banks in the surrounding farmed landscape (200 species).

The total pool of 252 plant species was divided into five categories of plant species; regionally extinct species (39 species), species that have not recolonized the target site but are present in the surrounding landscape (21 species), species that are present in all three species pools (85 species) and species that have recently invaded the surrounding landscape and/or the target site (57 and 50 species, respectively).

The dispersal mechanism, dispersal capacity and seed bank strategy of these categories were compared; in most cases the observed frequencies did not differ significantly from expected, indicating that some of the missing desirable species with long-range dispersal and/or permanent seed banks will recolonize the site. However, analysis showed that the first phase of restoration has only partly succeeded; (i) 60 out of the 145 meadow species present in the former meadows have not yet recolonized the target site because of insufficient seed dispersal, depleted soil seed banks and/or too few appropriate microsites for germination and establishment, and (ii) 57 weedy species not recorded on the former meadows are still present in spite of the restoration measures taken.

An increase in the number of meadow species would be attainable if the accessibility and suitability of the target site are maximized. The effectiveness of water, animals and humans as dispersal vectors is extremely limited in the study area, leaving wind as the principal dispersal vector. This observation implies that restoration of the former species-rich meadows in this particular case will remain incomplete unless species are introduced deliberately.

INTRODUCTION

In modern agricultural landscapes, plant species of wet nutrient-poor meadows have become rare or even regionally extinct as a result of intensive farming practices. The surviving plant species of such habitats have become restricted to small isolated nature reserves and to refugia on ditch banks. Yet, the efforts to restore these former species-rich meadows on land that has been taken out of agricultural production are now intensifying (e.g. Gibson et al. 1987; Bakker 1989; Buckley 1989; Ministerie LNV 1990).

In the Netherlands, Berendse et al. (1992) have carried out ecosystem experiments on different soil types with the aim of restoring species-rich meadows on formerly farmed fields. They concluded that low productivity levels are a prerequisite for, but do not guarantee, successful restoration of such meadow ecosystems. Other factors assumed to be important are the proximity of source populations, the presence of a seed bank in the soil and the frequent appearance of microsites appropriate for germination and establishment.

We report here on the first results of the restoration of species-rich meadows on a grassland site that experienced over 20 years of intensive farming. The study site is located in an open and heavily exploited farmed landscape in which the level fields are bordered by drainage ditches. In 1978, it was taken out of production and the application of fertilizers was ceased. Since then, the vegetation has been managed by mowing and removing the harvested biomass, by grazing, by locally stripping the sod and since 1986 by restoring the high water table that had long been a feature of these soils (Oomes 1991). The structure and botanical composition of these meadows is gradually changing (Altena and Oomes *unpubl. results*).

The study described in this paper involved a comparison of the recent list of higher plant species of the target site with historical data on on the botanical composition of the former species-rich meadows and with recent data of the ditch banks in the surrounding farmed landscape. Combination of these three species lists yields seven potential categories of plant species which are present in either one, two or all three lists. The main question is which species have indeed recolonized the Veenkampen since restoration started in 1978 and which species have failed to do so. Data on seed dispersal and seed bank strategy could provide some possible explanations for the success or failure of individual species. To determine the relative importance of seed dispersal and recruitment from the soil seed bank during restoration, we posed the following questions:

1. How many plant species are present in these seven species categories and what is their habitat preference?
2. Are differences in species composition between these categories related to differences in dispersal mechanism, dispersal capacity or to the ability to recruit from buried seeds?
3. Which vegetation management strategy gives the best results in terms of restoring the species richness of the former meadows?
4. Are the species absent from the vegetation likely to recolonize through dispersal of seeds or through recruitment from the soil seed bank?

STUDY AREA

The study area (c. 1,200 ha) is located in the centre of the Netherlands between two moraines (*Veluwe* and *Utrechtse Heuvelrug*) 4 km northwest of Wageningen (51°54' N; 5°38' E) (Figure 1). It is part of the *Binnenveld* valley (5 to 8 m above sea level) where peaty soils predominate, but with clay layers in the south, deposited in historic times by the river *Rhine*. Towards the ridges in the east and west of the valley, the peat attenuates and ultimately disappears.

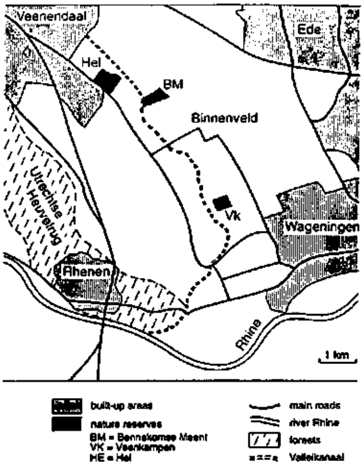

Figure 1. Location of the study area in the Netherlands. The meadows and ditch banks in the botanical surveys were all located within 1 to 2 km of the Veenkampen (Vk). The moraine *Veluwe* (not shown) is located further to the east of Ede and Wageningen.

Before 1950, species-rich meadows covered large parts of the valley and were part of large areas of communal land called 'marken' (Elzebroek 1990). Only small fragments (<15 ha) such as *Bennekomse Meent* and *Hel* remain (Figure 1). The soils of these meadows were originally very poor in nutrients because of the high groundwater levels and the removal of the mowings through hay-making. Inorganic fertilizers were not applied until the first decades of this century. Annual production was therefore low, from 1 to 4 tons per ha. The grass was usually cut by hand once a year, in late August or September. In some very wet years it could not be harvested because of the poor drainage of the valley. Until 1945, the valley was regularly inundated in winter and occasionally during heavy rains in spring and summer (A. Zijlstra *unpubl. data*).

After 1945, the valley was drained by the *Valleikanaal* and fertilized. The subtle differences in microtopography disappeared after the fields had been levelled and ploughed. The water table dropped, to 30 cm below the surface in winter and 80 cm in summer. Inundations no longer occurred. The use of fertilizers increased, with inputs from 50 kg N per ha in the 1950s to 400 kg N per ha in 1980 (van der Meer 1982). Reseeding with modern mixtures of grasses and herbicidal control of weeds are still common practices in the valley.

Veenkampen experimental site

Within the study area, a long-term study of the restoration of species-rich meadows is in progress in the *Veenkampen* experimental grassland site (13.2 ha). Here the soil consists of humic clay 20-80 cm deep, overlying peat above aeolian sandy deposits more than 120 cm below the surface (Berendse et al. 1992). Farming on the Veenkampen has been intensified since 1956. Three of the eight fields were partially ploughed and reseeded in 1956. In 1969 and 1970 two other fields were completely ploughed or reseeded. Three fields have never been ploughed or reseeded as far as is known. In the 1970s these fields were very poor in plant species and were completely dominated by common grassland species such as *Lolium perenne, Poa trivialis,* and *Elymus repens* (Altena and Oomes *unpubl. results*). In 1978, the application of fertilizers was stopped and vegetation management changed to mowing and removal of the harvested biomass in June and September.

In 1986, the site was divided into five compartments, each subjected to hydrological manipulations, so as to form a series from dry to wet meadows (Oomes 1991). In each compartment, three management treatments were established. The first treatment was *mowing and* *removal* of the mowings in June and September which is also the standard treatment on the Veenkampen. The plots measured 10 x 10 m and were replicated five times on each compartment. The total area is 0.25 ha (n=25 plots). The second treatment was seasonal *grazing* by two or three young bulls from May until October on paddocks varying in size from 0.3 to 0.8 ha, with a total area of 3.65 ha (n=5 plots). The third treatment, *sod stripping*, involved removing the upper 5 cm of the topsoil in plots measuring 15 x 25 m, with a total area of 0.19 ha (n=5 plots).

MATERIAL and METHODS

Species lists

Information on the presence of plant species of (i) the former species-rich meadows, (ii) the ditch banks surrounding the Veenkampen and (iii) the Veenkampen itself was collected from respectively:

- the botanical surveys conducted by D.M. de Vries between 1939 and 1950. The botanical composition of 24 species-rich meadows in the study area (1,200 ha) with the Veenkampen as the centre had been sampled over 35 years ago (Kruijne et al. 1967). The meadows in that survey were all located within 2 km of the Veenkampen. The list of species was supplemented with information from six relevés recorded within 0.5 km of the Veenkampen in 1947 (Ott 1992).
- a survey in 1991 of all plants species on 103 locations on 35 ditch banks in the landscape surrounding the Veenkampen. This list was complemented by information from species mapping in 1989, 1990 and 1991. All sampled sites are located within a radius of 1 km from the Veenkampen.
- annual samples of the botanical composition of the mown, grazed and sod-stripped plots on the Veenkampen between 1987 to 1991 (J. Bokdam *unpubl. results*; Altena and Oomes *unpubl. results*).

Categories of plant species

Seven categories of species were distinguished on the basis of plant species being present on either one, two or three species lists:

- species of the former meadows now regionally extinct (A)
- species of the former meadows present on the ditch banks surrounding the Veenkampen, but absent from the Veenkampen proper (B)
- species of the former meadows present on the Veenkampen as well as on the ditch banks of the surrounding landscape (C)
- species absent from the former meadows, but present on the Veenkampen and the surrounding ditch banks (D).

- species absent from the former meadows and the Veenkampen, but present on the ditch banks in the surrounding landscape (E).
- species of the former meadows present on the Veenkampen, but absent from the ditch banks in the surrounding landscape (F)
- species present on the Veenkampen, but absent from the former meadows and the ditch banks in the surrounding landscape (G).

Categories F and G were empty and omitted from further analysis (*see below*). Information on the following attributes was collected for each of the remaining five species categories:

– **major habitat types** in which the listed plant species optimally occur, i.e. dry grasslands (Gd) and moist to wet grasslands (Gw), heaths and moors (Hm), aquatic habitats such as banks and ponds (Aq), ruderal and arable land (Ra) and woodland and scrub (Wo) (CBS 1992; Appendix 1).

– **dispersal mechanism(s)**; taken from Grime et al. (1988), Feekes (1936) and Feekes and Bakker (1954). Species were labelled as dispersed by *wind, water, animals* or *unassisted* on the basis of specific adaptations to seed dispersal. In several plant species two dispersal mechanisms (*dichory*) could be involved in the dispersal of seeds (Appendix 1).

– **maximum distances** over which seeds can be transported during storms or by water as determined empirically by Feekes (1936) and Feekes and Bakker (1954). For our purposes it is sufficient to classify the listed plant species as capable of travelling distances <0.1 km (*short*), 0.1-1.0 (*medium*) or >1.0 km (*long*) from a seed source (Appendix 1).

Short distances apply to species which have heavy seeds that are dispersed no more than several dozens of metres during storms and have short floating times (hours to days). These species generally lack specific adaptations to dispersal (i.e. dispersal is *unassisted*), are dispersed by ants, or adhere to the fur of animals.

Medium distances apply to species whose seeds float on the water for weeks to months and can travel up to several hundred metres during storms.

Long distances apply to species which have dust-like seeds, such as orchid and fern species, or have other specific adaptations to wind dispersal, e.g. a pappus of hairs as in most composites. They include weed species that are widely distributed as a result of agricultural activities, and seeds ingested as fruits by wide-ranging animals such as birds (Appendix 1: columns 8 and 9).

– the **capacity of species to survive as buried seeds** in the soil as given by Grime et al. (1988), and supplemented with information from other studies by Chippendale and Milton (1934), Ryser and Gigon (1985), Verhoeven and van der Valk (1987), Bakker (1989) and Poschlod (1991). For the purpose of this study, species were classified as species with (Bs) or without (non-Bs) a persistent seed bank and unclassified species (no information available).

- the **contents of the soil seed bank** of the *Veenkampen* (Wind *unpubl. results*; Altena *unpubl. results*; Bootsma and Zemmelink *unpubl. results*). In these studies, soil cores were laid out in the laboratory and all emerging seedlings were identified and counted (Appendix 2).

RESULTS

Species pool and habitat type

The combined species pool consists of 252 vascular plant species. The former species-rich meadows contained 145 plant species, the ditch banks surrounding the Veenkampen 200 species and the fields of the Veenkampen 142 species. One-third of all plant species (85 spp., 33.7%) was present in all three species lists (Table 1).

Table 1. Number of plant species present on the former species-rich meadows (list 1), the ditch banks in the surrounding landscape (list 2) and the fields of the Veenkampen (list 3), for categories A to E separately. For explanation of species categories see *Material and Methods*.

		SPECIES CATEGORY					
LIST	**PERIOD**	**A**	**B**	**C**	**D**	**E**	**Total**
former meadows	1939-50	39	21	85	-	-	145
surrounding ditch banks	1989-91	-	21	85	44	50	200
restored grasslands	1987-91	-	-	85	57	-	142
Total number of species		39	21	85	57	50	252

The starting condition in 1978 for the restoration of species-rich meadows on the Veenkampen was heavily exploited species-poor fields of grass. According to a qualitative survey in 1980, the Veenkampen fields were very poor in plant species and dominated by *Lolium perenne, Poa trivialis, Elytrigia repens* and *Taraxacum spp.* (Altena and Oomes, *unpubl. results*). On the basis of the distribution and habitat preferences of the grassland species present, an estimated 35 species (30 category C species and 5 D category species) were present two years after restoration started. In the period 1987-91 the Veenkampen fields were richer in species and contained 142 species: 85 species of the former species-rich meadows (category C) and 57 species that are typical of ruderal and arable land and semi-aquatic habitats and had not been recorded on the former meadows (category D) (Table 1).

Despite the restoration efforts, the Veenkampen still lack 60 species which are nearly all typical of dry, moist and wet meadows, heaths and moors (Table 2). The missing species have either become regionally extinct (category A; 39 species) or are present on ditch banks in the surrounding landscape, but have not yet recolonized the site (category B; 21 species) (Table 1).

Table 2. Percentages and total number of species that have been recorded on the Veenkampen in the period 1987-1991 separated for six habitat types and species categories A to E. For explanation of species categories see *Material and Methods*.

	SPECIES CATEGORY					
HABITAT TYPE	**A**	**B**	**C**	**D**	**E**	**Total**
Dry meadows	23	19	2	-	-	15
Heaths and moors	51	24	11	7	6	41
Moist and wet meadows	21	38	40	9	2	56
Ruderal and arable land	5	5	29	54	30	74
Ponds and banks	-	14	14	23	34	45
Woodland and scrub	-	-	4	7	28	21
Total number of species	39	21	85	57	50	252

The 60 missing species represent 41.4% of the species pool of the former species-rich meadows. Another 50 species that did not occur on the former meadows and that are typical of non-grassly habitats (category E) have not yet colonized the site, although they were present on ditch banks in the surrounding landscape. The habitat spectrum of this category is similar to that of category D which suggests that some of the category E species may soon invade the Veenkampen too (Table 2).

Dispersal mechanism

Wind dispersal was the most common dispersal mechanism in 80 species, ranging from 28 to 41% of the species present in the five species categories. Animals (ants, mammals etc.) were involved in the dispersal of seeds in 57 species (range 9 to 28%). Adaptations for dispersal by water were prominent in 45 species (range 10 to 26%). A large group of species was unassisted in the dispersal of seeds (range 25 to 47%) (Figure 2). The observed frequencies of the dispersal mechanisms wind, water, animals and unassisted of the five species categories (A to E) did not differ significantly from the expected frequencies (χ^2 tests of goodness of fit; df=3 p>0.25) (Figure 2).

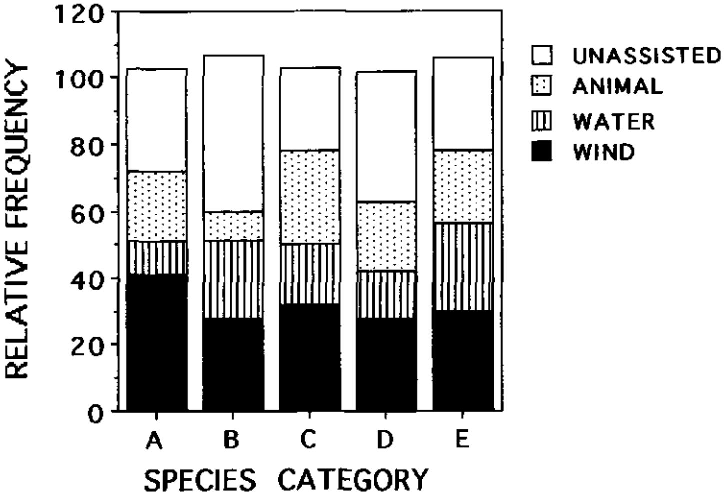

Figure 2. Relative frequency of four dispersal mechanisms for species categories A to E. Total frequencies can exceed 100% because dichory is taken into account (N=249 species).

Dispersal capacity

Similar results were obtained for the maximum dispersal distances (Figure 3). Most species disperse their seeds over short distances of less than 0.1 km (113 species, 45%), about one-third have a medium range dispersal (89 species, 35%), and only one-fith are capable of travelling distances greater than 1 km during storms (50 species, 20% of the entire species pool). In one category of species, the regionally extinct species (category A), the observed frequencies of species with long-distance and short range dispersal were significantly more frequent (12 vs. 7.7 species and 20 vs. 17.5 species respectively) and medium range dispersal less frequent than expected (7 vs. 13.8 species) (χ^2 tests of goodness of fit; df=2, p<0.05). In all other species categories (B to E) the observed frequencies of these three dispersal classes did not differ significantly from expected (χ^2 tests of goodness of fit; df=2, p>0.10).

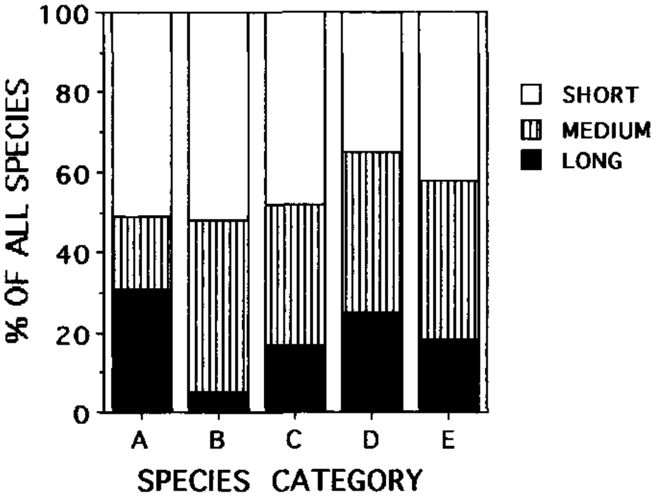

Figure 3. Percentage of species with dispersal distances < 0.1 km (SHORT), < 1.0 km (MEDIUM) and > 1.0 km (LONG) for species categories A to E (N=252 species).

Seed bank strategy

On the basis of the literature survey, 73.4% of all classified species (n=192 species) were characterized by a persistent seed bank and the remainder were characterized by other regeneration strategies such as seasonal regeneration in vegetation gaps and long range dispersal. Sixty species could not be classified because of a lack of information. In category A, species with persistent seed banks were significantly less frequent than expected ($\chi^2 = 22.578$; df=1, p<0.001), whereas in category D species with persistent seed banks were significantly more frequent than expected ($\chi^2 = 9.836$; df=1, p<0.01). No statistically significant differences were found in the other three categories (Table 3a).

Table 3. Number of plant species with or without a persistent seed bank (Bs) and unclassifed species (3a) and number of plant species detected as seeds in soil seed bank studies on the Veenkampen, per habitat type and species category (3b). Sources: Wind (*unpubl. results*), Altena (*unpubl. results*) and Bootsma and Zemmelink (*unpubl. results*). For explanation of species categories see *Material and Methods*.

	SPECIES CATEGORY					
3a. PERSISTENT SEED BANK	**A**	**B**	**C**	**D**	**E**	**Total**
species with Bs	10	13	53	44	21	141
species without Bs	19	2	19	3	8	51
unclassified species	10	6	13	10	21	60
Total number of species	39	21	85	57	50	252

3b. HABITAT TYPE	**A**	**B**	**C**	**D**	**E**	**Total**
Dry meadows	0	0	1	0	0	1
Heaths and moors	0	0	2	0	0	2
Moist and wet meadows	0	0	15	0	0	15
Ruderal and arable land	0	0	14	16	0	30
Ponds and banks	0	1	3	2	0	6
Woodland and scrub	0	0	1	1	0	2
Total number of species	0	1	36	19	0	56

Seed bank contents

The three seed bank studies on the Veenkampen revealed the presence of 56 plant species with viable seeds in the soil, which represents only 38.7% of the Veenkampen species pool (Table 3b). The seed bank was dominated by established species with profusely reproducing populations on the Veenkampen proper and by species which are adapted to remain dormant for a long period in the soil. Species of moist and wet meadows (15 spp.) and of ruderal and arable land (30 spp.) were most common (categories C and D).

The seed bank studies detected only one species that has no seed sources on the Veenkampen proper (the semi-aquatic *Lycopus europaeus*, category B). Sparsely occurring meadow species present in the vegetation of the Veenkampen and detected by the seed bank studies include *Ajuga reptans*, *Lychnis flos-cuculi* and *Ranunculus flammula* (Appendix 1). No seeds of the other 45 missing species of moist and wet meadows, heaths and moors from categories A, B and E were detected.

Species richness

The management treatments mowing, grazing and sod stripping showed large differences in restoring species richness in the period 1987 to 1991. On the 25 mown plots (total area 0.25 ha) 65 plant species were recorded during five years, on the five grazed paddocks (total area 3.65 ha) 112 species and on the five sod-stripped plots (total area 0.19 ha) 104 species (*Table* 4).

Table 4. Percentages and total number of species recorded on the Veenkampen in the period 1987-1991 on plots with mowing (n=25), grazing (n=5) and sod stripping (n=5) as treatments. Species were classified according to their habitat preferences.

HABITAT	MOWING	GRAZING	SOD STRIPPING	TOTAL
Dry grassland	0	1	1	2
Heaths and moors	6	4	12	13
Moist and wet grassland	35	29	30	39
Ruderal and arable land	43	43	38	56
Ponds and pond margins	9	16	16	25
Woodland and scrub	6	6	3	7
Total number of species	65	112	104	142

To enable the species richness between the treatments to be compared properly, the differences in area were removed by means of fitted species-area curves established by combining the information on area and species richness of individual plots and compartments. Using a log-linear (S-lnA) regression model, the calculated number of species for sites 0.1 ha, 0.25 ha and 0.5 ha was about twice as high on sod-stripped plots than on mown and grazed plots (Table 5).

Table 5. Log-linear regression models for the number of species (S) on plots with the treatments mowing, grazing and sod stripping (5a). Models with log-transformed values of area (A) gave the highest percentage of explained variance. Using these models, species richness was calculated for plots of 0.1, 0.25 and 0.5 ha. The percentage of the predicted number of species in relation to the entire species pool of the Veenkampen (n=142 spp.) is shown in brackets (5b).

5a.	**REGRESSION MODEL**	**df**	**R^2**	**F**	**p**
Mowing	$S = 16.3 \ln A + 87.2$	19	.832	89.362	<0.0001
Grazing	$S = 22.5 \ln A + 83.9$	15	.928	180.38	<0.0001
Sod stripping	$S = 24.2 \ln A + 146.7$	16	.801	60.514	<0.0001

5b.	**PREDICTED NUMBER OF SPECIES**		
	0.1 ha	**0.25 ha**	**0.5 ha**
Mowing	50 (35)	65 (45)	76 (53)
Grazing	32 (23)	53 (37)	68 (48)
Sod stripping	91 (64)	113 (80)	130 (92)

The numbers of plant species that are typical of heaths, moors, moist and wet meadows and were found exclusively in one management treatment was 1 species on mown plots, 11 species on sod-stripped plots and 7 species on grazed plots (Table 6). These numbers were biased because of differences in total area. Yet, several species with very few or no reproducing populations outside the Veenkampen proper were recorded almost exclusively on sod-stripped plots. Ten rare plant species were exclusive to the sod-stripped plots: *Agrostis canina, Carex disticha, C. hostiana, C. nigra, C. oederi, C. pallescens, Cynosurus cristatus, Luzula multiflora, Potentilla erecta* and *Viola canina.* Two rare species were exclusive to the paddocks: x *Festulolium loliaceum* and *Veronica scutellata* (Table 6). All other species exclusive to one treatment were common on ditch banks surrounding the Veenkampen during the study period.

Table 6. Meadow species exclusive to one management practice (mowing, grazing or sod-stripping). Species with less than 10 populations in the surrounding agricultural landscape are in italics, all other species were common on ditch banks surrounding the Veenkampen.

MOWING	**GRAZING**	**SOD STRIPPING**
Achillea ptarmica	*x Festulolium loliaceum*	*Agrostis canina*
	Filipendula ulmaria	*Carex disticha*
	Hypericum quadrangulum	*Carex hostiana*
	Lathyrus pratensis	*Carex nigra*
	Stellaria graminea	*Carex pallescens*
	Valeriana officinalis	*Carex oederi*
	Veronica scutellata	*Cynosurus cristatus*
		Epilobium palustre
		Luzula multiflora
		Potentilla erecta
		Viola canina

DISCUSSION

The main question concering the restoration of species-rich meadows is whether the plant species of the former wet nutrient-poor meadows will recolonize the former farmed fields when restoration measures are applied. In this study, we wanted to find out which species have indeed recolonized the Veenkampen since restoration started in 1978 and which have failed to do so. The data on dispersal mechanism, dispersal capacity and seed bank strategy could provide some possible explanations for success or failure.

In order to fully restore the former meadow ecosystems, two prerequisites must be met. Firstly, the abiotic conditions such as the pH, soil moisture content and soil fertility must be adjusted to the appropriate growing conditions of the desirable species. General measures to achieve this goal include restoring the former high moisture content of the soil by increasing the upwelling of base-rich groundwater in the valley (Grootjans 1985) and reducing the soil fertility by mowing and removing the mowings or, more drastically, by sod stripping (Bakker 1989). The second prerequisite is for sufficient numbers of buried seeds to be available or, if seed banks have been depleted, for seed dispersal that ensures that seeds from neighbouring source populations are deposited on the target site.

Floristic changes

The Veenkampen fields experienced more than two decades of intensive drainage and fertilizer application prior to restoration. Thus, the starting point for restoration was heavily exploited species-poor fields of grass dominated by species which are indicators of intensive agricultural use (*Poa trivialis* and *Lolium perenne*) and frequent soil disturbance (*Elymus repens, Taraxacum spp.* and *Rumex obtusifolius*). The ditch banks fringing the fields served as a refugium for many species such as *Ajuga reptans, Cardamine pratensis, Lotus uliginosus* and *Lychnis flos-cuculi* (Altena and Oomes *unpubl. results*).

After fertilizer applications ceased in 1978, the annual yields on the clay-on-peat soils of the Veenkampen initially fell rapidly from 12 tons per ha to 7 tons per ha but then remained constant. Because the conditions had improved, many of the species still present on the ditch banks were able to successfully recolonize the Veenkampen fields, either through short-range dispersal of seeds from the adjacent ditch banks or through direct recruitment from buried seeds. Assuming that 30 species had been present at the start, 55 species of the former species-rich meadows (i.e. 85 minus 30 category C species) have successfully recolonized the Veenkampen fields since then.

However, restoration has not been as successful as expected; two observations stress this point. The first observation is that 60 species present on the former meadows have not yet recolonized the Veenkampen fields. The reasons for this failure are complex and are related to (i) a depletion of their soil seed banks, (ii) too few seeds dispersed from local or regional source populations reaching the target site and/or (iii) too few microsites appropriate for germination and establishment. One could expect that regionally extinct species (category A) which do not form persistent seed banks but produce numerous long range dispersed seeds, such as *Cirsium dissectum, Eriophorum angustifolium* and several orchid species, will eventually establish on the Veenkampen *via* seed dispersal. Their absence indicates that dispersal and/or germination events are still not sufficiently frequent to allow their recolonization. Seed addition experiments may reveal the process which is responsible for this absence (see Chapter 4).

The second observation concerns the 57 weedy species, typical of ruderal, arable and semi-aquatic habitats (category D) which were not recorded on the former meadows but are still present in the vegetation of the Veenkampen fields. These species were introduced as a result of agricultural activities and are capable of surviving for long periods in the soil as dormant seeds; 94% of the classified category D species have a persistent seed bank (Table 3). The reason that the semi-aquatic species have been able to colonize is probably because the restored high water table in the Veenkampen soil since 1986 has allowed seeds that had been transported by wind and agricultural machinery to germinate.

These observations raise the more general question about the role of dispersal of seeds and the role of recruitment from soil seed banks during the restoration process. The 60 missing species may enter the vegetation through dispersal of seeds and/or recruitment from the soil seed bank, but in the Veenkampen area both pathways are problematic, as will be elucidated below.

Dispersal of seeds

Seeds of the 60 missing species of the former species-rich meadows may be brought to the target site by wind, water, animals and humans some time in the future. The small size of the source populations and of the target site reduces the probability of windborne seeds being deposited on the right spot. The Veenkampen (13.2 ha) is in fact a point target in a vast area of non-habitat which can easily be missed by seeds dispersed over long distances. As seed dispersal by wind is controlled by wind direction and wind speed, the location of the small source populations in a landscape relative to the target site becomes very important. Given the prevailing southwesterly winds, the closest source populations of meadow species such as *Bennekomse Meent* (Figure 1) are located downwind from the Veenkampen and are therefore unlikely to be very effective sources of immigrant propagules.

With regard to wind speed, dispersal by wind will most effectively bridge distances between sources and target when strong winds occur. In the study area, mean wind speeds >20 m/s during seed dispersal (August-September) are rare and have a probability of returning every 10 years; wind speeds >25 m/s return every 25 years and wind speeds >30 m/s every 200 years, but gusts of those wind speeds are far more frequent than the mean wind speeds (Rijkoort and Wieringa 1983). Chance dispersal by such extreme gusts must have played and probably continues to play an important role in stocking the regional species pool, not only for species adapted to wind dispersal, but also for unassisted or animal-dispersed species. According to a field study conducted by Feekes (1936), seeds of many species will be indiscriminately transported over hundreds to thousands of metres during storms. The value of erratic wind dispersal events becomes more important the longer a site is allowed to develop during a restoration process. We should think in terms of decades and centuries rather than in years.

Many meadow species produce seeds which are buoyant and may float on the water for weeks, months or even years (*hydrochory*) (Ridley 1930; Feekes 1936; Romell 1954). Inundations of the valley in winter time and during seed ripening and dispersal have frequently occurred during the past centuries. These inundations resulted in widespread dispersal of seeds (see Skoglund 1990) and in meadows becoming richer in species over time. Today, the hydrology of the *Binnenveld* valley is controlled to the extent that inundations no longer occur; this has minimized the role of water as a dispersal mechanism in the present agricultural landscape. Ditches may transport masses of seeds, but as the surface water is channelled away from the Veenkampen, no seeds will arrive there.

The role of humans in the dispersal of seeds (*anthropochory*) was probably substantial in historic times. The grass of the former meadows was traditionally cut by hand late in the growing season and then transported to the farms as hay on carts. Many ripe seeds were dropped on the field or along the route. Today, modern equipment used for ditch cleaning and hay-making will transport thousands of seeds from one field to another (Strykstra and Verweij 1995). However, their contribution to restoring species diversity is limited. In the case of the Veenkampen, it is more likely that seeds of established meadow species will leave the site than that seeds of missing desirable meadow species present in remote patches will accidentally enter it.

Recruitment from buried seeds

When immigration via dispersal of seeds is not very likely, recolonization can only occur by recruitment from seeds that have remained buried in the soil since the species-rich meadows were drained and fertilized. The small-scale seed bank studies conducted on the Veenkampen suggest that the recruitment of missing species from the seed bank is extremely unlikely. Viable seeds of only one species (*Lycopus europaeus*) out of the 60 potential immigrant species (categories A and B) were detected (Table 5). Yet, on plots from which the sod had been removed, 12 meadow species were recorded in the second or third year after sod stripping (Table 6). Species of the monocotyledonous genera *Carex, Luzula* and *Juncus* and species such as *Ajuga reptans* and *Lychnis flos-cuculi* frequently reappeared on these plots (Appendix 1). Since most of these monocotyledonous species have no or very few reproducing populations within a radius of at least five km around the Veenkampen, recruitment has most probably resulted from the germination of buried seeds that have remained for at least 30 years in the soil of these intensively used fields. It is unlikely that their establishment is an effect of directed dispersal by animals, in particular ducks, because the Veenkampen is not an attractive site for waterfowl throughout the year (Van Dorp *pers. obs.*).

Bakker (1989) suggested that it is useful to distinguish between species with a *persistent* seed bank which allow species to cope with poor seed set and species with a *permanent* seed bank which allow a species to regenerate in situ many years after it has disappeared from the vegetation. In the case of the Veenkampen, 23 of the 44 species classified as potential immigrants (categories A and B) are characterized by a seed bank strategy (Table 3). Several of these 23 species will not be recruited however, because their seed banks in the Veenkampen soil are expected to have been depleted by now. Probably only an extra five to ten species with expected permanent seed banks including *Carex pulicaris* and *Campanula rotundifolia* might be recruited from the soil seed bank of the Veenkampen. After field work had been completed, *Viola persicifolia* and *Gentiana pneumonanthe* were present on a few sod-stripped plots in 1994 (Oomes *pers. obs.*), presumably also as a result of recruitment from the soil seed bank.

The most vulnerable meadow species and those least likely to recover from buried seeds are species with transient seed banks (sensu Grime et al. 1988). Species such as *Briza media, Danthonia decumbens* and *Succisa pratensis* depend on the seasonal regeneration in vegetation gaps, but do not form persistent seed banks and disperse their seeds over short distances only. These species will therefore not be able to recolonize the target site and will remain absent from the restored Veenkampen fields. Introduction of seeds or plants would be the only solution to their preservation, on the precondition that the growing conditions allow their persistence.

Conclusion

The full restoration of the species composition of the original meadow communities requires the recolonization of all category A and B species, the extinction of all category D species and the prevention of colonization by category E species. Twelve years of restoration have demonstrated that this is not a realistic objective. The 1991 species pool of the Veenkampen still reflected the high soil fertility. Nevertheless, a slow and small increase in the species diversity of the restored Veenkampen fields is attainable, primarily as a result of chance dispersal .

Acknowledgements

We sincerely thank our colleagues H. Altena and J. Bokdam for the use of some of their unpublished data. H. van Dalen, M. de Groot, P. Ketner, H. Klees and H. van Oeveren participated in collecting the field data. F. Berendse and J.M. van Groenendael critically reviewed earlier drafts of this paper.

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Inundated experimental field in winter

Appendix 1 (*see* p. 41-47)

Information on the presence in the landscape of plant species and their attributes. Species are arranged alphabetically within plant families. Scientific names are according to van der Meijden (1990).

Column 1 : status of species (see Table 1).
Column 2 : major habitat type (see Methods section).
Columns 3-5 : presence on the Veenkampen in plots with treatment mowing (3), grazing (4) and sod stripping (5). Abundance of species: 0 =sparse, 1 = frequent, 2 = (co-)dominant.
Column 6 : species detected in seed bank study by Wind (a), Altena (b) and Bootsma and Zemmelink (c) (see Appendix 2).
Column 7 : regenerative strategy Bs = capacity of species to form persistent seed banks, according to Grime et al. (1988) and supplemented with data from the literature (see *Methods*). Dash means no persistent seed bank being developed, ? strategy uncertain.
Column 8 : dispersal mechanism based on Grime et al. (1988). H = dispersal by water, W = wind, U = unassisted, Uag = unassisted seeds widely distributed as a result of agricultural activities, Ad = animals by means of adhesive structures, E = animals (ants) by means of elaiosome, B = animals (birds) by means of berry.
Column 9 : dispersal mechanism based on Feekes (1936) and Feekes and Bakker (1954). H = seeds dispersed by water; seeds floating weeks to years, Zw = seeds dispersed by wind; transported over kilometres during storms, V = seeds dispersed by wind; transported over hundreds of metres during storms, Z = endozoochores and Au = autochores.
Column 10 : three levels of effectiveness of seed dispersal based on information from columns 8 and 9: SHORT (<0.1 km), MEDIUM (<1.0 km) and LONG (>1.0 km) range dispersal.

Species name	1	2	3	4	5	6	7	8	9	10
ALISMATACEAE										
Alisma plantago-aquatica	D	Aq	.	1	1	c	Bs	H/W	H	2
BORAGINACEAE										
Myosotis arvensis	D	Wo	1	1	1		Bs	Ad		1
Myosotis laxa ssp. cespitosa	D	Ra	1	.	.	c	?Bs	H	V	2
Myosotis palustris	C	Aq	.	1	.	c	Bs	U	V	2
Symphytum officinale	C	Aq	.	1	.		?	H/E	Au	1
CAMPANULACEAE										
Campanula rotundifolia	B	Gd	.	.	.		Bs	W		1
CARYOPHYLLACEAE										
Cerastium fontanum	C	Gw	1	1	1	ac	Bs	U	V	2
Lychnis flos-cuculi	C	Gw	1	1	2	ac	Bs	W	V	2
Silene noctiflora	D	Ra	.	.	1		?	W		1
Stellaria graminea	C	Gw	.	1	.		?	U		1
Stellaria media	D	Ra	1	1	1	abc	Bs	U	V	3
Stellaria uliginosa	E	Wo	.	.	.		Bs	U		1
CHENOPODIACEAE										
Atriplex patula	E	Ra	.	.	.		Bs	U	H	2
Atriplex prostrata	D	Ra	.	0	.		Bs	U	H	2
Chenopodium album	D	Ra	.	1	.	a	Bs	U		1
Chenopodium polyspermum	E	Ra	.	.	.		?	U	V	2
COMPOSITAE										
Achillea millefolium	B	Gw	.	.	.		?	W	V	2
Achillea ptarmica	C	Gw	1	.	.		?Bs	W	V	2
Artemisia vulgaris	E	Ra	.	.	.		Bs	U	V	2
Bellis perennis	D	Gw	.	1	1		Bs	W		1
Carduus crispus	E	Ra	.	.	.		?	W	Zw	3
Centaurea jacea	B	Gw	.	.	.		Bs	W		1
Cirsium arvense	C	Ra	1	1	1	c	Bs	W	Zw	3
Cirsium dissectum	A	Hm	.	.	.		-	W	Zw	3
Cirsium palustre	C	Gw	1	1	1	c	Bs	W	Zw	3
Cirsium vulgare	D	Ra	.	1	0		?Bs	W	Zw	3
Crepis biennis	A	Gw	.	.	.		?	W		3
Gnaphahlium uliginosum	D	Ra	.	0	0		Bs	W	Zw	3
Hieracium pilosella	A	Gd	.	.	.		?Bs	W	Zw	3
Hypochaeris radicata	C	Gd	.	.	1		-	W	Zw	3
Leontodon autumnalis	C	Ra	1	1	1	a	Bs	W	Zw	3
Leontodon saxatilis	A	Gd	.	.	.		-	W	Zw	3
Leucanthemum vulgare	C	Gw	.	1	1	c	Bs	W	V	2
Matricaria discoidea	D	Ra	.	1	1	a	Bs	U	V	2
Matricaria recutita	D	Ra	.	1	0		?	Uag		3
Picris hieracioides	A	Gd	.	.	.		?	W		3
Senecio aquaticus	E	Gw	.	.	.		-	W	Zw	3

Senecia jacobaea	B	Gd	.	.	.		Bs	W	V	2
Senecio vulgaris	D	Ra	.	1	1	ac	Bs	W	Zw	3
Sonchus asper	D	Ra	.	1	.		?Bs	W	Zw	3
Sonchus oleraceus	D	Ra	.	0	.		Bs	W	Zw	3
Taraxacum officinale	C	Ra	2	2	2	abc	-	W	Zw	3
Tussilago farfara	E	Ra	.	.	.		-	W	Zw	2
CONVOLVULACAEA										
Calystegia sepium	D	Aq	.	.	0		Bs	U	Au	1
CRUCIFERAE										
Alliaria petiolata	E	Wo	.	.	.		Bs	U		1
Barbarea stricta	D	Aq	.	1	.		?	U		1
Barbarea vulgaris	D	Aq	.	.	1		Bs	W		1
Capsella bursa-pastoris	C	Ra	1	1	1	ab	Bs	W		1
Cardamine hirsuta	D	Ra	1	1	.	b	Bs	W		1
Cardamine pratensis	C	Gw	1	1	2	bc	-	W		1
Erysimum cheiranthoides	E	Ra	.	.	.		?	U		1
Rorippa amphibia	D	Aq	.	.	1		?	U	V	2
Rorippa microphylla	D	Aq	.	1	.	c	?	U		2
Rorippa palustris	D	Ra	.	1	1	bc	Bs	H	V	2
Rorippa sylvestris	E	Ra	.	.	.		?	U	V	2
CYPERACEAE										
Carex acuta	C	Aq	0	.	1		?	H		1
Carex acutiformis	E	Aq	.	.	.		Bs	H		2
Carex disticha	C	Gw	.	.	1		Bs	U		1
Carex elata	E	Aq	.	.	.		Bs	U		1
Carex elongata	E	Wo	.	.	.		?	U		1
Carex flava	A	Hm	.	.	.		?	H	H	2
Carex hirta	C	Ra	.	1	1		?	U		1
Carex hostiana	C	Hm	.	.	1		Bs	U	H	2
Carex nigra	C	Hm	.	.	1		Bs	U		2
Carex oederi spp. oedocarpa	D	Hm	.	.	1		?	H		2
Carex ovalis	D	Ra	.	.	1		?Bs	U		1
Carex pallescens	C	Gw	.	.	1		Bs	U		1
Carex panicea	C	Hm	0	1	1		Bs	H		2
Carex pseudocyperus	E	Aq	.	.	.		?	H		2
Carex pulicaris	A	Hm	.	.	.		?	U		1
Carex rostrata	E	Hm	.	.	.		?	H		2
Carex vesicaria	E	Aq	.	.	.		?	H	H	2
Eleocharis acicularis	E	Aq	.	.	.		?	Ad		1
Eleocharis palustris ssp. palustris	D	Aq	.	1	1		Bs	Ad	H	2
Eriophorum angustifolium	A	Hm	.	.	.		-	W	Zw	3
Scirpus lacustris ssp. lacustris	E	Aq	.	.	.		?	H	H	2
DIPSACACEAE										
Succisa pratensis	A	Hm	.	.	.		-	Ad	H	2
EQUISETACEAE										
Equisetum arvense	C	Ra	.	1	.		?	W	Zw	3
Equisetum fluviatile	C	Aq	.	1	.		?	W		3
Equisetum palustre	C	Ra	1	1	1		-	W	Zw	3

GENTIANACEAE										
Gentiana pneumonanthe	A	Hm	.	.	.		Bs	U		1
GERANIACEAE										
Geranium dissectum	C	Ra	.	1	.		Bs	Ad		1
Geranium molle	E	Ra	.	.	.		Bs	Ad		1
Geranium pusillum	E	Ra	.	.	.		?	Ad		1
GRAMINAE										
Agrostis canina	C	Hm	.	.	1	b	Bs	Ad	V	2
Agrostis capillaris	C	Gd	.	0	.	a	Bs	U	V	2
Agrostis stolonifera	C	Ra	2	2	2	ab	Bs	U	V	2
Alopecurus geniculatus	C	Ra	1	1	2	ab	-	U	V	2
Alopecurus pratensis	C	Gw	1	2	2	a	-	U	V	2
Anthoxanthum odoaratum	C	Gw	0	1	1		Bs	Ad	V	2
Apera spica-venti	D	Ra	.	1	.		?	U	V	2
Arrhenatherum elatius	C	Gw	1	1	1		-	Ad		1
Briza media	A	Gw	.	.	.		-	U		1
Bromus carinatus	E	Ra	.	.	.		?	Ad		1
Bromus hordeaceus ssp. hord.	C	Gw	1	1	1		-	Ad		1
Bromus racemosus	B	Gw	.	.	.		?	Ad		1
Calamagrostis canescens	B	Hm	.	.	.		?	U	Zw	3
Cynosurus cristatus	C	Gw	.	.	1		-	U		1
Dactylis glomerata	C	Gw	1	1	1		-	Uag		3
Deschampsia cespitosa	C	Ra	1	1	.		Bs	Ad		1
Echinochloa crus-galli	D	Ra	.	1	.		?	Ad		1
Elymus repens	C	Ra	1	1	2		Bs	U		1
Festuca arundinacea	C	Ra	.	1	.		-	Ad		1
Festuca ovina ssp. tenuifolia	A	Gd	.	.	.		-	Ad		1
Festuca pratensis	C	Gw	2	1	1		-	Ad		1
Festuca rubra	C	Gw	1	1	1		-	Ad		1
x Festulolium loliaceum	D	Gw	.	1	.		?	Uag		3
Glyceria fluitans	D	Aq	1	1	1		Bs	U		1
Glyceria maxima	C	Aq	1	1	1		Bs	H	H	2
Holcus lanatus	C	Gw	2	1	2	b	Bs	U	V	2
Holcus mollis	E	Wo	.	.	.		?	Ad	V	2
Hordeum secalinum	C	Gw	.	1	1		?	Ad		1
Lolium perenne	C	Ra	1	2	1		-	Uag		3
Molinia caerulea	A	Hm	.	.	.		?Bs	U	H	2
Nardus stricta	A	Hm	.	.	.		-	Ad		1
Phalaris arundinacea	D	Aq	1	1	1		?Bs	H	V	2
Phleum pratense ssp. pratense	C	Gw	1	1	1		-	Ad	V	2
Phragmites australis	C	Aq	.	1	.		-	W	Zw	3
Poa annua	D	Ra	.	1	1	ab	Bs	U	V	2
Poa palustris	B	Aq	.	.	.		?	U	V	2
Poa pratensis	C	Gw	2	1	1	b	?Bs	Uag	V	3
Poa trivialis	C	Ra	2	2	2	ab	Bs	U	V	2
Trisetum flavescens	A	Gw	.	.	.		-	Ad	V	2
GUTTIFERAE										
Hypericum maculatum	D	Hm	1	.	1		Bs	W		1
Hypericum quadrangulum	D	Gw	.	1	.		Bs	W		1

IRIDACEAE										
Iris pseudacorus	C	Aq	.	.	1		?	H	H	2
JUNCACEAE										
Juncus acutiflorus	D	Gw	1	.	1		Bs	Ad		2
Juncus articulatus	C	Ra	1	1	1	abc	Bs	Ad	V	2
Juncus bufonius	D	Ra	.	1	0	ac	Bs	Ad	V	2
Juncus bulbosus	E	Aq	.	.	.		Bs	Ad		2
Juncus conglomeratus	C	Hm	1	1	1		Bs	Ad	V	2
Juncus effusus	C	Ra	1	1	2	ab	Bs	Ad	V	2
Juncus inflexus	D	Ra	.	1	.		Bs	Ad	V	2
Juncus subnodulosus	E	Hm	.	.	.		Bs	Ad	V	2
Luzula campestris	A	Gd	.	.	.		Bs	E		1
Luzula multiflora	D	Gw	.	.	1		Bs	E		1
LABIATAE										
Ajuga reptans	C	Gw	1	1	2	bc	Bs	E		1
Galeopsis tetrahit	E	Wo	.	.	.		Bs	U	Au	1
Glechoma hederacea	C	Wo	1	1	1	b	?	U	Au	1
Lamium album	E	Wo	.	.	.		Bs	E	Au	1
Lamium purpereum	D	Ra	0	1	.		Bs	E	Au	1
Lycopus europaeus	B	Aq	.	.	.	c	Bs	H/W	H	2
Mentha aquatica	C	Aq	.	.	1		Bs	H	H	2
Mentha arvensis	C	Ra	1	1	.		Bs	H	Au	1
Prunella vulgaris	C	Gw	.	1	1		Bs	Ad	Au	1
Scutellaria galericulata	B	Aq	.	.	.		Bs	H	H	2
Stachys palustris	C	Aq	0	.	1		?Bs	H	Au	1
Stachys sylvatica	E	Wo	.	.	.		Bs	Ad	Au	1
LILIACEAE										
Allium vineale	C	Wo	.	1	.		?			1
Ornithogalum umbellatum	E	Wo	.	.	.		?			1
LINACEAE										
Linum catharticum	A	Gd	.	.	.		Bs	U		1
LYTHRACEAE										
Lythrum salicaria	C	Aq	.	1	1	bc	Bs	H	Au	1
MENYANTHACEAE										
Menyanthus trifoliata	A	Hm	.	.	.		?	H	H	2
ONAGRACEAE										
Chamerion angustifolium	E	Wo	.	.	.		-	W	Zw	3
Epilobium hirsutum	D	Aq	.	1	1		Bs	W	Zw	3
Epilobium obscurum	D	Aq	.	1	.		Bs	W		3
Epilobium palustre	D	Hm	.	.	1		Bs	W	Zw	3
Epilobium parviflorum	E	Aq	.	.	.		Bs	W	Zw	3
Epilobium tetragonum	E	Wo	.	.	.		?	W		3
OPHIOGLOSSACEAE										
Ophioglossum vulgatum	A	Hm	.	.	.		-	W		3

ORCHIDACEAE										
Dactylorhiza maculata	A	Hm	.	.	.		-	W		3
Dactylorhiza majalis	A	Hm	.	.	.		-	W		3
Epipactis helleborine	E	Wo	.	.	.		. -	W		3
Gymnadenia conopsea	A	Hm	.	.	.		-	W		3
Plathantera bifolia	A	Hm	.	.	.		-	W		3
OXALACEAE										
Oxalis fontana	E	Ra	.	.	.		?	U		1
PAPLIONACEAE										
Genista tinctoria	A	Hm	.	.	.		?	U		1
Lathyrus palustris	B	Gw	.	.	.		?	U		1
Lathyrus pratensis	C	Gw	.	1	.		Bs	U		1
Lotus corniculatus	B	Gd	.	.	.		Bs	U	Au	1
Lotus uliginosus	C	Gw	1	1	2	a	Bs	U	Au	1
Medicago lupulina	A	Gw	.	.	.		Bs	U	Au	1
Ononis repens ssp. spinosa	A	Gw	.	.	.		?Bs	U		1
Trifolium dubium	C	Gw	.	1	1		Bs	Ad	Au	1
Trifolium pratense	C	Gw	1	1	1	c	Bs	Ad	Au	1
Trifolium repens	C	Ra	2	2	2	abc	Bs	Ad	Au	1
Vicia cracca	C	Gw	1	1	.		?Bs	U	Au	1
Vicia hirsuta	E	Ra	.	.	.		Bs	U	Au	1
PLANTAGINACEAE										
Plantago lanceolata	C	Gw	.	0	1	c	Bs	Ad		1
Plantago major ssp. major	C	Ra	.	1	1	b	Bs	Ad	V	2
POLYGALACEAE										
Polygala vulgaris	A	Gd	.	.	.		-	E		1
POLYGONACEAE										
Polygonum amphibium	C	Ra	1	1	1	b	?Bs	H		2
Polygonum aviculare	C	Ra	1	1	1	abc	Bs	Uag	V	3
Polygonum convolvolus	D	Ra	.	.	1	c	Bs	Uag		3
Polygonum hydropiper	D	Ra	.	0	1	c	Bs	H		2
Polygonum lapathifolium	E	Ra	.	.	.		Bs	U	V	2
Polygonum persicaria	D	Ra	.	1	.	c	Bs	Uag		3
Rumex acetosa	C	Gw	2	2	2	b	-	W		1
Rumex acetosella	B	Gd	.	.	.		Bs	U	V	2
Rumex conglomeratus	E	Ra	.	.	.		?Bs	H		2
Rumex crispus	D	Ra	1	1	1		Bs	U	H	2
Rumex hydrolapathum	D	Aq	.	1	.		?Bs	H	H	2
Rumex obtusifolius	D	Ra	1	1	2	c	Bs	Ad		1
PRIMULACEAE										
Hottonia palustris	E	Aq	.	.	.		?	H		2
Lysimachia nummularia	B	Ra	.	.	.		?	U	Au	1
Lysimachia thyrsiflora	E	Hm	.	.	.		?	H	H	2
Lysimachia vulgaris	B	Gw	.	.	.		-	H	Au	1
RANUNCULACEAE										
Caltha palustris	B	Gw	.	.	.		-	H	H	2

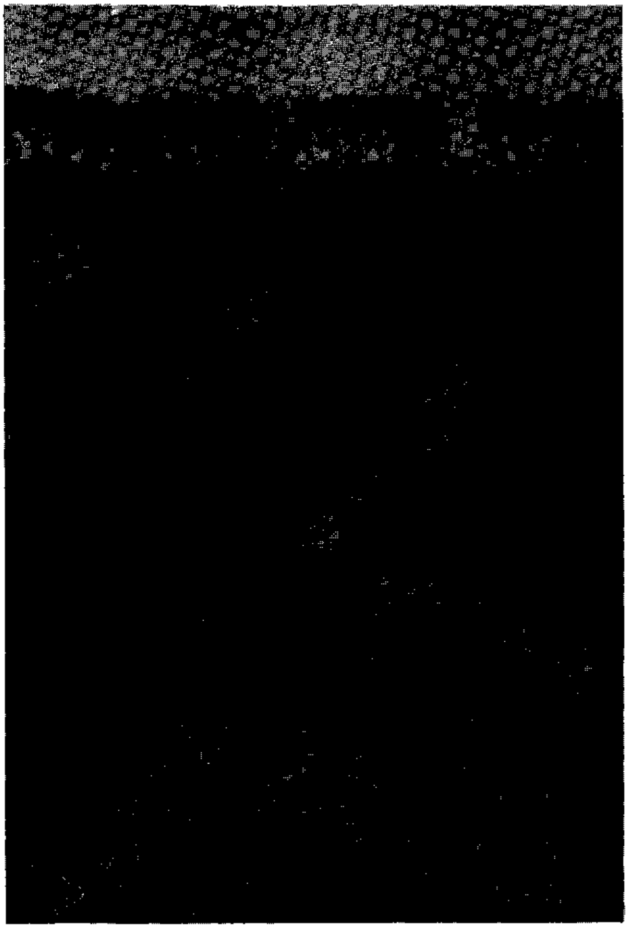
Myosurus minimus	E	Ra	.	.	.		?Bs	Ad		1
Ranunculus acris	C	Gw	2	1	1	a	Bs	Ad		1
Ranunculus ficaria	D	Wo	.	1	.		-	E		1
Ranunculus flammula	C	Hm	0	1	1	ac	Bs	H		2
Ranunculus repens	C	Ra	2	2	2	abc	Bs	H/W	H	2
Ranunculus sceleratus	D	Ra	0	1	0	ac	Bs	H	H	2
Thalictrum flavum	C	Aq	1	0	1	b	?Bs	H/W		1
ROSACEAE										
Agrimonia eupatoria	A	Gw	.	.	.		-	Ad		1
Filipendula ulmaria	C	Gw	.	1	.		Bs	H		1
Potentilla anglica	A	Ra	.	.	.		?	U		1
Potentilla anserina	C	Ra	0	.	1		?	U		1
Potentilla erecta	C	Hm	.	.	1		Bs	U	Au	1
Potentilla palustris	B	Hm	.	.	.		?	U	H	2
Potentilla reptans	C	Ra	.	.	0		?Bs	U	Au	1
RUBIACEAE										
Galium aparine	C	Wo	.	1	1		-	Ad	Au	1
Galium mollugo	B	Gw	.	.	.		Bs	U		1
Galium palustre	C	Aq	.	1	1		Bs	H	H	2
Galium uliginosum	C	Hm	.	1	1		Bs	U		1
Galium verum	A	Gd	.	.	.		?Bs	U		1
SCROPHULARIACEAE										
Euphrasia stricta	A	Hm	.	.	.		-	W		1
Linaria vulgaris	D	Ra	.	.	0		Bs	W	V	2
Pedicularis palustris	A	Hm	.	.	.		Bs	W		1
Rhinanthus angustifolius	A	Gw	.	.	.		?	H/W	H	2
Rhinanthus minor	A	Hm	.	.	.		-	W		1
Scrophularia nodosa	E	Wo	.	.	.		Bs	W	Au	1
Veronica arvensis	D	Ra	1	1	1		Bs	U	V	2
Veronica beccabunga	E	Aq	.	.	.		Bs	Ad	H	2
Veronica chamaedrys	C	Gw	1	1	0	bc	Bs	U	V	2
Veronica officinalis	B	Hm	.	.	.		Bs	U	Au	1
Veronica scutellata	D	Hm	.	0	.		?	U		1
Veronica serpyllifolia	D	Ra	1	1	1	a	Bs	U		1
SOLANACEAE										
Solanum dulcamara	D	Aq	.	0	0		-	B	Z	2
SPARGANIACEAE										
Sparganium erectum	E	Aq	.	.	.		?Bs	H/W		1
TYPHACEAE										
Typha angustifolia	E	Aq	.	.	.		?	W	Zw	3
Typha latifolia	E	Aq	.	.	.		-	W	Zw	3
UMBELLIFERAE										
Aegopodium podagraria	E	Wo	.	.	.		-	U		1
Anthriscus sylvestris	D	Wo	1	1	.		-	U		1
Berula erecta	E	Aq	.	.	.		Bs	H	H	2
Carum carvi	A	Gw	.	.	.		?	U		1
Daucus carota	B	Gw	.	.	.		Bs	Ad		1

Heracleum sphondylium	E	Wo	.	.	.		-	W	H	2
Hydrocotyle vulgaris	A	Ra	.	.	.		-	H	H	2
Oenanthe aquatica	E	Aq	.	.	.		?	H/W		1
Oenanthe fistulosa	E	Aq	.	.	.		-	H/W		1
Peucedanum palustre	B	Hm	.	.	.		Bs	H/W	H	2
Pimpinella saxifraga	A	Gd	.	.	.		-	U		1
Sium latifolium	E	Aq	.	.	.		?	H/W	H	2
URTICACEAE										
Urtica dioica	D	Wo	1	1	.	b	Bs	Ad	V	2
VALERIANACEAE										
Valeriana dioica	A	Hm	.	.	.		?	W		3
Valeriana officinalis	C	Gw	.	1	.		-	W	Zw	3
VIOLACEAE										
Viola arvensis	D	Ra	.	.	0	c	?Bs	Uag	Au	3
Viola canina	C	Hm	.	.	1		?	U	Au	1
Viola persicifolia	B	Hm	.	.	.		Bs	U	Au	1

Appendix 2

Information on three seed bank studies conducted on the Veenkampen fields between 1980 and 1988.

Author	**Wind** (a)	**Altena** (b)	**Bootsma & Zemmelink** (c)
Year	1980	1986	1988
Season	summer	spring	spring
Soil layer sampled (in cm)	0-20	0-20	0-20
Diameter of the core (cm)	7.5	4.0	2.7
Number of samples	20	320	400
Total volume (dm^3)	17.7	80.4	34.4
Number of seeds recovered	1706	1849	13731
Number of species	23	31	43



Ditch bank typical of the farmed landscape

CHAPTER 2

Dynamic distribution and regenerative strategies of ten perennial grassland species in a Dutch agricultural landscape

with H. van Oeveren.

submitted to Journal of Vegetation Science

Abstract

In this study, the distribution of ten perennial plant species typical of species-rich meadows were mapped in a Dutch agricultural landscape (220 ha) in 1990, 1991 and 1992 to assess their metapopulation dynamics and to relate changes in distribution between years and differences between species to their regeneration strategies. The location of individual populations were digitized and transformed onto grid cells with a mesh size of 50 m.

Mapping showed that ditch banks in the study area (a set-aside area and the surrounding farmed landscape) formed an important refugium for the selected species; the relative frequencies of species varied from 3.7% to 33.8% of all available ditch bank cells (n= 737). Ditch banks were managed by regular mowing plus removing the harvested biomass on the set-aside area and by grazing, mulching, dredging in the farmed landscape. In the set-aside area, seven species were more frequent, two species were less frequent. One species did not differ in frequency between the two areas.

The distribution of the selected species varied greatly between years, suggesting frequent extinction and colonization events. Variation was expressed in two indices (E/C= mean ratio of the number of extinctions and colonizations and P/(T+P) = ratio of permanently occupied cells to temporarily and permanently occupied cells). The overall E/C index for all species and all years was 0.99. Four species appeared to be decreasing in distribution in the study area (E/C>1.0), six species appeared to be stable (E/C=1.0) or increasing (E/C<1.0).

The possible relations between the variation in distribution and five life-history attributes (seed weight, dispersal capacity, dispersal distance, ability to vegetatively spread and seed bank type) were examined for each species. None of these attributes showed significant associations with the indices. It is concluded that different combinations of life-history attributes (i.e. regeneration strategies) could lead to species stability in this type of agricultural landscape.

INTRODUCTION

In many cases the restoration of species-rich meadows on land that used to be farmed is strongly hampered by the limited recolonization capacity of a number of plant species (Primack and Miao 1992). Although the growing conditions at such cases appear to be appropriate for germination and establishment, species may be absent because none of their seeds have yet arrived (Tilman 1994). Seeds must immigrate from neighbouring sources in order to establish new populations, but in intensively farmed landscapes such sources are few, do not always produce sufficient seed and are often restricted to small and isolated patches.

The metapopulation concept (Levins 1970; Hanski 1989; Opdam 1990), that the *distribution of a species in a landscape is composed of a* system of local populations interacting through the dispersal of seeds, is an important contribution to the conservation biology of species in fragmented landscapes. Individual patches in fragmented landscapes may frequently experience extinction and colonization events, but the metapopulation persists if the rate of local extinctions (E) is less than the rate of establishment of new local populations (C), i.e. if $E/C < 1.0$ (Hanski 1989). In this context, restoring species-rich meadows on former agricultural land and connecting them with existing reserves through a network of ecological corridors would increase the time the metapopulation persists.

Here, we report on the dynamic distribution of ten perennial meadow species in a fragmented landscape. In the study area, an intensively farmed landscape in the centre of the Netherlands, the only potentially suitable patches for such species occur on the banks of the drainage ditches that delimit the almost flat rectangular fields. These ditch banks are managed e.g. by mowing, grazing and dredging and are assumed to function as refugia and corridors for the selected species. Within the study area, an area of formerly intensively used grassland has been set-aside on which it is being attempted to restore the former species-rich meadows. The species selected for this study are typical of these former species-rich meadows and show profound differences in their regenerative strategies, i.e. strategies based on dispersal of seeds, vegetative spread, recruitment from a seed bank in the soil or on a combination of processes (Grime et al. 1988).

Our hypothesis was that the distribution of the selected plant species in the study area would vary in two ways: *between years* when extinction and colonization events are frequent and *between species* because of differences in regenerative strategies. The aim of this study was to map the distribution of the selected plant species in the study area during three years (1990/91/92) and to answer the following questions:

1. What are the frequencies and distribution patterns of the selected plant species in the study area and how are they related to the management of ditch banks?
2. What are the frequencies of extinction and colonization in individual patches and how are they related to population size?
3. Is the variation in distribution between years and between species related to the variation in life-history attributes?
4. Is restoration of species-rich meadows in fragmented landscapes feasible, given the management of ditch banks and the regenerative strategies of the selected species?

THE LANDSCAPE

The study area (220 ha) is located in the centre of the Netherlands between two glacial ridges (*Veluwe* and *Utrechtse Heuvelrug*) and forms part of the *Binnenveld* valley near Wageningen ($51^{0}54'$ N; $5^{0}38'$ E). The landscape is very open, almost treeless and contains long and narrow fields delimited by drainage ditches, which are intensively used for livestock grazing and silage cutting. The fields have become uninhabitable to meadow species because of high fertilizer inputs of up to 400 kg N/ha/yr (van der Meer 1982).

The only patches still suitable for meadow species in the study area occur on ditch banks. These linear strips of land vary in aspect and slope and are between 0.5 m and 5 m wide and 0.2 to 0.7 km long. The environment of ditch banks is often adversely affected by spill-over of inorganic fertilizers, application of herbicides to suppress *Urtica dioica, Rumex spp.* and *Cirsium spp.*, and trampling and grazing by livestock. The *Veenkampen* experimental set-aside area (13.2 ha) was established in the study area in 1978 with the aim of restoring the species-rich meadows that used to be common in the region (Berendse et al. 1992).

PLANT SPECIES

In the study area, the intensification of farming started around 1950. Since then, many plant species of the former species-rich meadows have disappeared from the fields and either have become regionally extinct or have managed to survive on ditch banks. Van Dorp and Oomes (*submitted*; Chapter 1) have shown that 106 of the 145 species (73%) recorded on the former species-rich meadows are still present on ditch banks in the study area, although some have very small populations. Ten of these surviving species were selected for this study because they are characteristic perennial herbs of moist and wet meadows dominated by grasses such as *Molinia caerulea* and *Anthoxanthum odoratum* and show large differences in regeneration strategies.

MATERIAL and METHODS

Species mapping

The distribution of the selected species was mapped in the last ten days of July and the first ten days of August (the period during which most plant populations are at their peak of flowering or fruiting and are very conspicuous) in 1990, 1991 and 1992. A distinction was made between populations with *generative* plants which bear flower buds, flowers or fruits and *vegetative* plants which lack such reproductive parts. All populations of the selected species were plotted in the field on 1:3500 maps. The size of all reproducing plant populations except *H. quadrangulum* was estimated from the number of flowering heads, umbels, flowering stems, individuals or size of patches (Table 1).

Table 1. Species-specific units used to estimate the size of reproducing populations of the ten selected species in the field and corresponding cut-levels for the three size-classes: small, medium and large.

SPECIES	UNIT	SMALL	MEDIUM	LARGE
Achillea ptarmica	head	1-50	51-500	>500
Centaurea jacea	head	1-10	11-50	>50
Cirsium palustre	stem	1	2-10	>10
Leucanthemum vulgare	head	1-50	51-500	>500
Lotus uliginosus	area (m^2)	1	2-3	>3
Lychnis flos-cuculi	individual	1	2-5	>5
Peucedanum palustre	umbel	1-10	11-50	>50
Thalictrum flavum	stem	1-3	4-10	>10
Viola persicifolia	individual	1	2-5	>5

GIS analysis

The locality of each population was digitized from field maps onto species maps for each year (1990, 1991 and 1992) separately, using the Geopakket 3.01 package (Geops 1991), which characterizes populations in a vector-oriented database by species, estimated size and field coordinates. To be able to compare the distribution of species between years, the spatial information was transformed onto a raster of 50 x 50 m grid cells. This resolution was chosen instead of a finer grid (e.g. 25 x 25 m) because it reduced the matching errors between years resulting from possible mapping inaccuracies in the field. Using a width of 50 m gave a total number of 1218 grid cells over the entire study area; this number was divided into 481 grid cells of inhospitable farmed fields (39.5%) and 737 grid cells of ditch banks (60.5%). The latter figure includes 41 ditch banks cells of the set-aside area (3.3%) and 696 ditch bank cells in the surrounding farmed landscape (57.2%).

Transformation of the spatial information onto a raster with a 50 m mesh produced total maps which give the total size of the reproducing population in terms of grid cells. The variation in population sizes among cells was subsequently reduced to three species-specific size-classes of *small, medium* and *large* sources. This procedure was necessary because of the species-specific approach to estimate the size of reproducing populations in the field. Total maps were then used for each species: (i) to determine the frequency and distribution of cells occupied by generative and vegetative plants during 1, 2 or 3 years, (ii) to establish the relation between the frequency of occurrence and the management of ditch banks and (iii) to establish the relation of the frequency of extinctions and colonizations with the size-class of cells. Presence/absence data were used to analyse (i) and (ii) and semi-quantitative data were used to analyse (iii).

Management of ditch banks

The management of ditch banks within the study area was monitored for two years from August 1990 until August 1992, at 2-week intervals from summer until autumn and once a month from winter until spring (van Dorp *unpubl. results*). Monitoring revealed that the management of ditch banks and fields on the set-aside area consisted of mowing and then removing the harvested biomass twice a year, in June and September. The ditch banks in the surrounding farmed landscape are managed differently by farmers who either dredge, mulch or allow livestock to graze the ditch banks. Dredging involves removing debris from the ditch bottom, cutting the ditch bank vegetation and depositing all organic material on the upper part of the ditch bank; mulching refers to mowing and shredding the biomass and leaving it in situ. Some ditch banks had not been managed at all for several years, allowing Willow (*Salix* *aurita*), Hawthorn (*Crataegus monogyna*) and Reed (*Phragmites australis*) to establish. Over the study period, 54% of the ditch banks surrounding the set-aside area received the same treatment every year, 46% were managed inconsistently with a different treatment the following year (van Dorp *unpubl. results*). This prevented a statistical comparison on the frequency of species between the various treatments. Instead, treatments were summarized into two distinct categories; mowing and removing the harvested biomass on the set-aside area (*set-aside area*) and a combination of dredging, mulching, grazing and no management on the ditch banks in the landscape surrounding the Veenkampen (*farmed landscape*). The frequency of the ten selected species for each category was determined for 1990, 1991 and 1992 separately and expressed as the percentage of all available cells being occupied.

A way of assessing the prevalence of species in the two categories of ditch bank management was to compare the *observed* frequency of species in the set-aside area with its *expected* frequency (i.e. the number of cells occupied on the basis of the frequency of a species in the surrounding landscape). The following procedure was adopted to determine the expected frequency of each species. The perpendicular distance of each occupied cell in the surrounding landscape to the boundary of the set-aside area was determined. Using these distances, the cumulative number of occupied cells was plotted against the distance to the set-aside area. Each number-to-distance curve was then fitted with third-order polynomial regression. The slope of the curve indicates the general frequency of a species in the study area, the Y-intercept can be regarded as the expected frequency for the set-aside area. Deviations between expected and observed frequencies may indicate the degree in which the set-aside area is accessible and/or suitable for the selected species.

Dynamics

Between any two years, an occupied cell could remain occupied (no change) or become empty (extinction) the following year, whereas an empty cell could become occupied (colonization) or remain empty for another year (no change). During the study period (1990-92), individual cells may have been occupied temporarily (1 or 2 years) or permanently (3 years) by a species. To obtain a measure of the changes in occupancy between years for generative plants, two indices were identified:

- E/C, gives the ratio of the number of extinctions to the number of colonizations from year t_n to year t_{n+1}, with values <1 (distribution shrinking), 1 (distribution constant) or >1 (distribution expanding)
- P/(T+P), gives the ratio of the number of permanently occupied cells (P) to the number of temporarily and permanently occupied cells (T+P), with values between 0 (no cells permanently occupied) and 1 (all cells permanently occupied).

Life-history attributes

In order to investigate the relation between the indices of dynamic distribution and life-history variation, information was collected for each of the selected species on the following life-history attributes (Table 2; *see* Appendix 1 for species accounts):

Table 2. Autecological data on five life-history attributes: seed weight (1: ≤ 0.25 mg; 2: 0.26 - 1.00 mg; 3: >1.00 mg); dispersal mechanism (B= seed dispersed ballistically; W= wind-dispersed; Wc= wind-dispersed from a capsule; Wp= wind-dispersed seed with a pappus); dispersal distance (S= short, <0.1 km; M=medium, 0.1-1.0 km; L=long, >1.0 km); vegetative spread (1: diameter of plants <10 cm; 2: 10-25 cm; 3: 25-100 cm; 4: >100 cm); seed bank type (1: a small amount of seed persists but concentrations of seeds in the soil are high only immediately after seed has been shed; type 2: a large bank of seeds is present throughout the year).

ATTRIBUTE	PLANT SPECIES									
	Vp	Pp	Hq	Cj	Ap	Tf	Lf	Cp	Lv	Lu
Seed weight	2	3	1	3	1	3	1	3	2	2
Dispersal mechanism	B	W	Wc	Wc	W	W	Wc	Wp	W	B
Dispersal distance	S	M	S	S	S	S	M	L	M	S
Vegetative spread	2	1	3	2	4	3	2	1	2	4
Seed bank type	2	1	2	1	1	2	2	1	1	2

- **seed size**; the propagules collected in the study area were weighed and classified into three classes: 1, weight ≤ 0.25 mg; 2, 0.26 - 1.00 mg; 3, >1.00 mg.
- **seed dispersal mechanism**; the dispersal mechanism was classified on the basis of information collected by Grime et al. (1988) and van Dorp and Oomes (*submitted*; Chapter 1). The following abbreviations are used: B, seeds dispersed ballistically from drying pods or capsules; W, wind-dispersed including Wc, wind-dispersed seeds that are shed from capsules held above the surrounding vegetation and Wp, wind-dispersed seed with a pappus.
- **seed dispersal capacity**, the maximum distance travelled by seeds during storms or on water was classified as short (S) if seeds travel distances up to 0.1 km, medium (M) for distances up to 1 km and long (L) for distances greater than 1 km, according to information collected by van Dorp and Oomes

(*submitted*; Chapter 1) .

- **vegetative spread**, four classes were identified: 1= perennials forming small tussocks and unbranched compact rhizomes (<10 cm in diameter), 2= perennials attaining 10-25 cm in diameter, 3= perennials attaining 25-100 cm in diameter, 4= perennials attaining >100 cm in diameter (Grime et al. 1988).
- **recruitment from a persistent seed bank**, two types of seed bank were identified: in type 1 a small amount of seed persists in the soil but concentrations of seeds in the soil are high only immediately after seed has been shed and in type 2 a large seed bank is present throughout the year. The seed bank types of the selected species are based on Grime et al. (1988), Bakker (1989) and van Dorp (*unpubl. results*) and Harvey and Meredith (1981) for *Peucedanum palustre*.

RESULTS

Frequency and distribution

Although none of the selected species were present on the farmed fields, they still occurred on ditch banks, locally with profusely flowering populations. Four species were relatively sparse in the study area, occupying less than 10 % of all available ditch bank cells. Six species were relatively common, occupying more than 10 % of all available cells over the three-year study period (Table 3). *L. uliginosus* was the most widespread species (33.8%). Mapping also revealed that each species had its own characteristic pattern of distribution (Figure 1). The distribution of *H. quadrangulum, L. vulgare* and *L. uliginosus* showed a relatively high degree of clustering of individual populations, while *A.ptarmica, C. palustre, L. flos-cuculi* and *T. flavum* showed a more even distribution over the landscape. Populations of *C. jacea, P. palustre* and *V. persicifoilia* tended to be isolated from each other (Figure 1). The number of cells with plants that did not flower or set seed over the entire study period was exceptionally high in one species, *T. flavum* (Table 3).

Figure 1. Distribution of ten meadow species during three years (1990-92). Squares are cells of 50 x 50 m with generative plants and occupied for 1 (open), 2 (with dot) or 3 (filled) years. Crosses are cells which contained vegetative plants only during the three-year period. Species are arranged from sparse (left) to common (right). *See* page 57.

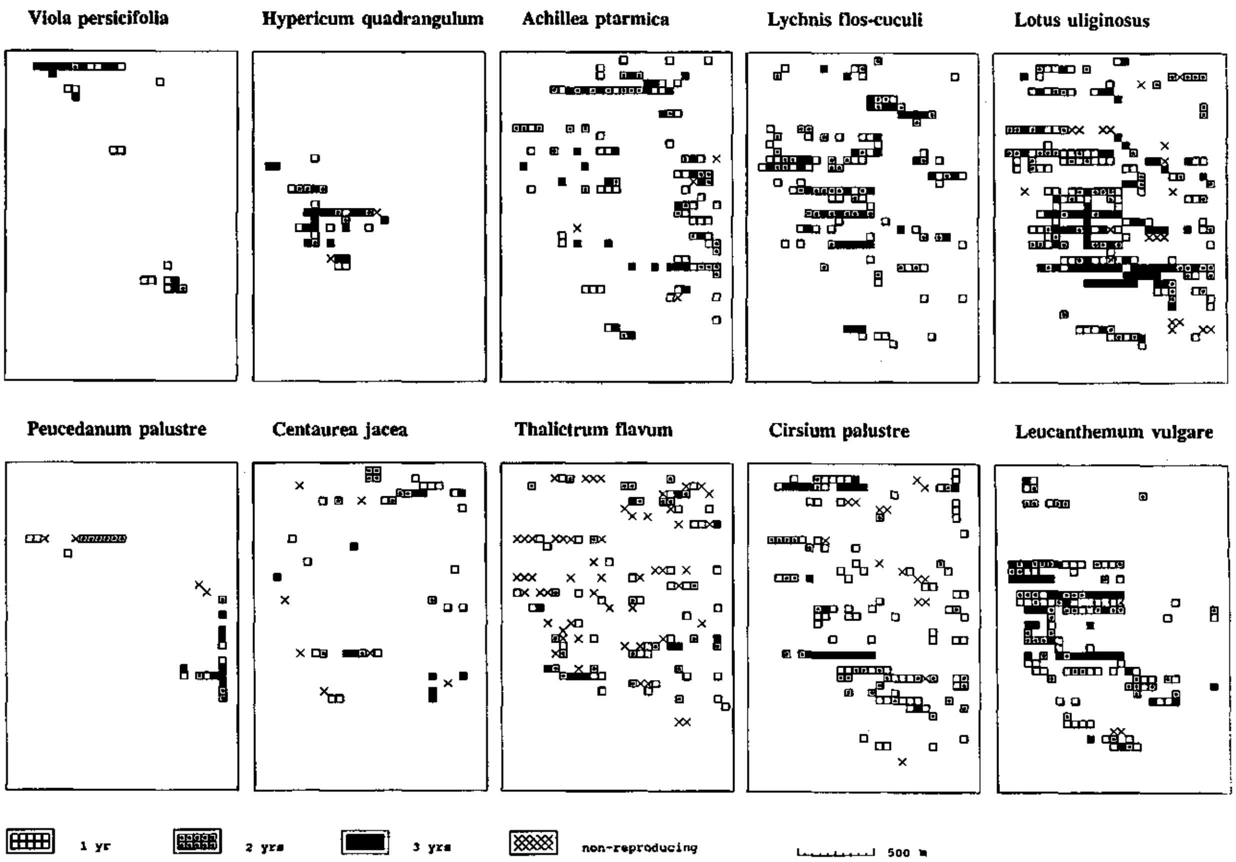

Viola persicifolia
Hypericum quadrangulum
Achillea ptarmica
Lychnis flos-cuculi
Lotus uliginosus
Peucedanum palustre
Centaurea jacea
Thalictrum flavum
Cirsium palustre
Leucanthemum vulgare
1 yr
2 yrs
3 yrs
non-reproducing
500 m

Table 3. Number of cells occupied by generative plants in 1990, 1991 and 1992 separately and over the three-year period 1990/92 (top), the number of cells occupied by exclusively vegetative plants over the three-year period 1990/92 (middle) and the total number of cells occupied by generative and vegetative plants over the three-year period 1990/92 (bottom), expressed as the percentage occupied of all available ditch bank cells in the study area (n=737 cells). Species are ranked by increasing frequency. Species codes are *Ap=A. ptarmica, Cj=C. jacea, Cp=C. palustre, Hq=H. quadrangulum, Lf=L. flos-cuculi, Lu=L. uliginosus, Lv=L. vulgare, Pp=P. palustre, Tf=T. flavum* and *Vp=V. persicifolia.*

	PLANT SPECIES									
	Vp	**Pp**	**Hq**	**Cj**	**Ap**	**Tf**	**Lf**	**Cp**	**Lv**	**Lu**
1990	19	18	25	20	70	26	88	83	81	155
1991	17	18	24	24	70	46	83	56	96	141
1992	17	15	29	28	65	50	85	66	103	164
∑ Gen. cells	27	24	35	39	111	75	137	128	147	229
∑ Veg. cells	0	5	2	7	4	53	0	15	3	20
Total	27	29	37	46	115	128	137	143	150	249
% of all cells (n=737)	3.7	3.9	5.0	6.2	15.6	17.4	18.6	19.4	20.4	33.8

Effect of ditch bank management

The mean frequency of the ten selected species was significantly higher on the ditch banks of the set-aside area (ranging from 18.9% to 27.1%) than on the ditch banks of the surrounding farmed landscape (ranging from 7.0% to 7.3%) (one factor ANOVA after arc-sine transformation, Scheffé's F-test p<0.05; Table 4). The mean frequencies of both ditch bank types were not significantly different between years (Scheffé's F-test, p>0.05). Seven of the ten species had the highest frequency on the ditch banks of the set-aside area; this was particularly striking in *H. quadrangulum* and *L. uliginosus*. Only one species was more frequent on the ditch banks in the surrounding farmed area. Two species were absent from the set-aside area during the study period (Table 4).

Table 4. Percentage of cells occupied by generative plants separated into those on ditch banks in the surrounding farmed landscape (n=696 cells) and those in the set-aside area (n=41 cells). Frequencies of the two ditch bank types were compared with one-factor ANOVA after arc-sine transformation (Scheffé's F-test), species were ranked in order of increasing frequency.

PLANT SPECIES	FARMED LANDSCAPE			SET-ASIDE AREA		
	90	91	92	90	91	92
Viola persicifolia	2.7	2.4	2.4	0	0	0
Peucedanum palustre	2.6	2.6	2.2	0	0	0
Hypericum quadrangulum	1.9	1.9	1.9	29.3	26.8	39.0
Centaurea jacea	2.6	2.9	3.2	4.9	9.8	14.6
Achillea ptarmica	9.3	9.8	8.5	12.2	4.9	14.6
Thalictrum flavum	3.7	6.5	6.6	0	2.4	9.8
Lychnis flos-cuculi	9.6	10.2	9.9	51.2	29.3	39.0
Cirsium palustre	9.5	6.5	7.9	41.5	26.8	26.8
Leucanthemum vulgare	9.3	12.1	11.9	39.0	29.3	48.8
Lotus uliginosus	18.5	16.8	19.0	63.4	58.5	78.0
Mean % (n=10 species)	7.0^a	7.2^a	7.3^a	24.1^b	18.9^b	27.1^b
SE	1.7	1.6	1.7	7.5	5.9	7.8

Prevalence of species in the set-aside area

The relationship between the cumulative number of occupied cells and the distance to the set-aside area is shown in Figure 2. The slopes and intercepts of these third-order polynomial curves correlated positively with the total frequency of the species within a 1 km radius of the set-aside area (slope: R^2= .818, df=9, p<0.001, intercept: R^2= .595, df=9, p<0.01). These results suggest that the *regional* abundance of a species to some extent determined its *local* abundance in a target area. The expected frequencies (Y-intercepts) correlated significantly positively with the observed frequencies in the set-aside area (R^2= .67, df=9, p<0.01), yet deviations were also apparent. One species was as frequent as expected: *A. ptarmica* (4 occupied cells expected versus 5 observed); seven species were more frequent than expected: *C. jacea* (-9 vs. 7), *C. palustre* (3 vs. 21), *H. quadrangulum* (5 vs. 19), *L. vulgare* (5 vs. 21), *L. flos-cuculi* (8 vs. 25), *L.uliginosus* (11 vs. 38) and *T. flavum* (3 vs. 11); two species were absent although one species was expected to be present (*P. palustre* (-9 vs. 0) and *V. persicifolia* (5 vs. 0) (Figure 2).

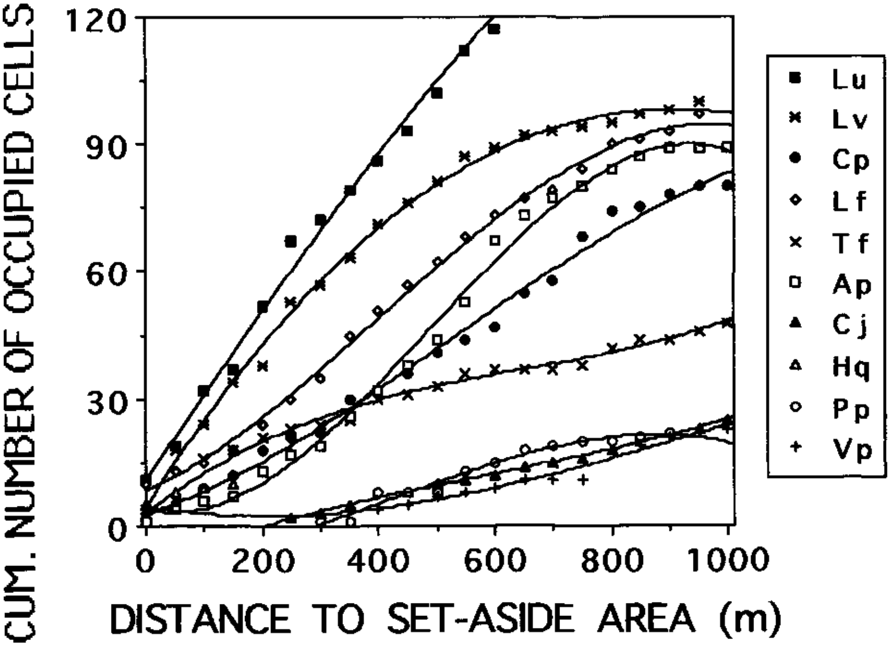


Figure 2. Relationship between the cumulative number of occupied cells for ten meadow species and the distance of occupied cells within a 1 km radius (m) to the set-aside area where species-rich meadows are being restored. The shown curves of all species except H. quadrangulum are third-order polynomials that were fitted to the data; in all cases R^2 ≥0.97.

Dynamic distribution

The ten selected plant species together occupied 468 cells (i.e. 63.5% of all 737 available ditch banks cells) 1059 times over the three-year study period (Table 5); an average occupied cell harboured plants for 1.78

years between 1990 and 1992. In 71% of all cases, generative (i.e. flowering and/or fruiting) plants occupied the cells, in 11% by vegetative plants only and in 18% by both generative and vegetative plants. No cells had exclusively vegetative plants during the three-year period.

Most cells were not occupied by plants of the selected plant species each year. Almost half (46%) of all occupied cells had generative and/or vegetative plants of the selected species for only 1 year, 29% had plants present for 2 years and 25% had plants present for 3 years (Table 5). This suggests that the occupancy of patches by flowering and fruiting plants fluctuates greatly and that the *total* distribution of a plant species in the study area over the three-year study period was much wider than in a single year. Yet, the variation in the total number of cells occupied by a species between the three years (1990/91/92) was relatively small, except for some of the more common species such as *C. palustre* and *L. vulgare* (Table 3).

Table 5. Frequency of cells occupied by (i) generative, (ii) generative and vegetative or (iii) exclusively vegetative plants during one, two or three years, using the data of ten selected plant species for the entire study period1990-92 (n=1059 cases of cells being occupied by plants).

REPRODUCTIVE MODE	NUMBER OF YEARS OCCUPIED			TOTAL FREQUENCY
	1	2	3	
Generative	326	210	220	756 (71%)
Generative + Vegetative	72	71	44	187 (18%)
Vegetative	94	22	0	116 (11%)
Total frequency	492 (46%)	303 (29%)	264 (25%)	1059 (100%)

Frequency of extinctions and colonizations

The degree of change in the numbers of occupied cells between years was expressed by the indices E/C and P/(T+P) (Table 6). The comparisons of the distribution between 1990/91 and between 1991/92 showed that extinctions and colonizations occurred in every species. Out of 20 cases, the E/C ratio was <1.0 in ten cases, 1.0 in three cases and >1.0 in seven cases (Table 6). In three species (*C. jacea, L. vulgare* and *T. flavum*), the E/C ratio was <1.0 in both years, indicating that the species was becoming more widespread over the three-year study period. In three species (*A. ptarmica, P. palustre* and *V. persicifolia*), the E/C was ≥1.0, indicating a general decline, and in the remaining four species (*C.palustre, H. quadrangulum, L. flos-cuculi* and *L. uliginosus*), the E/C values were not constant but varied from >1.0 between 1990/91 to <1.0 between 1991/92. The mean E/C ratios of all ten species for 1990/91 (1.08) and 1991/92 (0.87) did not differ significantly from 1.0 (t-tests, df=9, p=0.60 and p=0.39 respectively). Moreover, the E/C ratios did not differ significantly between the two periods (t-test, two-tailed, df=9, p=0.366). The two species (*T. flavum* and *C. palustre*) with relatively low P/(T+P) values (0.15 and 0.17) showed the most dynamic distribution whereas the three least abundant species (*V. persicifolia, P. palustre* and *H. quadrangulum*) and the most abundant species (*L. uliginosus*) with relatively high P/(T+P) values (ranging from 0.32 to 0.51) showed the least dynamic distribution (Table 6).

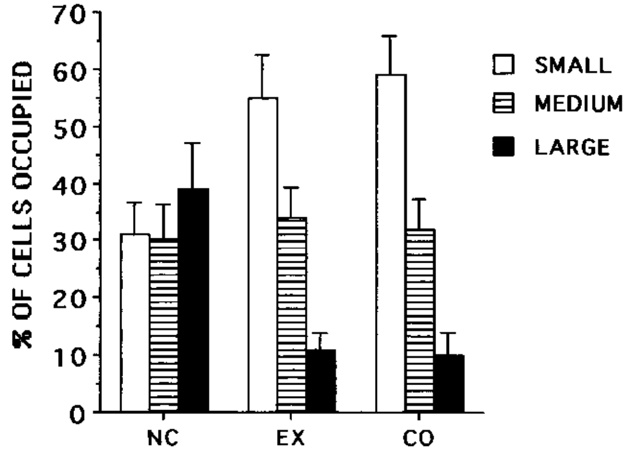


Figure 3. Percentage of cells that remained occupied (NC=no change), became extinct (EX) or were colonized (CO) between two years, separated into cells with small, medium and large total population size. Values are means (± SE) for ten species and two years (1990/91 and 1991/92).

Table 6. Number of cells that became empty (extinction) or were filled (colonization) between 1990/91 and 1991/92 (top) and the ratio between extinctions and colonizations (E/C) and the proportion of all occupied cells that were occupied permanently (P/(T+P)) (bottom). Species codes are *Ap=A. ptarmica, Cj=C. jacea, Cp=C. palustre, Hq=H. quadrangulum, Lf=L. flos-cuculi, Lu=L. uliginosus, Lv=L. vulgare, Pp=P. palustre, Tf=T. flavum* and *Vp=V. persicifolia.*

NUMBER OF CELLS	**PLANT SPECIES**									
	Vp	**Pp**	**Hq**	**Cj**	**Ap**	**Tf**	**Lf**	**Cp**	**Lv**	**Lu**
EXTINCTION										
1990/91	7	4	5	8	27	9	36	56	26	53
1991/92	4	7	5	6	27	18	29	25	33	33
COLONIZATION										
1990/91	5	4	4	12	27	29	31	29	41	39
1991/92	4	4	10	10	22	22	31	35	40	56
E/C										
1990/91	1.4	1.0	1.3	0.7	1.0	0.3	1.2	1.9	0.6	1.4
1991/92	1.0	1.8	0.5	0.6	1.2	0.8	0.9	0.7	0.8	0.6
mean **E/C**	1.2	1.4	0.9	0.6	1.1	0.6	1.0	1.3	0.7	1.0
P/(T+P)	.44	.32	.51	.28	.28	.15	.28	.17	.28	.36

The correlation between the size-class of the population and the percentage of cells that became occupied (*colonization*) or empty (*extinction*) the following year was investigated. Extinctions were significantly more frequent in cells with small populations than in cells with large populations (55% and 11% of all cells in the appropriate size-class, respectively) (one-factor ANOVA, Scheffé's F-test, df=8, $p<0.05$). Colonizations were also significantly more frequent in cells with small sources the following year than in cells with large sources (59% and 10% of all cells, respectively) (one-factor ANOVA, Scheffé's F-test, df=8, $p<0.05$) (Figure 3). All other comparisons between size-classes for the percentages of cells experiencing no change, extinction or colonization events did not show significant differences (one-factor ANOVA, Scheffé's F-test, df=8, p>0.05).

Table 7. Results of Mann-Whitney U and Kruskal-Wallis tests for the indices E/C and P/(T+P). Index values were related to five life-history attributes: seed weight, dispersal mechanism, dispersal capacity, vegetative spread and seed bank type. All ten comparisons between indices and life-history attributes were not significant (p>0.10).

	df	E / C	P/(T+P)
Seed weight	2	H=0.018 n.s.	H=2.581 n.s.
Dispersal mechanism	3	H=2.318 n.s.	H=3.913n.s.
Dispersal capacity	2	H=2.218 n.s.	H=1.919n.s.
Vegetative spread	3	H=5.755 n.s.	H=0.447 n.s.
Seed bank type	1	z= -0.731 n.s.	z= -0.740 n.s.

The two indices E/C and P/(T+P) were not significantly related to either seed size, dispersal mechanism, dispersal capacity, ability to spread vegetatively or seed bank type (Mann-Whitney U tests and Kruskal-Wallis tests; p>0.10) (Table 7).

DISCUSSION

This study analysed the distribution of ten perennial plant species typical of species-rich meadows in a farmed landscape and the changes in their distribution between years. Although the selected species had disappeared from the farmed fields, they were still present on ditch banks, and often in surprisingly large numbers (e.g. the Dutch Red List species *Viola persicifolia*). It has been established that linear landscape elements such as ditch banks represent important refugia for a number of species in intensively exploited landscapes (Melman 1991; van Strien 1991).

This study also suggests that only one out of four patches was permanently occupied with reproducing plants and that three out of four patches were colonized and became extinct after being occupied for 1 or 2 years. The question remains whether such changes in distribution at the level of grid cells represented true extinctions and colonizations of individual populations. This study cannot fully answer this question because of the following problems:

- During the surveys of the ditch banks, some plant populations might have been overlooked, although this is unlikely because of the time taken to conduct the surveys and because the plants were at the peak of flowering or fruiting at that time. Most of the selected species are very conspicuous when flowering or fruiting because of tall stems and striking colours, but some of the small vegetative plants (especially those on grazed ditch banks) may have been overlooked.
- The location of a population in year t may in some cases not have been identical to the location in year t+1 because of inaccuracies in mapping and digitizing. This was indeed a serious problem. In order to reduce this type of error, it was necessary to use grid cells with a mesh size of 50 m. It is possible that some of the changes in occupancy of cells could have been caused by inaccuracies of the method rather than by extinction and colonization events. Another consequence of upscaling was that any within-cell variation in numbers and distribution could not be detected. The frequency of extinctions and colonizations should therefore be discussed at the level of grid cells instead of at the level of individual populations.

We also demonstrated that there were large differences in distribution between ditch banks of the set-aside area and those managed by farmers. Frequencies were significantly higher in the Veenkampen. This indicates that the measures taken on the Veenkampen to restore the abiotic conditions of the former species-rich meadows (no fertilizer inputs, higher water tables, removal of the harvested biomass) are beginning to succeed for species still present in the farmed landscape. The comparison between the set-aside area and the surrounding farmed landscape also indicated that: (i) for one species the conditions on the set-aside area (in particular mowing in June and September) were not different from those in the surroundings, (ii) the relatively benign environment on the set-aside area has favoured the spread of seven species over the set-aside area, (iii) the set-aside area is inaccessible to propagules of two species, i.e. seed dispersal is inadequate to bridge the distance between sources and the set-aside area.

The various management treatments (mowing, dredging, grazing etc.) have both beneficial and adverse effects on the growing conditions for plants. The beneficial effects include the creation of sites appropriate for germination and establishment for seeds dispersed or buried in the soil and the release from intensive grazing and mowing which prevents the flowering and fruiting in plants. The first effect could lead to the colonization of newly available sites, the second to the reproduction in populations consisting of plants formerly surviving only vegetatively. The adverse effects include the increased competition from tall fast-growing herbs and grasses on the subordinate species and the prevention of flowering and fruiting because of intensive grazing and mulching. Both adverse effects could lead to plants surviving the short adverse periods as vegetative plants and to the extinction of individual plant populations when adverse conditions last too long. We believe that the changes in cell occupancy between years are partly the effect of true extinctions and colonizations and partly the effects of established plant individuals going from a generative (very conspicuous) to a vegetative state (very inconspicuous).

Dynamics and life-history attributes

The degree of change in occupancy at landscape level (expressed by the indices E/C and P/(T+P)) had no statistically significant relations with the life-history attributes seed weight, dispersal capacity, dispersal distance, vegetative spread and seed bank type. We expected that short-lived species with long range dispersal, without a capacity to build up a persistent seed bank or to spread vegetatively would show a more dynamic distribution than long-lived species with short range dispersal, a persistent seed bank and the capacity to spread vegetatively. This was indeed the case when *Cirsium palustre* was compared with *Lotus uliginosus* (Table 7). However, using the data of all ten species, the relationships between single life-history attributes and the two indices were not statistically significant. This finding can be explained by the idea that to secure a population on a site, plants have developed regeneration strategies, i.e. a combination of attributes which allow them to compensate for weakly developed attributes. For example, the short range dispersal of seeds in *Lotus* is compensated for by a permanent seed bank and great ability to spread vegetatively.

Grime et al. (1988) distinguised four such regenerative strategies in higher plants: vegetative spread (V), long range dispersal of numerous seeds (W), seasonal recruitment in vegetation gaps (S) and recruitment from a seed bank (Bs) and stated that these strategies are not mutually exclusive. Frequently, species exhibit two or three regenerative strategies, and in fact such species should persist longer in a landscape under various forms of stress than species with a single strategy. The selected species were characterized by a combination of recruitment from a persistent seed bank with either vegetative spread or seasonal recruitment in vegetation gaps. This is in contrast with the regionally extinct species of the former species-rich meadows which depend more frequently on a single strategy, often seasonal recruitment in vegetation gaps (van Dorp and Oomes *submitted;* Chapter 1). The multiple-attribute character of the regenerative strategies of the selected species may explain their persistence in this type of landscape. The complex relations that exist between distribution, dynamics and life-history traits can be demonstrated by examining two species in some detail, *Peucedanum palustre* and *Cirsium palustre.*

Peucedanum palustre was one of the least dynamic species. This short-lived perennial species was also one of the spatially most restricted species. It has survived on the least disturbed patches in the landscape which escape frequent mowing and dredging. Such patches are very scarce in the study area. To regenerate, *P. palustre* relies mainly on seasonal regeneration in by seed, since it does not spread vegetatively and buried seeds are viable for only 1 to 2 years. This suggests that adult plants may survive and reproduce in the favourable but scarce patches, but it is highly unlikely that the species will colonize other more distant sites in the study area. In contrast, *Cirsium palustre* is one of the most dynamic and widespread species. It is a monocarpic biennial or short-lived perennial thistle that produces numerous long range dispersed seeds, is resistant to grazing and recruits seedlings from a persistent seed bank. This strategy has led to many small ephemeral populations becoming established around the few large source populations in the study area.

Recolonization of the set-aside area

The distribution patterns at landscape scale were all different and characterize the individualistic behaviour of each species. In the study area, stretches of ditch banks with a high density of occupied patches alternate with stretches with a low density, nowhere forming a cohesive network of ecologically well-managed ditch banks. At landscape scale, this implies that the scattered populations on the present-day network of ditch banks do not function as a metapopulation. Ditch banks that are intensively grazed and frequently mulched lack the effective seed sources completely. Ditch banks with 'good quality' patches are connected to banks with 'low quality' patches. Another implication is that species with a poor dispersal capacity are unable to cross these unfavourable stretches of bank in the landscape and that the restored fields on the set-aside area (acting as a *target*) will remain inaccessible for new species for a long time. By the same token, species established on the set-aside *area* (acting as a *source*) will find it difficult to migrate along ditch banks to restored sites elsewhere in the landscape.

Acknowledgements

We thank P. Ketner and H. Klees (Wageningen Agricultural University) for their contribution to the species mapping. F. van den Berg and C.R. Jurgens assisted with GIS. F. Berendse, J.M. van Groenendael and W. Joenje critically reviewed earlier drafts of this paper.

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Appendix 1

Achillea ptarmica L. : a perennial composite species up to 0.9 m tall, with large individuals attaining maximally 10 m in diameter (**V** - **3**) and 3000 flowering heads. Seeds (0.25 mg) are flattened (achenes) and well dispersed by wind and water during late summer and autumn (*medium range* dispersal). Germination is immediate in gaps. A.p. probably forms a persistent seed bank (**?B** - **1**)

Centaurea jacea L. : a perennial composite species up to 1.2 m tall (**V** - **2**) . Seeds (2.22 mg) are launched from capsules and dispersed by the wind during summer (*short range* dispersal). Seeds may also survive passage through vertebrate gut. Germination is immediate in gaps and in closed turf (**S?**). C.j. forms a persistent seed bank (**B** - **1?**)

Cirsium palustre (L.) Scop. : a monocarpic biennial or short-lived perennial thistle, up to 1.5 m tall (**V** - **1**). Pappus-bearing seeds (2.00 mg) are widely dispersed by wind on warm days with turbulence (*long distance* dispersal) (**W**). Germination is immediate in gaps and in closed turf. C.p. forms a persistent seed bank (**B** - **1**)

Hypericum quadrangulum L. : a perennial hemicryptophyte, up to 0.6 m tall (**V** - **2**). Numerous small and light (0.03 mg) seeds are launched from capsules and dispersed by the wind during autumn and winter (*short range* dispersal) and probably externally on animals. Dry period is required for germination. Germination is the following spring in gaps. H.q. forms a persistent seed bank (**B** - **1**).

Leucanthemum vulgare Lamk. : a short-lived winter green perennial composite species of dry to moist places, up to 0.6 m tall (**V** - **2**). Seeds (0.36 mg) are achenes and dispersed by wind and (largely?) as a result of agricultural activities (*medium range* dispersal) during summer. Germination is immediate in gaps (**S**). L.v. forms a persistent seed bank (**B** - **1**)

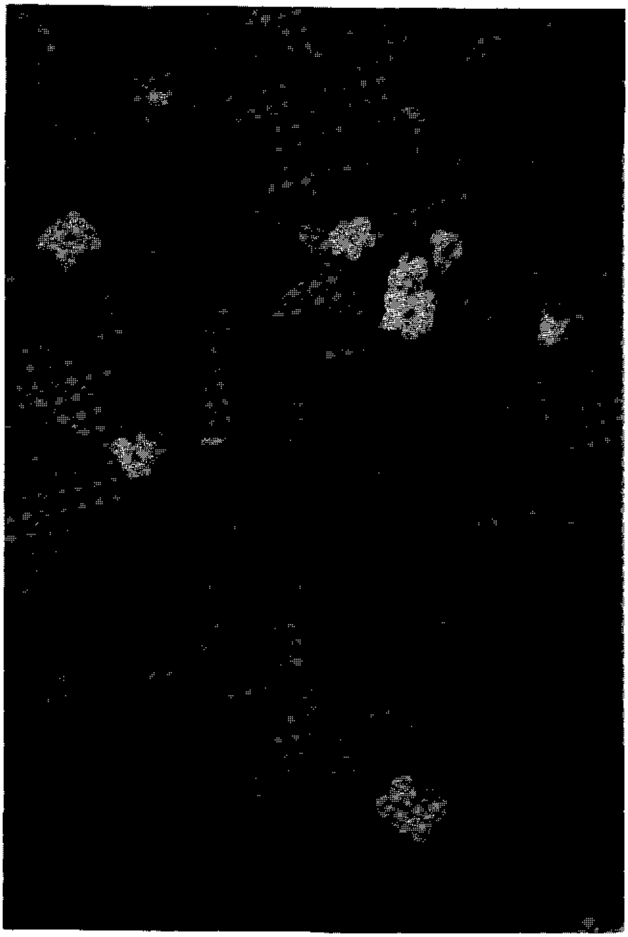
Lotus uliginosus Schkuhr : a perennial legume with spreading stoloniferous shoots, up to 1.0 m tall (**V** - **4**). When ripe pods burst open, seeds (0.57 mg) disperse over short distances during summer (*short range* dispersal). Scarification of the hard seed coat and chilling is required for germination. Germination is the following spring. L.u. forms a persistent seed bank (**B** - **2?**)

Lychnis flos-cuculi L. : a short-lived perennial , up to 0.9 m tall (**V** - **3**). Seeds (0.15 mg) are launced out of capsules and dispersed by wind during summer (*short range* dispersal) and also by hay-making machines. Germination is immediate in gaps (**S?**). L.f. forms a persistent seed bank (**B** - **2?**).

Peucedanum palustre (L.) Moench : a short-lived perennial umbellifer with monocarpic rosettes, up to 1.5 m tall (**V** - **1**). Large flattened and winged seeds (2.61 mg) are wind dispersed during summer and early autumn (*medium range* dispersal) and float on water for >6 months. Chilling and fluctuating temperatures are required for germination. Germination is the following spring in gaps (**S**). P.p. probably forms a persistent seed bank (**?B** - **1**)

Thalictrum flavum L. : a hemicryptophyte perennial species of tall herb communities, river banks and grasslands, up to 0.9 m tall (**V** - **3**). The nutlets (1.49 mg) are dispersed by wind (*short range* dispersal) and float on water for >6 months. Scarification of the nutlets is required to break dormancy. Germination is the following spring, mostly in gaps (**S?**). T.f. forms a persistent seed bank (**B - 2?**).

Viola persicifolia Schreber : a cleistogamous stoloniferous perennial violet, up to 0.3 m tall (**V - 3**). The species is a national rarity (Red List 1). Seeds (0.78 mg) are dispersed ballistically from drying capsules (*short range* dispersal); ants are not involved in the dispersal. Chilling is required for germination. Germination is the following spring in gaps (**S**). V.p. forms a persistent seed bank (**B - 2?**).



Viola persicifolia and the ruderal Chenopodium album recruiting on a disturbed soil

CHAPTER 3

Seed dispersal capacity of six perennial grassland species measured in a wind tunnel at varying wind speed and height

with W.T.M. van den Hoek and C. Daleboudt
submitted to Canadian Journal of Botany

Abstract

In this study, the dispersal capacity of six barochorous grassland perennials was experimentally assessed in a wind tunnel. The selected species (*Centaurea jacea, Hypericum quadrangulum, Lotus uliginosus, Lychnis flos-cuculi, Peucedanum palustre* and *Thalictrum flavum*) have difficulty in recolonizing restored ecosystems in agricultural landscapes, primarily because of their poor dispersal capacities. Special attention was paid to the behaviour of long-range dispersed seeds under conditions of strong wind gusts.

Variation in dispersal distances within a seed population and between species with different aerodynamic attributes was assessed. Seeds of the selected species were released at five wind speeds (V; 2, 3, 6.5, 10 and 13.5 m/s) and release heights (H; 0.2, 0.3, 0.4 0.5 and 0.6 m) in experiments in a wind tunnel. Variation in their dispersal distance was expressed as 1-percentile, mode and 99-percentile. Regression analyses showed that a model with three terms (V, V*V and V*H) best explained the variance in the dispersal distance across all species.

According to the regression models, the dispersal distances of seeds in the tail of a frequency distribution (99-percentile values) increase exponentially with wind speed. At wind speeds of 14 m/s, predicted maximum distances are 10 to 15 m for small and relatively heavy spherical seeds (3 spp.) and 20 to 30 m for large and relatively light cylindrical or disk-like seeds (3 spp.). A review of meteorological data for an inland restoration site showed that maximum wind gusts >10 m/s at plant height occur at least annually. The longevity of plant individuals of the selected species varies from <5 years to several decades, suggesting a large potential for long-range dispersal of seeds during the life-time of plants.

Two strategies are open to plants to increase their spatial dispersal of seeds: (i) increasing the release height (e.g. taller infructescences), (ii) requiring stronger winds to release seeds, e.g. by extending or shifting the time of dispersal to periods with stronger winds (autumn and winter).

INTRODUCTION

Restoration of species-rich meadows on former agricultural land contributes importantly to the conservation of species diversity in agricultural landscapes. However, the success of restoring such endangered plant communities, especially in the case of depleted soil seed banks, depends largely on the accessibility of sites to the seeds of desirable plant species (Berendse et al. 1992). The dispersal of seeds is a key factor in the regeneration process when the distances between restored sites and their closest source populations in agricultural landscapes are too large to ensure that sufficient seeds are deposited to allow re-establishment. Seeding experiments have shown that lack of seeds is indeed one of the main causes of the slow recolonization of restored meadows (Primack and Miao 1992, van Dorp *submitted*; Chapter 4).

Seeds of the most frequent immigrant species during recolonization in Western Europe are ubiquitous anemochorous ruderals such as *Cirsium arvense* and *Tussilago farfara* which can be transported over large distances (Bakker 1960a; Burrows 1986). Seeds of barochorous perennial grassland species are also dispersed by wind, but generally remain within a few metres of the parent plant (Howe and Smallwood 1982; Fenner 1985; Willson 1992). As a consequence of their limited dispersal capacity, seeds of perennial grassland species have rarely been recorded in the local seed rain (e.g. Jefferson and Usher 1989). But, because of their long life spans (up to several decades), relatively rare events such as extreme wind gusts could create important opportunities for the dispersal of seeds over longer distances (Ridley 1930; Feekes 1936; Berg 1983). This implies that a small proportion of the seeds produced will be dispersed by wind over relatively large distances.

In practice, it is very difficult to ascertain the dispersal distance in the field, particularly of those seeds that occur in the tail of a frequency distribution (e.g. Bakker 1960b). In this study, we investigated the factors which control the frequency distributions of dispersal distances of seeds by experimentally releasing batches of seeds in a wind tunnel. In particular, wind speed (V) and release height (H) are known to affect the dispersal distances of relatively large particles with high terminal velocities (V_s > 10 cm/s) such as seeds (Burrows 1986; McCartney 1990).

Seeds of six barochorous species were chosen for this study; these species are expected to recolonize the restoration sites in Dutch farmed landscapes where the previous soil conditions have been restored. They are grassland perennials which vary in longevity from relatively short-lived to long-lived and show large differences in aerodynamically important attributes such as the shape, size and mass of their seeds. We were interested in three questions in particular:

1. What are the effects of wind speed and release height on the frequency distribution of dispersal distances of seeds?
2. What are the actual frequencies of wind speeds, including extreme wind gusts, for a particular restoration site in the Netherlands?
3. What are the implications of 1 and 2 for the mobility of the selected species in fragmented agricultural landscapes.

MATERIAL AND METHODS

Plant species

Six plant species were selected for this study: *Centaurea jacea*, *Hypericum quadrangulum*, *Lotus uliginosus*, *Lychnis flos-cuculi*, *Peucedanum palustre* and *Thalictrum flavum*. They are characteristic of species-rich meadows in the Netherlands but also occur on linear landscape elements such as road verges and banks of ditches that characteristically separate the level, drained plots of land in Dutch rural landscapes. The selected species are all perennial but vary in longevity. *Lychnis* and *Peucedanum* plants are relatively short-lived (less than five years) once they have become established as adults (Biere et al. 1989; Harvey and Meredith 1985), the other four species live long periods, i.e. up to several decades.

Seeds of the selected species lack specific adaptations to long-range dispersal by wind or animals. Seeds of *Centaurea*, *Hypericum* and *Lychnis* are launched from swaying capsules, whereas the seeds of *Peucedanum* and *Thalictrum* are detached individually from the plant by forces of the wind. Seeds of *Lotus* are released explosively from pods that dry out. The seeds of *Peucedanum* are flattened and have winged edges, indicating some degree of adaptation to dispersal by wind, but are also able to float on water for several months to years (Harvey and Meredith 1985).

Wind speeds

The baseline information on wind speeds for an inland restoration site near Wageningen in the centre of the Netherlands was taken from Wieringa and Rijkoort (1983). The wind speeds were tabulated for two-month periods as the cumulative percentages of hourly mean wind speeds at a standard height of 10 m. To obtain the frequency of wind speeds that are relevant to the dispersal ecology of the selected species, wind speeds were calculated for (i) an average infructescence height of 0.4 m instead of the standard height of 10 m and for (ii) maximum wind gusts with relatively short gust wavelengths (i.e. gusts which last 5 to 20 s) instead of hourly mean wind speeds.

To (i) determine the wind speed at the level of an average infructescence of 0.4 m height, the formula of a logarithmic wind profile was used for wind speeds > 6 m/s under neutral conditions,

$$\overline{u} = 2.5\, u_* \ln(z/z_0)$$

where $\overline{u}$ is the hourly mean wind speed (m/s) at 10 m, u_* is the friction velocity (m/s) which scales the wind speed, z_0 is the roughness length (m) which scales the height. For a flat open and treeless farmed landscape z_0 was set at 0.02 m and the selected height z was set at 0.4 m (Wieringa and Rijkoort 1983).

To estimate (ii) the maximum wind gust the gust factor $G = u_{max} / \overline{u}$ was used. The gust factor is the ratio of the median maximum wind gust u_{max} and the mean wind speed $\overline{u}$ on the basis of 1-hour sampling periods (Wieringa 1983). It was assumed that at the height of 0.4 m under neutral conditions with z_0=0.02 m, the gust factor G is approximately 1.6; thus the maximum wind gust u_{max} with a 50% probability during an 1-hour period is 1.6 $\overline{u}$ (Wieringa 1983).

SEED DISPERSAL EXPERIMENT

Wind tunnel

The seed dispersal experiment was carried out in the wind tunnel of the DLO-Institute for Agrobiology and Soil Fertility at Haren (Groningen, the Netherlands). This wind tunnel is normally used to study soil erosion, but with minor adjustments it can also be used to experimentally study the dispersal of seeds. The wind tunnel has a fan (electromotor 1460 rpm, 20 HP) with eight blades (diameter 1 m) that sucks the air through a closed circuit at wind speeds up to 21 m/s. Wind speeds can be adjusted by opening or closing the blinds in front of the fan. The observation section of the wind tunnel measures 0.75 m by 0.75 m and is 18 m long, with side walls consisting of removable glass windows. At the end of the observation section a settling box (2.2 x 1.5 x 2.5 m) collects the seeds that are still in flight at the end of the wind tunnel.

Experimental procedure

Seeds of the selected species were released in the wind tunnel from a thin hollow steel tube (inside diameter 5 mm) that was wide enough to contain seeds but narrow enough not to cause too much turbulence around it. The tube was the only obstacle in the wind tunnel during a trial. It was filled by hand with seeds of the selected species that had been collected in 1990 and *stored in the laboratory under dry conditions at 20 °C until use.* The seeds were released mechanically from the open tip of the tube by expelling them with a piston rod. Seeds were airborne in the wind tunnel for short periods of time before being trapped by a sticky wallpaper that was firmly taped to the floor throughout the wind tunnel. To minimize the possibility of minor turbulences during the experiment, a 13.1 m long section of the wind tunnel in front of the settling box was used. The use of the taped wallpaper limited the range of wind speeds in the wind tunnel to a maximum of 13.5 m/s, at higher wind speeds the reproducibility of the trials was no longer guaranteed. The height at which seeds were released from the tube was varied from 0.2 to 0.6 m above the floor of the wind tunnel. Seeds trapped on the wallpaper were counted at 0.1 m intervals over the entire 13.1 m observation section. This procedure gave 131 data entries for each trial.

Statistical analysis

The dispersal experiment was designed to determine the effect of wind speed (V) and release height (H) on the frequency of dispersal distances of seeds. A rotating design by Cochran and Cox (1968) was used, to be able to efficiently analyse potential second order responses (V^2 and H^2). It consisted of eleven combinations of five wind speeds and five release heights (Figure 1). The five selected wind speeds were 2.0, 3.0, 6.5, 10.0 and 13.5 m/s and release heights were 0.2, 0.3, 0.4, 0.5 and 0.6 m. In the centre of the design at V = 6.5 m/s and H = 0.4 m three replicate trials were run. Trials were carried out in May 1991 and March 1992 using eleven trials per species and 250 to 350 seeds per trial (Figure 1). In the entire experiment, sixty-six trials were carried out with a total number of 19,284 seeds.

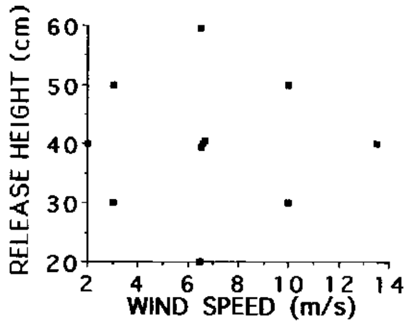


Figure 1. Experimental design of the wind tunnel experiment showing the selected values of wind speed (m/s) and release height (m). In the centre of the design (V=6 m/s and H=0.4 m) three replicate trials were run, with a total of eleven trials per species.

As stated above, the raw data from each trial consisted of the 131 seed counts at 0.1 m intervals. Graphical inspection of the various seed number to distance relationships revealed different forms of right-skewed frequency distributions of dispersal distances. In the matching cumulative frequency distributions, the left and right aymptotes were asymmetrical around the mode. To obtain accurate estimates of the various parameters (*see below*), the 131 equidistant classes of 0.1 m were reduced to an arbitrarily smaller number of 22 classes, each of which had a similar number of seeds. The distances of these new classes varied between 0.1 and 0.6 m, depending on the shape of the cumulative frequency distribution.

The NLIN procedure (SAS 1987) was used to fit an exponential curve for each of the 66 cumulative distributions using the Gompertz function:

$$Y=a_1e^{-e^{(a_2+a_3x)}}$$

where Y is the cumulative number of seeds, x is the distance from the point of seed release, coefficient a_1 is the total number of seeds counted (the number near the right asymptote) and coefficients a_2 (values > 0) and a_3 (values < 0) are estimated in the regression analyses and describe the shape of the curves. The chosen function can be applied to a wide range of cumulative distributions with two asymptotes that are not symmetrical. To obtain ecologically meaningful parameters, the 1-percentile, mode and 99-percentile values of the cumulative distribution were calculated. The dispersal distances of the 99-percentile values are particularly indicative of the conditions for long-range dispersal of seeds.

Regression models were subsequently set up for individual species to account for the variance in the 1-percentile, mode and 99-percentile. The RSQUARE procedure (SAS 1987) was used to select the best regression model with three, four or five possible terms (V, H, V^2, H^2 and $V * H$). Inspection of the output of the regression analyses showed that second order models selecting the terms V, V^2 and $V * H$ were the most consistently significant models across all six species. This led to a fixed model for all species and parameters:

$$\log (Y+1) = b_0 + b_1 * V + b_2 * V^2 + b_3\ V * H$$

where Y is the distance (m) of the 1-percentile, mode or 99-percentile of the cumulative frequency distribution. Such a fixed model enabled inter-species comparisons to be made about the effects of wind speed and release height on the dispersal distances of seeds. The selection of the terms in the fixed model was thus based on the combined information of all species, but the values of the coefficients b_0, b_1, b_2 and b_3 were based on the data on single species (i.e. values of 11 wind speed - release height combinations). The effect of release height (H) per se was not sufficiently strong and consistent across all species to be selected as an independent factor in the model. The final result was 18 regression models for six species and the three selected parameters. Finally, the fixed model (with H = 0.4 m) was used to calculate the dispersal distances of the 1-percentile, mode and 99-percentile for wind speeds varying between 2 and 10 m/s and extrapolated for wind speeds of 14 m/s.

RESULTS

Seed attributes

The seeds of the selected species represented four different shapes: rod (*Hypericum*), sphere (*Lychnis* and *Lotus*), cylinder (*Centaurea* and *Thalictrum*) and disk (*Peucedanum*) (Figure 2). The first three species are relatively small (length <1.5 mm) and light (<1 mg), the last three species are relatively large (length >3 mm) and heavy (>1 mg). Seeds of the selected species are released from individual infructescences at maximum heights of 0.6 to 1.5 m off the ground in early summer (*Lychnis*) and from late summer until autumn (other five species) (Table 1). Together, these attributes determine the terminal velocity V_s of falling seeds and thus the time seeds are airborne.

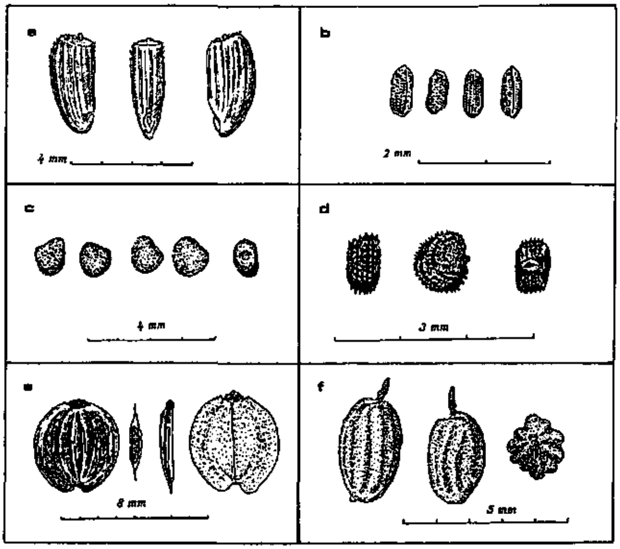


Figure 2. Seeds of (a) *Centaurea jacea*, (b) *Hypericum quadrangulum*, (c) *Lotus uliginosus*, (d) *Lychnis flos-cuculi*, (e) *Peucedanum palustre* and (f) *Thalictrum flavum*. (Source: Beyerinck 1947).

Table 1. Information on the shape, length, width and mass of seeds (n=20), the height of the infructescence (min. and max. in m) and dispersal season (months) for six plant species. Abbreviations of species names are Cj=*Centaurea jacea*, Hq=*Hypericum quadrangulum*, Lu=*Lotus uliginosus*, Lf=*Lychnis flos-cuculi*, Pp=*Peucedanum palustre* and Tf=*Thalictrum flavum*.

ATTRIBUTE	**SPECIES** **Hq**	 **Lf**	 **Lu**	 **Tf**	 **Cj**	 **Pp**
SHAPE	ROD	SPHERE	SPHERE	CYL.	CYL.	DISK
LENGTH (mm)	0.92	1.01	1.39	3.17	3.77	6.65
SD	0.06	0.06	0.14	0.29	0.44	0.83
WIDTH (mm)	0.39	0.89	1.24	1.94	1.76	4.22
SD	0.02	0.09	0.11	0.20	0.21	0.48
MASS (mg)	0.03	0.15	0.57	1.49	2.22	2.61
SD	0.01	0.03	0.11	0.35	0.47	0.68
HEIGHT (m)	0.3-0.6	0.3-0.9	0.3-1.0	0.4-0.9	0.1-1.2	0.6-1.5
DISPERSAL SEASON	VIII-IX	VI-VII	VIII-IX	VIII-IX	VII-IX	VIII-IX

Frequencies of wind speeds

The data on the cumulative frequencies of mean wind speeds show that frequency declines with increasing wind speed. At a standard height of 10 m, mean wind speeds up to 10 m/s are most frequent in the inland restoration site and occur for 95% of the time in the period July-August and for 93% of the time in September-October. Winds stronger than 10 m/s still occur annually, but winds stronger than 18 m/s return statistically only once every ten years (22.0 m/s) to once every two-hundred years (30.0 m/s). Closer to the ground at the height of 0.4 m, winds stronger than 10 m/s are very rare and statistically do not occur every year (Table 2). In fact, the strongest wind speeds in the dispersal experiment (10 and 13.5 m/s) are extremely rare at the level of an average infructescence of 0.4 m and occur approximately once every ten to one-hundred years (Table 2).

Such extreme wind conditions are very rare if based on the means of 1-hour sampling periods, but maximum wind gusts of this magnitude are more frequent. If we take e.g. a mean wind speed of 14.0 m/s at a standard height of 10 m and assume a gust factor G = 1.6, then the corresponding mean wind speed at 0.4 m is 6.7 m/s with a maximum peak gust of 10.8 m/s (Table 3). The cumulative frequencies for wind speeds ≥14.0 m/s are 0.2% for July-August (3.0 hours) and 0.9% for September-October (13.2 hours). These figures imply that at the level of a 0.4 m tall plant such maximum wind gusts occur statistically during 16.2 hours with a 50% probability every year between July and October (Table 2).

Table 2. Wind speeds (m/s) at standard heights of 10.0 m and 0.4 m with corresponding maximum gusts U_{max} for an inland restoration site in the Netherlands; the wind speed at 0.4 m was calculated with the formula of a logarithmic wind profile (z_0 = 0.02 m) and the maximum gust by calculating mean wind speed at 0.4 m with gust factor G (=1.6) (*top*) and cumulative percentages of time for wind speeds greater than 2 to 30 m/s between July and October (based on hourly means of two-months periods) (*bottom*). Dash means calculation of wind speed not permitted, 1:10 means a frequency of once every 10 years; 1:25 once every 25 years; 1:200 once every 200 years. (Source: Wieringa and Rijkoort 1983).

HEIGHT (m)	**WIND SPEED (m/s)**							
10	2	6	10	14	18	22	26	30
0.4	-	-	4.8	6.7	8.7	10.6	12.5	14.5
U_{max} at 0.4 m	-	-	7.7	10.8	13.9	17.0	20.0	23.1
PERIOD	**CUMULATIVE FREQUENCY (%)**							
July/August	88	34	5	0.2	0.01	1:10	1:25	1:200
September/October	86	36	7	0.9	0.05	1:10	1:25	1:200

Dispersal experiment

The regression analyses of the dispersal experiment in the wind tunnel showed that the best model across all species consisted of three terms including wind speed (V, V*V) and the interaction between wind speed

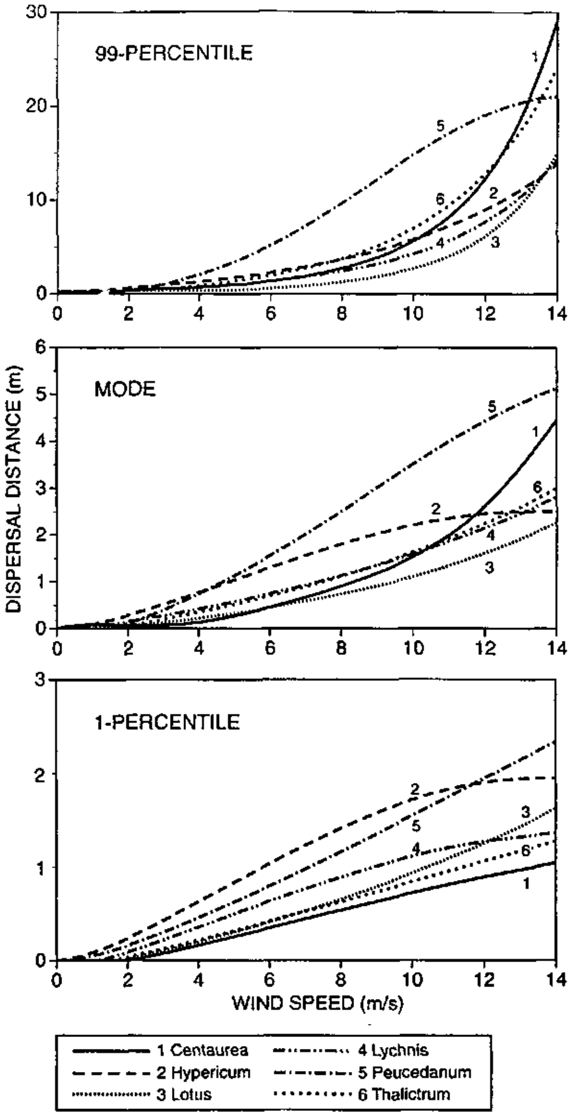


Figure 3. Relation between wind speed (m/s) and dispersal distance (m) for 1-percentile, mode and 99-percentile. Distances were calculated for a release height of 0.4 m with the regression models of the six selected species.

and release height (V*H) (Table 3). The fixed model showed higher percentages of explained variance in the parameters 1-percentile, mode and 99-percentile than the models with other combinations of terms. Generally, the models indicate that the dispersal distances of individual seeds were statistically significantly and positively correlated with wind speed (Figure 3). The effect of release height (H) on the dispersal distances consisted of a positive interaction with wind speed (Figure 4); there was no overall statistically significant effect of release height per se.

The models were used to calculate the dispersal distances at a release height of 0.4 m. The distance at which 1 percent of all seeds was deposited increased approximately linearly in all species (except in *Hypericum*) with wind speed. At wind speeds between 10 and 14 m/s hardly any seeds will be deposited less than 1 to 2.5 m from the point of release (Figure 3). For the 99-percentile, the rate of increase of dispersal distance with wind speed was even exponential, because of a strong quadratic effect of wind speed (V*V) (Figure 3). The distances at which most of the seeds (mode) was deposited increased linearly to slightly exponentially (except in *Hypericum*) (Figure 3). The values of coeffient b_2 (indicating the strength of the quadratic effect of wind speed) increased from negative values for the 1-percentile to positive values for the 99-percentile (Table 3). The ranges between the 1- and 99-percentile distances also increased exponentially with wind speed, indicating that the frequency distributions of dispersal distances became more right-skewed, thus with longer tails.

The differences between species in their dispersal behaviour were very pronounced in the tail of the frequency distribution at the highest wind speeds (Figure 3). At wind speeds of 14 m/s, predicted maximum distances are 10 to 15 m for small and relatively heavy spherical seeds (*H. quadrangulum, L. uliginosus* and *L. flos-cuculi*) and 20 to 30 m for large and relatively light cylindrical or disk-like seeds (*C. jacea, P. palustre* and *T. flavum*). Interestingly, the disk-like *Peucedanum* seeds travelled farther than all other seed forms at all wind speeds, except at the strongest wind speed of 14 m/s.

The time that shed seeds remained airborne in the wind tunnel can be estimated by dividing the distance travelled (m) by the constant wind speed (m/s). The flight time (s) of seeds released in a single trial were far from constant and varied one to two orders of magnitude, between 0.05 and 2 s. Most of the seeds in the trials were airborne for only 0.1 to 0.3 s. Only at wind speeds of 10 and 14 m/s did some seeds exceed the calculated flight times of 1 s.

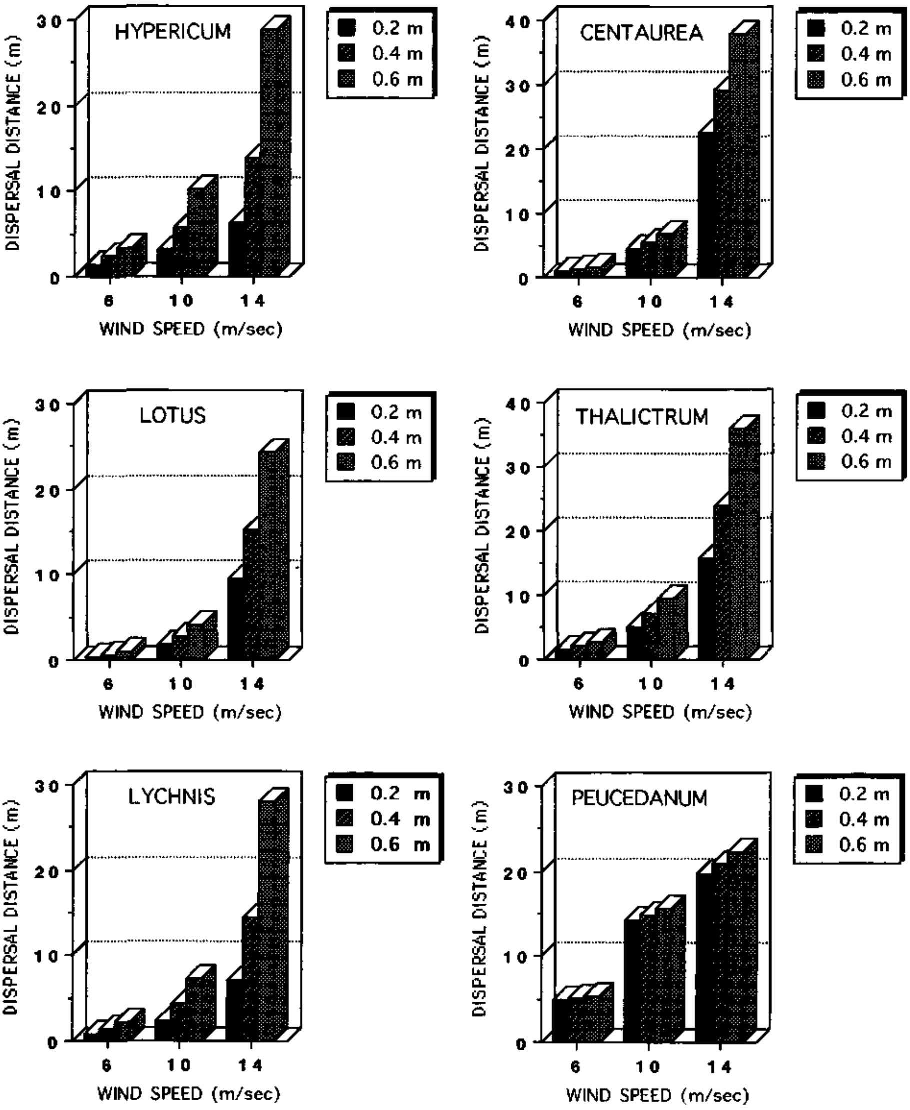


Figure 4. Effect of release height on the dispersal distance (m) for wind speeds of 6, 10 and 14 m/s. Distances were calculated with the regression models for the 99-percentile.

Table 3. Regression models per species for 1-percentile, mode and 99-percentile of the cumulative frequency distribution of dispersal distances. The coefficients of the fixed model are b_0, b_1, b_2 and b_3: $\log(Y+1) = b_0 + b_1.V + b_2.V^2 + b_3.H*V$. Note that in the regression models the unit of wind speed V is m/s and release height H is cm. Significance levels of the coefficients are * p<0.05, ** p<0.01, *** p<0.001.

1-percentile	b_0	b_1	b_2	b_3	R^2	F	P
H. quadrangulum	-0.114	0.100**	0.0065**	0.0019***	.956	51.6	<0.0001
L. flos-cuculi	-0.172***	0.078***	-0.0046***	0.0015***	.995	497.1	<0.0001
L. uliginosus	-0.143*	0.042	-0.0002	0.0010**	.979	110.4	<0.0001
T. flavum	-0.133	0.061	-0.0015	0.0007	.909	23.3	<0.0005
C. jacea	-0.202	0.036	-0.0022	0.0015**	.936	34.7	<0.0001
P. palustre	-0.099	0.057	-0.0026	0.0018*	.846	12.9	<0.0001

mode	b_0	b_1	b_2	b_3	R^2	F	P
H. quadrangulum	- 0.142	0.125**	-0.0078**	0.0021**	.975	92.1	<0.0001
L. flos-cuculi	-0.075	0.040	-0.0005	0.0017***	.959	80.1	<0.0001
L. uliginosus	-0.085	0.020	0.0019	0.0011***	.982	131.5	<0.0001
T. flavum	-0.178*	0.082**	-0.0007	0.0010**	.984	151.7	<0.0005
C. jacea	-0.010	-0.028	0.0070*	0.0013*	.927	83.0	<0.0001
P. palustre	-0.414**	0.238***	-0.0082**	0.0009*	.988	192.5	<0.0001

99-percentile	b_0	b_1	b_2	b_3	R^2	F	P
H. quadrangulum	0.169	0.061	0.0014	0.0025***	.978	104.7	<0.0001
L. flos-cuculi	0.166	-0.026	0.0084	0.0023*	.927	29.6	<0.0001
L. uliginosus	0.399	-0.170	0.0197**	0.0016	.951	45.4	<0.0001
T. flavum	-0.121	0.117	0.0047**	0.0014	.983	34.8	<0.0005
C. jacea	0.235	-0.023	0.0153	0.0009	.937	141.1	<0.0001
P. palustre	-0.726**	0.531***	-0.0190***	0.0002	.978	104.5	<0.0001

DISCUSSION

In this study, thousands of seeds were released in a wind tunnel to establish the effects of wind speed and release height on the dispersal distances of seeds of six barochorous perennial meadow species. Although these seeds lack specific adaptations to wind dispersal, most were dispersed up to several metres and a small proportion unexpectedly travelled more than ten metres. Extrapolations with the regression models suggest that the dispersal distances of seeds in the tail of frequency distribution (99-percentile) increase exponentially up to tens of metres under stormy conditions with winds stronger than 14 m/s. Such predicted distances are obviously much longer than the dispersal distances determined by short-term field studies which trap seeds up to 2 to 5 m from their source (e.g. Verkaar et al. 1983). Clearly, strong winds at the height of an average infructescence (0.4 m) are not very frequent during the dispersal season. But, the significance of extreme wind gusts for the seed dispersal in perennial plant species which live up to several decades should not be underestimated. The wind tunnel experiment also demonstrated substantial and ecologically significant variation in the dispersal distances of seeds *within trials* and *between species*. This variation will be elucidated first.

variation within a trial

The seeds released during the trials were not deposited as one clump of seeds but in various degrees of scatter. The variation in dispersal distances of seeds within a single trial was clearly expressed by the 99-percentile and 1-percentile distances (Figure 3). The mean ratio of the estimated 99-percentile and 1-percentile distances for the six selected species at a wind speed of 4 m/s was 3 (1.0 m versus 0.3 m; i.e. 98% of the seeds were deposited at distances between 0.3 m and 1.0 m from the point of release); at a wind speed of 14 m/s the ratio increased to 12 (19.6 m versus 1.6 m; i.e. 98% between 1.6 m and 19.6 m). The principal factors which could have contributed to the observed variation in dispersal distances were variation in wind speeds (*turbulence*) in the wind tunnel due to the experimental set-up and variation in the aerodynamic properties of seeds.

If the seeds released in the wind tunnel all had identical seed attributes, then the apparent variation in dispersal distances could have been caused entirely by the variation in horizontal wind speed. Since no significant variation in wind speeds was detected with Pitot tubes (van den Hoek *unpubl. data*), we assumed that the degree of variation in horizontal wind speed (*turbulence*) in the wind tunnel was actually very small. Furthermore, the seeds released are relatively heavy particles with terminal velocities higher than 10 cm/s and less sensitive to slight turbulence in a wind tunnel than e.g. spores or pollen (Burrows 1986; McCartney 1990). Note, however, that very small seeds were simultaneously released from the tube as very small clumps of seeds rather than as individual seeds. This method of releasing the seeds may have caused small eddies and consequently small differences in the trajectories of falling seeds. At higher wind speeds, such differences become magnified and are apparent as a wider scatter of seeds.

Measurements of important aerodynamic attributes of seeds such as the length and width of seeds and mass suggest that variation in these seed attributes contributed to the observed scatter in dispersal distances. The coefficient of variation (SD/MEAN) of the seed population used in this experiment was between 5% and 15% for length and width of seeds and more than 20% for seed mass across all six species (Table 1).

variation between species

The variation in dispersal distances between species was less than the variation within a trial (Figure 3). In fact, groups of species behaved rather similarly in the wind tunnel, despite the differences in shape and other attributes between species. In the trial with strong winds of 10 to 14 m/s, the differences between groups of species became most clear; as a group, the small and relatively heavy seeds (*Hypericum, Lychnis* and *Lotus*) showed slightly shorter dispersal than the large and relatively light seeds (*Thalictrum, Centaurea* and *Peucedanum*). The size (or diameter), mass and specific mass of seeds are important attributes in the dispersal process, as they determine the forces upon a seed during its fall (McCartney 1990).

ecological implications

The high wind speeds that occur in the field at frequencies that cannot be ignored have important ecological consequences. Four of the six selected plant species are iteroparous perennials and may produce seeds during several decades. There are no reliable data on their longevity, but the point is that during the life-time of such plant individuals strong gusts of wind are not rare during the dispersal season but are actually rather frequent. The probability that reproducing plants will take advantage of such strong wind gusts increases with their life-span, e.g. in the case of long-range seeds colonizing remote sites. The distances over which barochorous seeds are transported by extreme winds are likely to be in the order of several tens to hundreds of metres rather than of decimetres to metres.

In the context of ecosystem restoration, it is important to investigate whether plants are able to increase the spatial dispersal of their seeds. In principle, two strategies are open to them: (i) increasing the release height of seeds and (ii) requiring stronger winds to release the seeds from the parent plant. In these scenarios, the time that seeds are airborne (*flight time*) will increase. Longer flight times imply a wider scatter of seeds and hence a greater chance for an individual seed to encounter a distant safe site.

The positive interaction in the fixed model between release height (H) and wind speed (V) suggests that there is an effect of increasing the release height (i.e. a taller fruiting stem) on the dispersal of seeds, particularly when strong winds occur. The interaction effect was weak for *Peucedanum* seeds but relatively strong for *Hypericum* seeds. In the field, the infructescences of the selected species are usually borne at greater heights than the release heights used in this experiment (Table 1). Some plants have stems more than one metre tall, but yet they protrude above the canopy of a grassland by only 0.2 to 0.6 metre. A taller infructescence thus means that more seeds will be distributed by wind over a larger area around the parent plant, especially under strong wind conditions. Seeds released from stems shorter than the canopy are likely to be intercepted instantly by the surrounding vegetation and are not transported by the wind. In the latter case, seed will remain close to its source unless other secondary dispersal mechanisms are operating.

From the regression models it can also be deduced that seeds will have wider dispersal if greater minimal wind speeds are required to release the seeds from the parent plant. As far as we know, no data are available on the variability of minimal release speeds among plant species, within plant populations, or during the dispersal season of an individual plant. In five of the selected plant species, a minimal wind speed is necessary to release seeds (i.e. to catapult seeds from open capsules on swaying stems of *Centaurea, Hypericum* and *Lychnis,* and to disrupt the connection between seed and infructescence as in *Peucedanum* and *Thalictrum*). Seeds of *Lotus* are independent of ambient wind speeds and are dispersed ballistically from dried out pods.

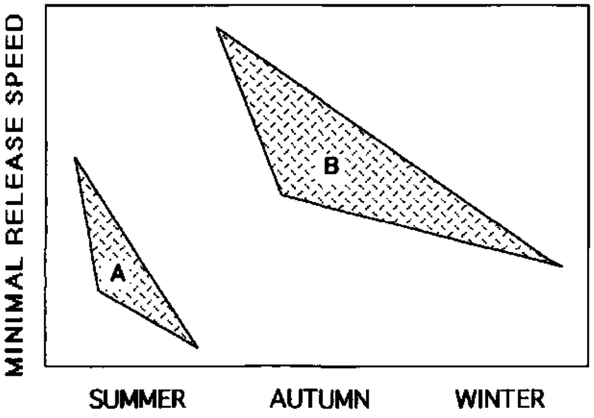


Figure 5. Time - wind speed windows for two hypothetical species. A: species dispersing seeds in summer with 'low' minimal release speeds; B: species dispersing seeds in autumn and winter over extended periods at 'high' minimal release speeds.
The sloping windows indicate that the minimal release speeds tend to decline over the dispersal period as a result of decay of the connection between seed and parent; the decline is faster in species A than in species B.

Various infructescences of *Peucedanum* containing ripe seeds were held in front of a fan. We observed that the minimal wind speeds necessary to release the ripe seeds exceeded 4.5 m/s. During the exposure at minimal release speeds, several ripe seeds remained attached to the infructescence by tiny strings, even at wind speeds of 9 m/s (van den Hoek *unpubl. results*). This connection between seed and parent deteriorates during the dispersal season as a result of decay and ensures that seed dispersal is limited in time. In their dispersal experiment, Kadereit and Leins (1988) found that several poppy species (*Papaver* spp.) started to disperse seeds at minimal wind speeds of 9 m/s. Even at peak gusts of 14 m/s some seeds were still retained in capsules. The rather tall and sturdy flowering stems of *Hypericum* often retain a fraction of the seed crop well into the winter when peak wind gusts are more frequent (van Dorp *pers. observ.*).

It can be suggested that there is a wide range of minimal release speeds depending on the strength of the connection between seed and parent plant and the shape of capsules. This range in wind speeds by which seeds are likely to be dispersed may range from say 4 to 14 m/s. It may change during the dispersal season of a species, thereby creating different "time - wind speed windows" (Figure 5). Two types of plant species may occur along this gradient. At one extreme, species A that sheds its seeds in a short period of time at a range of rather low wind speeds which results in highly localized distribution patterns of seeds around the parent plant. At the other extreme, species B has an extended dispersal period with a range of high wind speeds. In the latter species, a substantial proportion of the seed crop is dispersed far beyond the parent plant. This category of species probably includes *Hypericum spp.*, but also tree species such as *Fraxinus excelsior* which frequently retain their seeds year round.

Acknowledgements

We sincerely thank Dr. A.F.G. Jacobs (Dept. of Meteorology, Wageningen) for discussions on dispersal of seeds by wind, P. Kostense for drawing figure 3 and the DLO-Institute for Agrobiology and Soil Fertility at Haren for the permission to use their wind tunnel.

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Dehiscing fruits of the umbelliferous Peucedanum palustre

CHAPTER 4

Plant recolonization of grasslands undergoing restoration is limited by the availability of seeds and appropriate microsites

submitted to Journal of Applied Ecology

Abstract

The recolonization of former agricultural fields of grass by perennial grassland species is assumed to be delayed or even prevented by a lack of seeds, a lack of microsites offering opportunities for germination and establishment, or both. On the study site (13.2 ha) in the centre of the Netherlands, a scheme to restore species-rich meadows by restoring the shallow water table and mowing and removing the harvested biomass twice a year has been in progress since 1978. Despite these measures, sixty species of the former species-rich meadows have not yet recolonized, including ten desirable perennial grassland species which still occur on ditch banks in the surrounding agricultural landscape.

Sampling the seed rain with sticky traps recorded the deposition of seeds of resident species and ubiquitous wind-dispersed species of the genera *Betula*, *Cirsium* and *Epilobium* and the seeds of only one of the ten species selected for study (*Lychnis flos-cuculi*). Given the spatial distribution of source populations of the selected species in the surrounding agricultural landscape and the limited dispersal capacity of the selected species, the fields of the restoration site are largely inaccesssible. Lack of seeds is a major cause of their absence.

Addition of seeds revealed significantly higher establishment rates of the selected species on sod-stripped plots than on mown and clipped plots. Differences between treatments are explained by the low density and short duration of gaps in the intact (mown and clipped) vegetation. Differences between species are related to seed weight; species with large heavy seeds had significantly higher establishment rates than species with small light seeds. The lack of appropriate microsites, especially for species with small seeds, is another cause of species' absence. There are still too few appropriate microsites available because of the very fertile soil.

Recruitment from old buried seeds is another recolonization route. Burying seeds for two years revealed very low mortality rates in species with small, spherical and hard-coated seeds (*Hypericum*, *Leucanthemum*, *Lotus*, *Lychnis*, *Thalictrum* and *Viola*) and moderate mortality rates in species without special germination requirements and high area/content ratios (*Achillea*, *Centaurea*, *Cirsium* and *Peucedanum*). Species from the

first group are expected to be frequently recruited from old buried seeds during restoration that involves sod stripping.

The implications for the restoration management of species-rich meadows are discussed. More attention should be paid to spatial relations of the selected species in a landscape and to their regeneration ecology.

INTRODUCTION

The persistence of many plant species in agricultural landscapes is threatened by the isolation and fragmentation of their habitats (Bunce and Howard 1990). To stem the ongoing extinction of endangered plant species, efforts are being made to connect existing habitats and to restore former habitats on previously farmed land. During restoration, the plant species that return first recolonize either from viable seeds buried in the soil or from seeds that have immigrated from neighbouring source populations. Pioneer species with light plumed, winged or dust-type seeds and species with permanent seed banks can be expected to take particular advantage of available patches early in the restoration process (Bakker 1989). However, studies have indicated that several plant species do not rapidly recolonize available habitat patches (or "target areas"), not even after the appropriate growing conditions have been restored (Berendse et al. 1992; van Dorp and Oomes *submitted;* Chapter 1). Perennial grassland species with limited dispersal capacities are especially likely to show time lags in recolonizing those patches (Nip-van der Voort et al. 1979; Verkaar 1990; Primack and Miao 1992). Two hypotheses can be advanced to explain their absence from apparently suitable habitat patches.

The first hypothesis is concerned with the *accessibility* of patches to plant species. It states that seeds do not reach the patch because of their limited dispersal capacity and the large distances between source populations and target areas. The availability of seeds is then the factor limiting a species' distribution in the landscape. The accessibility of target areas can be increased by restoring their habitats and by providing corridors to facilitate the immigration of plant species. The second hypothesis is concerned with the *suitability* of patches to the deposited seeds. It states that seeds reach the patch, but do not germinate and establish because of a lack of appropriate microsites. It can be assumed that the structure of the vegetation is one of the most important factors affecting site suitability. It controls the availability of microsites as it creates gradients in temperature, light intensity and light quality (Silvertown 1980). Restoration of the former hydrological conditions or the management of the vegetation may increase the availability of appropriate microsites.

These two hypotheses concerning the absence of plant species were tested in an experimental grassland site in the centre of the Netherlands. The study site has been undergoing restoration since 1978 and is presumed to be suitable for the establishment of species characteristic of wet and infertile habitats. Ten perennial grassland species that were common on the former species-rich meadows were selected for this study. At the start of the investigation, they were absent from the fields undergoing restoration but still present on the banks of the ditches that typically delimit the flat fields in the surrounding farmed landscape. In this study, I investigated whether the absence of the selected species was due to a lack of seeds, a lack of suitable microsites, or both. The following observations and experiments were carried out:

- to test the accessibility hypothesis, the seed rain on the experimental field was sampled with sticky traps and the results were compared with theoretically derived deposition rates based on the dispersal capacity and the size and location of seed sources of the selected species.
- to test the suitability of the field for establishment, seeds of the selected species were added to small plots that showed large differences in the availability of microsites. To create such differences, the vegetation of the plots had been manipulated by: (i) mowing and removing the harvested biomass (this represents the standard treatment for the restoration site), (ii) by frequent clipping which reduced the above-ground competition, and (iii) by stripping the sod, to leave the soil bare.

Dispersed seeds may remain buried in the soil for some time and, depending on the dormancy patterns of species, will germinate after small-scale disturbances have created the appropriate microsites. To check the recruitment of the selected species from naturally buried seeds, I recorded the emergence of seedlings on the sod-stripped plots. To assess the ability of seeds to wait in the soil for the appearance of appropriate microsites, I carried out an experiment in which I buried seeds in the soil in order to obtain an estimate of the depletion rate of viable seeds in the soil.

MATERIAL and METHODS

Study site

The experiments and observations were done on the *Veenkampen* experimental grassland site (13.2 ha) near Wageningen, the Netherlands (51^0 54' N; 5^0 38' E). This site is situated in the centre of the *Binnenveld* valley, a clay-on-peat area between two glacial ridges. Extensive species-rich hay-meadows with several orchid species were present in the valley until 1950, when most meadows were drained, fertilized and used intensively for pasture. The fields became species-poor and inhospitable for the pre-1950 flora, but their enclosing ditch banks still function as refugia for some of the ousted plant species, which include the ten species selected for this research. Ditch banks are heavily stressed environments because of frequent spraying of herbicides, spill-over of inorganic fertilizers, overgrazing and trampling by cattle and mulching (van Dorp and van Oeveren *submitted*; Chapter 2).

After 1978, the intensive use of the Veenkampen fields ceased; fertilizer application was stopped and vegetation management changed to mowing and removing the harvested biomass twice a year in June and September. In addition, the groundwater levels of the fields were raised artificially in 1985 by pumping up deep groundwater and by conserving the rain water. The annual primary production of these fields fell from 12 ton of dry matter/ha in 1978 to 7 ton/ha in 1990 (Oomes 1991). The present management of the experimental site aims at the restoration of wet and unfertile growing conditions which enhance the recolonization of typical meadow species, including the ten selected plant species. The experiments were conducted on a wet grassland (1.3 ha) with a clay-on-peat soil that has not been ploughed or reseeded as far is known.

Plant species

The following ten species were selected for this study: *Achillea ptarmica, Centaurea jacea, Cirsium palustre, Hypericum quadrangulum, Leucanthemum vulgare, Lotus uliginosus, Lychnis flos-cuculi, Peucedanum palustre, Thalictrum flavum* and *Viola persicifolia*. They were selected from a total of sixty plant species present in the former hay-meadows before 1950 (D.M. de Vries *unpubl. data*). Detailed mapping in 1990 showed that the selected species had reproducing populations at distances of less than 1 km from the Veenkampen. Three species, *Hypericum quadrangulum, Lotus uliginosus* and *Lychnis flos-cuculi* had reproducing populations on the ditch banks bordering the experimental field. Since 1990, the early summer flowering *Lychnis flos-cuculi* was the only selected species that had successfully recolonized the Veenkampen fields (van Dorp and van Oeveren *submitted*; Chapter 2).

The selected species achieve good dispersal of their seed after mid June, i.e. after the first hay-cut. Dispersal is generally restricted to a few metres from the parent plant, since all but one of the selected species lack specific adaptations to long-distance dispersal by wind, water or animals (van Dorp and Oomes *submitted*; Chapter 1). The exception is *Cirsium palustre*, a wind-dispersed monocarpic thistle which produces numerous plumed seeds that are dispersed up to thirty metres from the parent plant (van Leeuwen 1987).

Seed rain measurement

The arrival of seeds of the selected species was recorded by sampling the seed rain on the experimental field for 77 days from June 27 until September 11 in 1990. Sixty sticky traps with a diameter of 14 cm were arranged in six parallel transects each containing ten traps spaced 1 m apart; three transects were placed in a patch dominated by various grass species (patch 1) and three transects in a patch dominated by *Juncus conglomeratus* and *J. effusus* (patch 2). The two patches were 50 m apart. The traps were 15 cm above the ground, so that only wind-dispersed seeds would be trapped. The traps had a sampling area of 154 cm^2 and were inspected every week; the trapped seeds were removed and identified when possible. Distances from the traps to the three nearest reproducing populations of the selected species were derived from the 1990 distribution maps which covered the experimental site and the ditch banks in the surrounding landscape (van Dorp and van Oeveren *submitted*; Chapter 2).

To be able to compare the seed rain with theoretical deposition rates of seeds, information on the dispersal capacity and the location and size of seed sources of the selected species was needed. The dispersal capacity of species was expressed by α which is the rate of density attenuation with distance; values of α were based on wind tunnel experiments (van Dorp et al. *submitted*; Chapter 3), literature and estimates from field observations. The location and size of seed sources were based on the mapping results of the selected species (van Dorp and Oeveren *unpubl. data*) and gave the distance of the three nearest seed sources (m) and a coarse estimate of their seed production. The deposition rate of seeds on patch (x,y) can be estimated by multiplying P (x,y) times Q, where P (x,y) is the probability of deposition of a single seed [$P = \alpha^2 . 2\pi^{-1} . e^{(-\alpha . D)}$ is based on the dispersal capacity α and the distance D between sources and target] and Q is the number of seeds produced annually in a source (van Dorp et al. *submitted*; Chapter 5).

Seed addition experiment

Seeds of the ten selected species were collected from nearby seed sources shortly before the experiment started on 28 September 1990 and sown uniformly on plots 50 x 50 cm. On these plots, large differences in the availability of microsites had been created as a result of three different treatments imposed on the vegetation: (i) sods 5 cm thick were cut and removed in order to create a bare soil at the start of the experiment (sod-stripped), (ii) the grass was clipped at 4 cm height at 2-week intervals during the 1991 growing season (April to October) to simulate a frequently grazed sward (clipping), (iii) on the control plots the grass was cut twice a year in June and September 1991, which was the normal practice for the rest of the experimental site (mowing). Each treatment-species combination was replicated in six blocks; the total number of plots was thus 180 (10 species * 3 treatments * 6 blocks) and the total number of seeds sown 18,000 (100 seeds/plot).

Seedlings and established plants of the introduced species were counted eight months (June 1991) and twelve months (October 1991) after the seeds had been sown. A final count was done in the middle of the 1992 growing season, when the aboveground biomass of all plants (resident and introduced) were harvested simultaneously. The first such harvest (for *Lychnis flos-cuculi*) was on June 1, and the last (for *Thalictrum flavum*) was on August 10. The plants were dried at 70 °C for 16 hours and weighed. The number of established individuals and their total weight indicate the suitability of the plots for the establishment of the introduced species. The introduced plants were not permitted to disperse their seeds, so as to permit the recording of natural recolonizations of the fields in the future.

Two tests were used in the statistical analysis of the seed addition experiment. Since none of the selected species showed significant block effects, the data from the plots with the same treatment were combined per species. To test the differences in the effects of the factors treatments and species on the probability of establishment and of flowering, it was necessary to transform the data to 0 (no establishment or flowering) and 1 (plants established and flowered) because of the many zeros in order to be able to use the procedure GLM (General Linear Models) (SAS 1987). The significance of the differences in the *total weight* of the introduced species per plot were normally tested with a one-way ANOVA for separate species with the Scheffé's F-test (with α=0.05).

Longevity of seeds

The longevity of seeds in soil was determined by burying small bags of seeds at a depth of five cm in the soil of the experimental field in situ. Each bag had a mesh size of 0.1 mm and contained 50 g soil from the Veenkampen mixed thoroughly with 50 seeds of a single species. The experiment started on September 24 1990 and continued for two years. After 5, 11, 19, 24, 29, 34, 43, 48, 54, 64, 71, 78, and 104 weeks, three bags per species were exhumed and thoroughly examined for seeds. All seeds recovered were put into incubators with a regime of twelve hours light and twelve hours darkness at temperatures alternating between 12 °C and 20 °C during three weeks. All germinated seeds were removed. Seeds that had not germinated after three weeks were inspected for viability by staining with tetrazolium (Moore 1972). This yielded three categories of seeds: germinated, dormant and dead. The percentage of seeds retrieved with this method was very high; after two years 91% of the initial seeds (including dead seeds) was retrieved. It was assumed that the seeds not retrieved after exhumation could be counted as dead seeds (incl. fatal germination).

In the statistical analysis, a negative exponential model $S = S_0 10^{-gt}$ was fitted to the data to extrapolate the survival of seeds over longer time spans. In the model, S is the number of viable (i.e. germinated and dormant) seeds at time t (in weeks), S_0 the initial number of viable seeds and g the depletion rate (Murdoch and Ellis 1992).

RESULTS

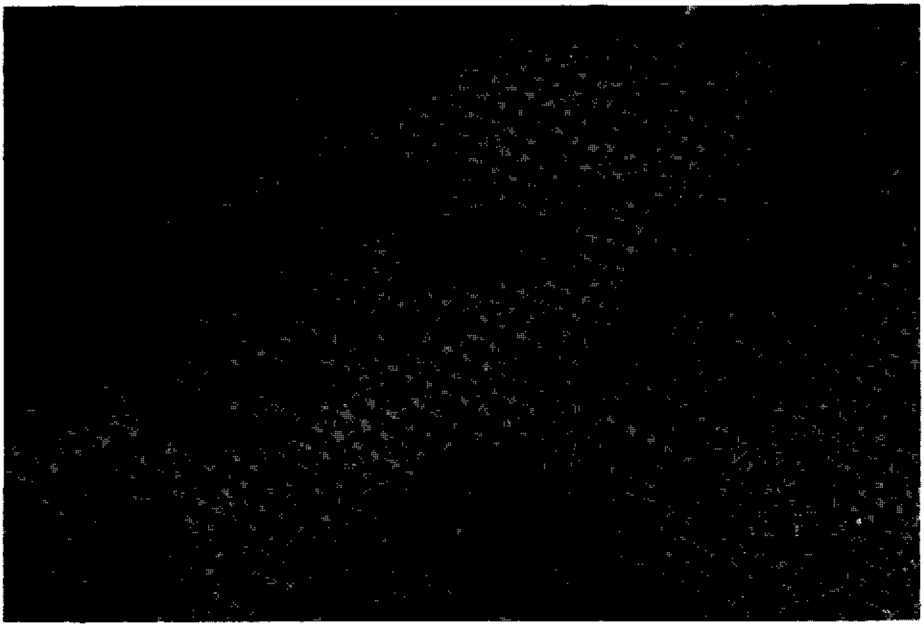
Seed rain

A total of 300 seeds was deposited on the traps between June 27 and September 11 1990 (Table 1). Seeds of only one of the ten selected species were recorded (9 seeds of *Lychnis flos-cuculi*). The nearest seed sources of *L. flos-cuculi* were within 3 m of the traps. No seeds of the other nine selected plant species were trapped. The rushes *Juncus conglomeratus* and *J. effusus* were the most abundant species, with 176 seeds (58.7%); their nearest seed sources were close (5 m and less) to the sticky traps. Eighty seeds (26.7%) belong to efficiently wind-dispersed species whose nearest seed sources were elsewhere on the Veenkampen (for *Epilobium spp.* at 15 m and for *Cirsium arvense* at 120 m upwind from the traps). The nearest seed source of *Betula spp.* was a large mixed hardwood forest at an elevation 45 m above the valley and 2.6 km southwest and also upwind from the Veenkampen. During the sampling period the deposition rate of *Betula spp.* varied between 3.0 and 3.5 seeds/week/m^2 (Table 1).

The distances of the three nearest seed sources to the traps varied between 3 m in *Lychnis flos-cuculi* and 645 m in *Viola persicifolia* (Table 2). The coarse estimates for the number of seeds in those source populations (i.e. number of plants times their seed production) vary three orders of magnitude from a thousand seeds in *Centaurea jacea* to a million seeds in *Hypericum quadrangulum.* The expected deposition rates of seeds on the experimental field (P(x,y) times Q; *see Methods*) is greater than 1 seed/m^2/year in only two species, *Lychnis flos-cuculi* and *Hypericum quadrangulum.* According to the method applied, the windborne deposition of seeds from the three nearest source populations is zero or not detectable for eight of the ten selected species (Table 2). Although *Lychnis flos-cuculi* seeds were trapped, no *Hypericum quadrangulum* seeds were trapped - probably because most of the sources in the latter species were on a ditch bank downwind from the

Table 1. Deposition of seeds (number of seeds per week/m^2) on patch 1 (with grasses) and patch 2 (with Juncus spp.) and the total number of seeds trapped on sticky traps placed in the experimental field at the Veenkampen. On each patch, 30 thirty traps of 154 cm^2 were exposed for 77 days in summer and early autumn 1990.

SPECIES	PATCH 1	PATCH 2	NUMBER OF SEEDS
Juncus conglomeratus/effusus	1.0	33.7	176
Cirsium arvense	4.3	2.4	34
Betula verrucosa/pubescens	3.0	3.5	33
Epilobium spp.	1.0	1.6	13
Lychnis flos-cuculi	0	1.8	9
not determined (no selected spp.)	2.9	4.0	35
Total number of seeds	12.2	46.9	300



Experimental field with sod-stripped, mown (tall grass) and clipped (short grass) plots

Table 2. Deposition rates of seeds of the selected plant species on the experimental field, based on the index of a species dispersal capacity α, the mean distance D of the three nearest source populations to the target field (m), the probability of deposition of a single seed $P = \alpha^2.2\pi^{-1}.e(\alpha.D)$, a coarse estimate of the number of seeds in a source Q and the expected deposition (P times Q) (*see text*). Species are listed in order of decreasing deposition probability.

Plant species	**Dispersal capacity** (α)	**Distance to target** (m)	**Deposition probability** P	**Size seed sources** (Q = number of seeds)	**Deposition of seeds** (number of seeds/m^2/ year)
L. flos-cuculi	-0.4	3	$7.7\ 10^{-3}$	10^{4}	77
H. quadrangulum	-0.4	20	$8.5\ 10^{-6}$	10^{6}	8.5
C. palustre	-0.1	85	$3.2\ 10^{-7}$	10^{5}	0.03
L. uliginosus	-2.0	10	$1.3\ 10^{-9}$	10^{4}	0
L. vulgare	-0.4	100	$1.1\ 10^{-19}$	10^{5}	0
C. jacea	-0.4	170	0	10^{3}	0
A. ptarmica	-0.4	175	0	10^{5}	0
T. flavum	-0.4	220	0	10^{5}	0
P. palustre	-0.4	635	0	10^{4}	0
V. persicifolia	-2.0	645	0	10^{4}	0

Establishment of introduced species

The seed addition experiment revealed highly statistically significant differences between treatments and between species in the probability of establishment and in the probabilityof flowering, two years after the addition of seeds. The interaction between species and treatment was not significant ($p>0.05$) (Table 3). On 93.3% of the sod-stripped plots, sowing of seeds resulted in the establishment of plants, compared with 28.3% of mown plots and 33.3% of the clipped plots. It seems that most of the sown species had difficulty establishing in the intact vegetation. The mean number of established plants per 100 sown seeds on sod-stripped plots (8.6 ± 0.8 s.e.) was significantly higher than on mown (1.1 ± 0.4 s.e.) and clipped (2.2 ± 0.7 s.e.) plots (Scheffé's F-test, $p<0.001$) (Figure 1).

Table 3. Analysis using GLM on the probability of establishment (above) and flowering (below) of the ten introduced plant species.

ESTABLISHMENT

Source	**df**	**Sum of squares**	**F-value**	**P**
Species	9	7.339	0.815	<0.0001
Treatment	2	15.833	7.917	<0.0001
Species x Treatment	18	3.611	0.201	0.0534
Error	150	18.167		

FLOWERING

Source	**df**	**Sum of squares**	**F-value**	**P**
Species	9	6.422	0.714	<0.0001
Treatment	2	13.300	6.650	<0.0001
Species x Treatment	18	5.144	0.286	<0.0001
Error	150	10.333		

The differences between these treatments were also reflected in the standing biomass of the resident species and introduced species (Table 4). The mean standing biomass at harvesting ranged from 3.9 (ton/ha) for sod-stripped plots to 5.2 and 5.4 (ton/ha) for clipped and mown plots, respectively. The relative contribution of the introduced species to the standing biomass was high for sod-stripped plots with 26.0%, but insignificant for mown and clipped plots (0.4% versus 1.6%) (Table 4).

There were also observable differences in establishment success between the selected species. *Centaurea jacea* and *Cirsium palustre* performed significantly better, while *Leucanthemum vulgare* and *Viola persicifolia* performed worse compared to all other species (Figure 1). In three species with large heavy seeds (seed weight >2 mg) *Centaurea jacea, Cirsium palustre* and *Peucedanum palustre,* the differences between treatments in the number of established plants were not significant (Scheffé's F-test, $p>0.05$). In all other species, numbers of established plants were significantly higher on sod-stripped plots than on mown or clipped plots. The differences between the treatments in the total biomass (g/m^2) of the introduced species upon harvesting confirm the results of the number of established individuals per plot. The biomass of five species was significantly higher on sod-stripped plots than on mown or clipped plots (Scheffé's F-test, $p<0.05$) (Table 5).

Table 4. Standing biomass (ton/ha) of resident and introduced plants species on plots with mowing, clipping and sod stripping as treatments (each treatment with 60 plots; figures with ± s.e.) and the minimum and maximum total standing biomass per treatment (means of 6 blocks). Signficance of differences between treatments were tested with Scheffé's F-test with $\alpha=0.05$.

CATEGORY	MOWING	CLIPPING	SOD STRIPPING
introduced	0.02^{a} ± 0.01	0.08^{a} ± 0.03	1.02^{b} ± 0.21
resident	5.41^{a} ± 0.13	5.07^{a} ± 0.14	2.90^{b} ± 0.15
all species	5.43^{a} ± 0.13	5.15^{a} ± 0.14	3.92^{b} ± 0.21

Table 5. Total biomass (g/m^2) of the selected species upon harvesting using treatment as the principal factor. For each species a separate one-factor ANOVA on total biomass was because of differences in harvesting date. Signficance of differences between treatments were tested with Scheffé's F-test with $\alpha=0.05$. Species are listed in order of increasing seed weight.

PLANT SPECIES	MOWING		CLIPPING		SOD STRIPPING	
Hypericum quadrangulum	0.01^{a}	± 0.01	0.05^{a}	± 0.04	39.0^{a}	± 22.5
Lychnis flos-cuculi	1.02^{a}	± 1.00	0.1^{a}	± 0.1	74.3^{b}	± 12.8
Achillea ptarmica	0.0^{a}	± 0	0.0^{a}	± 0	82.9^{b}	± 24.1
Leucanthemum vulgare	0.0^{a}	± 0	0.96^{a}	± 0.91	29.1^{a}	± 14.1
Lotus uliginosus	0.01^{a}	± 0.01	0.96^{a}	± 0.74	47.5^{b}	± 18.2
Viola persicifolia	0.0^{a}	± 0	0.0^{a}	± 0	0.37^{a}	± 0.20
Thalictrum flavum	0.02^{a}	± 0.01	0.01^{a}	± 0.01	1.83^{a}	± 0.90
Cirsium palustre	7.35^{a}	± 2.43	44.5^{a}	± 14.3	289.6^{b}	± 80.9
Centaurea jacea	15.5^{a}	± 10.4	34.5^{a}	± 20.4	421.1^{b}	± 79.3
Peucedanum palustre	0.52^{a}	± 0.45	2.35^{a}	± 2.35	37.6^{a}	± 25.9

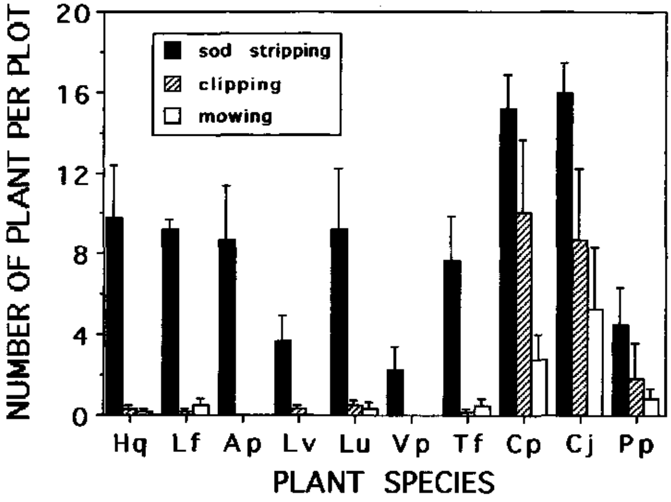


Figure 1. Mean number of established plants per plot (0.25 m^2) for the treatments mowing, clipping and sod stripping. The established individual plants were harvested two years after 100 seeds had been sown on each plot (50 x 50 cm). Species are listed in order of increasing seed weight. Vertical bars are the s.e. bars for six plots.

The recruitment of the selected species from naturally buried seeds was specifically scored on the sod-stripped plots of the seed addition experiment. In three of the 60 sod-stripped plots (5.0%), one seedling of three selected species (*Achillea ptarmica, Hypericum quadrangulum* and *Viola persicifolia*) was recorded on plots where no seeds of these species had been sown (*alien species*). The *Viola* seedling was recorded in the first growing season only. The latter two seedlings survived as vegetative adults until harvesting. No *alien* plants were recorded on clipped and mown plots.

Longevity of buried seeds

After two years of burial in soil, seed mortality was greater than 50% in only two plant species, *Achillea ptarmica* and *Peucedanum palustre*. In the other eight species, seed mortality was much lower (Figure 2). In four species (*Cirsium palustre, Lotus uliginosus, Thalictrum flavum* and *Viola persicifolia*), the regression coefficient of the negative exponential model did not significantly deviate from zero (F-tests, $p > 0.05$) (Table 6).

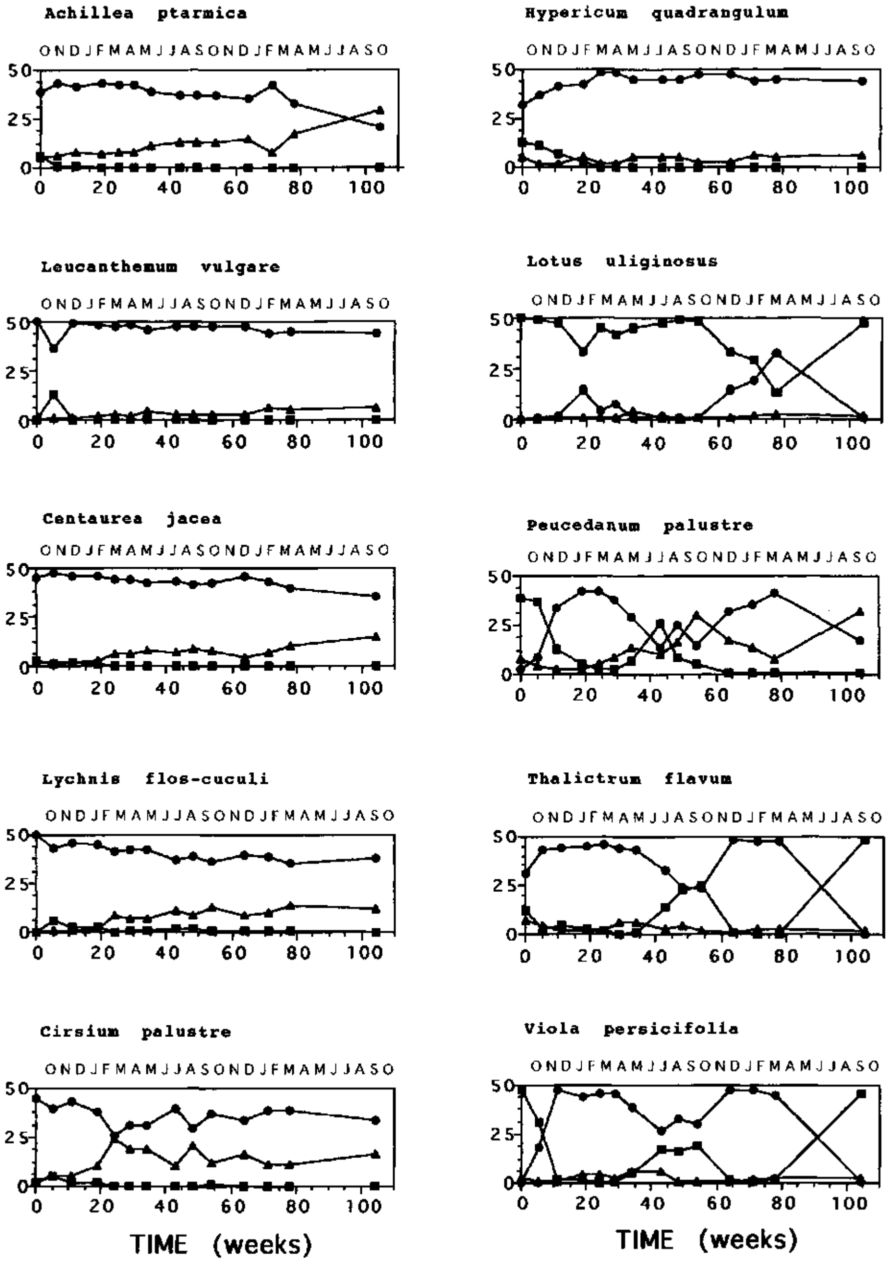


Figure 2. Number of seeds of the selected species that were dormant (squares), germinated (dots) or dead (triangles) upon exhumation after being buried in the Veenkampen soil for periods up to two years. Values are means of three batches per exhumation per species.

The last three species have hard seed coats and/or dormancy cycles (Figure 2). This finding indicated that the seed burial experiment was too short to detect a change in seed viability in those species. In the remaining six species the models were significant. If we assume a constant rate of decline in seed viability, then the time required to reduce the density of viable seeds in this grassland by a factor 10^5 (e.g. from 10 seeds m^{-2} to 1 seed ha^{-1}) can be calculated. In the absence of soil invertebrates larger than 0.1 mm, the seeds of these perennial grassland species are capable of surviving in soil at a depth of 5 cm for up to several decades. To reduce the density of buried seeds in a field by a factor 10^5 would take 32 years for *Peucedanum palustre* and 281 years for *Hypericum quadrangulum*.

Table 6. Regression models showing the decline of the number of viable seeds with time (in weeks) using the general model of $S= S_0 10^{-gt}$, where S is the number of viable seeds at time t (t in weeks) and S_0 the initial number of viable seeds and g the depletion rate. Models are based on the data of the seed burial experiment (n=13 exhumation periods plus a control at t=0). Species are listed in order of increasing seed depletion rate.

SPECIES	MODEL	R^2	P
Viola persicifolia	$S = 47 * 10^{(2.9\ 10^{-5} t)}$	0.003	n.s.
Thalictrum flavum	$S = 46 * 10^{(2.5\ 10^{-4} t)}$	0.186	n.s.
Lotus uliginosus	$S = 49 * 10^{(-1.6\ 10^{-4} t)}$	0.222	n.s.
Hypericum quadrangulum	$S = 47 * 10^{(-2.5\ 10^{-4} t)}$	0.266	$p<0.05$
Leucanthemum vulgare	$S = 49 * 10^{(-5.0\ 10^{-4} t)}$	0.812	$p<0.01$
Cirsium palustre	$S = 39 * 10^{(-7.3\ 10^{-4} t)}$	0.082	n.s.
Centaurea jacea	$S = 48 * 10^{(-1.1\ 10^{-3} t)}$	0.722	$p<0.01$
Lychnis flos-cuculi	$S = 48 * 10^{(-1.3\ 10^{-3} t)}$	0.717	$p<0.01$
Achillea ptarmica	$S = 47 * 10^{(-2.3\ 10^{-3} t)}$	0.691	$p<0.01$
Peucedanum palustre	$S = 49 * 10^{(-3.0\ 10^{-3} t)}$	0.492	$p<0.01$

DISCUSSION

The absence of plant species from a locality can be attributed in general to a lack of seeds (accessibility hypothesis), a lack of appropriate microsites (suitability hypothesis) or a combination of both factors. In the case of the Veenkampen experimental site, about sixty plant species that used to be present on the former species-rich meadows have not recolonized the fields at this stage of the restoration process (van Dorp and Oomes *submitted*; Chapter 1). These sixty species have either become regionally extinct or are restricted to refugia on ditch banks in the surrounding farmed landscape. The ten plant species examined in this study belong to the second category. The experimental field was assumed to be suitable for the establishment of the selected species because the groundwater level had been raised, the soil had become less fertile and the species had still survived in a rather hostile environment on ditch banks. The accessibility and suitability of the experimental field will be discussed on the basis of observations and results of the experiments in order to explain this absence.

Site accessibility

The seed rain measurements detected the seeds of only one of the ten selected plant species, *Lychnis flos-cuculi*, an early reproducing perennial species with seed sources close to the traps. The seed rain was dominated instead by local resident species (*Juncus spp.*) and ubiquitous wind-dispersed pioneer species of the genera *Betula, Cirsium* and *Epilobium*. These species have a great dispersal capacity (low values of α), occur at short distances upwind from the experimental field (low values of D) and/or have large populations producing huge quantities of seed (high values of Q). These characteristics are in sharp contrast with those of the selected plant species.

According to the 1990 mapping of the selected species, in all but three species the distances to nearest source populations of the selected species were several tens to hundreds of metres. Moreover, the estimated number of seeds produced annually in these populations were usually less than 10^6 seeds. Given these constraints, the limited dispersal capacity of the barochorous species and the sampling technique used, it would have been extremely unlikely to trap any wind-dispersed seeds of *Achillea ptarmica, Centaurea jacea, Cirsium palustre, Leucanthemum vulgare, Peucedanum palustre, Thalictrum flavum* or *Viola persicifolia.*

From this it can be inferred that the Veenkampen fields are largely inaccessible to seeds from source populations of the selected species. The present situation of negligible direct input of wind-dispersed seeds is probably also valid for several other desirable meadow species in the surrounding agricultural landscape.

However, it cannot be ruled out that seeds reached the field via another dispersal vector than wind and remained undetected. Several mechanisms may have operated, including a directed dispersal of seeds by birds (Howe and Smallwood 1982). This mechanism is suggested by the observation of a *Hypericum quadrangulum* seedling that was recorded on a sod-stripped plot where the species had *not* been deliberately sown. This seedling may have originated from a seed secondarily dispersed by birds. Starlings (*Sturnus vulgaris*) were observed foraging extensively on the recently exposed sod-stripped plots shortly after the seeds had been added to these plots (van Dorp *pers. observ.*). Very small light seeds like those of *Hypericum quadrangulum* may easily stick to birds' feet or feathers and be transported over tens to hundreds of metres to other denuded patches (Ridley 1930). I also found bird droppings containing seeds of the bird-dispersed shrub *Sambucus nigra* on these same plots. Another possibility is that the seedling emerged from a seed deposited by strong wind gusts and had been buried in the soil seed bank before being activated by the removal of the sod.

Recruitment from the soil seed bank

If the dispersal of seeds from various source populations to a target area is not a very likely event, another route is the recruitment from old seeds that were buried at the time of the former meadows. The seed burial experiment indicated that in the absence of seed predators larger than 0.1 mm, in most species the decline in seed viability proceeded (very) slowly over the two-year period (Table 3). This observation suggests that once seeds have entered deeper soil layers, several decades may be required before a soil seed bank from an undisturbed soil has been depleted completely. Seeds of the selected species, *Hypericum quadrangulum, Leucanthemum vulgare, Lotus uliginosus, Lychnis flos-cuculi, Thalictrum flavum* and *Viola persicifolia* are likely to have been transported vertically to deeper soil layers by rain through soil cracks and the tunnels of earthworms. These species have small, spherical and hard-coated seeds, show dormancy cycles and are probably less vulnerable to attacks by pathogens and seed predators than species with seeds with high area/content ratios (Crawley 1992). They may thus have formed the persistent seed banks in the soils of the former species-rich meadows which have become a vital asset in the restoration process. The selected species that would have failed to have seeds in the soil seed bank include those without special germination requirements and with high area/content ratios, such as *Achillea ptarmica, Centaurea jacea, Cirsium palustre* and *Peucedanum palustre.*

The following observations from the Veenkampen also suggest that recruitment of meadow species from old buried seeds can be stimulated by sod stripping. Altena and Oomes (*unpubl. data*) recorded the reappearance of several meadow species soon after sod stripping in 1985. These species included regionally rare species such as *Viola persicifolia,* a national Red List species, *Gentiana pneumonanthe* and sedges such as *Carex hostiana, C. pallescens, C. panicea* and *C. oederi* (van Dorp and Oomes *submitted;* Chapter 1). These species were abundant in the former species-rich meadows according to the data collected by D.M. de Vries (*unpubl. data*) before 1950. It is very likely that they were recruited from a soil seed bank that had been formed before 1950. Such buried seeds may thus have survived four decades of intensive agricultural management. Seed dispersal by e.g. birds is very unlikely, since these plant species are extremely scarce in the surrounding landscape. Other, more common species in the agricultural landscape that probably also reappeared through recruitment from the soil seed bank include *Ajuga reptans, Lychnis flos-cuculi* and *Thalictrum flavum.*

Site suitability

When immigration is unlikely and seed banks have been depleted by agricultural activities, the last resort and direct test of the suitablility of the patch is to introduce seeds. The seed addition experiment showed that species with large heavy seeds (*Centaurea jacea, Cirsium palustre, Peucedanum palustre* and perhaps *Thalictrum flavum*) have a higher probability of establishing successfully in the intact vegetation (whether mown or clipped) than species with small light seeds. The latter type of species obviously demanded large gaps (> 0.01 m^2) in the vegetation to establish. Such gaps in the vegetation are a prerequisite for their establishment (Fenner 1985) but occurred in low densities and were only temporarily available in the mown and clipped vegetation of the experimental field. Consequently, the probability of a dispersed seed landing on an appropriate microsite is extremely small and therefore a much larger number of seeds would be required to secure establishment.

The sod-stripped plots provided the appropriate growing conditions for all species as they were void of vegetation at the start of the experiment. After two growing seasons, the standing biomass of sod-stripped plots had rapidly increased to 73% and 76% of the standing biomass of mown and clipped plots respectively. Again, heavy-seeded species such as *Centaurea jacea* and *Cirsium palustre* performed better than the light-seeded species. Their seeds germinated in early spring 1991 and new recruits were able to outcompete the resident species or suppress the regrowth of stoloniferous grasses and herbs. Gradually, these plots became revegetated by a mixture of plants of resident and introduced species. On the clipped and mown plots, the establishment success of the introduced species was significantly smaller than on sod-stripped plots. The below-ground competition for water and nutrients between resident and introduced species in the mown grasslands may have been more severe than the above-ground competition for light. In a few years, the sod-stripped plots will be completely revegetated and 'closed' again for colonizing plant species until another disturbance takes place.

Implications for restoration

To restore the former species-rich meadows, it is necessary to improve both the *accessibility* and *suitability* of the Veenkampen fields. To improve the accessibility, we can increase the size of seed sources (Q) and/or decrease the distances to the nearest source populations (D). The option of increasing the size of local source populations can be pursued by mowing less frequently and delaying the onset of mowing (Smith 1990). This will increase the probability of seeds being dispersed to distant patches by agents such as birds and mammals. Even the role of water as a dispersal agent could be reactivated, because several meadow species have buoyant seeds that will float on water for several weeks to months (Ridley 1930; Bulle et al. 1994). If these measures all prove to be inadequate, deliberate reintroduction of seeds should be considered, to allow more populations to establish (Primack and Miao 1992).

This study was too short to accurately predict whether the introduced species would have persisted as adult individuals in the longer term or be replaced by more competitive plant species. Whether this will happen depends to a large extent on the soil fertility and the frequency of small-scale disturbances caused by grazing herbivores and small mammals such as moles and mice. The initial decrease in annual yields from 12 to 7 ton/ha on the Veenkampen fields was realized early in the restoration process. But after five years yields had stabilized at 7 ton/ha under a management of restoring the high water table and mowing and removing the harvested biomass twice a year. A further reduction to 5 ton/ha is required but it is uncertain whether this is attainable, given the large buffer of organic nitrogen in the soil and the heavy atmospheric deposition of nitrogen compounds (c. 60 kg N/ha/year). It may thus be difficult to restore the wet nutrient-poor conditions necessary for the establishment of many characteristic meadow species.

Conclusion

The study by Berendse et al. (1992) indicated that restoration of boundary conditions such as a low soil fertility and high soil moisture content is not easy to achieve and is above all no guarantee for the return of many desirable meadow species. The present study specifically showed that the absence of many plant species on a site undergoing restoration can be caused by a site's isolated postion in the landscape and by an insufficient habitat quality. Such a combination of factors prohibiting a successful restoration has not yet received the necessary attention from conservationists. It is also important to understand the regeneration ecology of the endangered plant species in order to know under which conditions a deliberate introduction of species will be both unavoidable and successful.

Acknowledgements

I sincerely thank the assistance of F. van den Berg, J. Blijenberg, M. Dannenburg, H. van Oeveren, H. Rap and I. Raemakers in the field and M. Lechowitz for his advice on statistical matters.

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CHAPTER 5

Migration rates of grassland plants along corridors in fragmented landscapes assessed with a cellular automaton model

with P. Schippers and J. M. van Groenendael
submitted to Landscape Ecology

Abstract

This study investigated the efficacy of linear landscape elements in fragmented landscapes as corridors for perennial grassland species with short-range dispersal of seeds. Corridors are essential for the persistence of metapopulations in fragmented landscapes, but it is unclear to what extent linear landscape elements such as ditch banks and road verges can function as corridors for those species. The principal factors that determine the rate of migration through corridors include the width and habitat quality of patches within a corridor (expressed as the population growth rate λ) and the dispersal capacity of plants (expressed as the slope α of the relationship between seed number and log-distance).

A cellular automaton model was used to simulate the effects of the principal factors on the rate of migration of imaginary species. Simulations with different levels of the principal factors were carried out and results indicated highly significant and positive main effects of dispersal capacity, habitat quality and width of corridors on the migration rate. Significant interactions existed between dispersal capacity x width and dispersal capacity x habitat quality ($p<0.0001$), indicating that the effects of width and habitat quality depended on the dispersal capacity. In narrow corridors, most of the dispersed seeds were deposited outside the corridor which significantly reduced migration rates, especially for species with long-range dispersal. In wide corridors (up to 20 m), seed losses were much smaller and migration rates approximated those of continuous habitats. The contribution of the few long-range dispersed seeds to the rate of migration was significant when habitat quality was high (i.e. population growth rates of 2.5). However, in all simulations migration rates were very low and less than 5 m/yr.

It is concluded that linear landscape elements are not effective corridors in fragmented landscapes for plants with short-range seed dispersal, because migration rates are low, landscape elements vary in the percentage of high quality patches, and refugia and suitable habitat patches are frequently several kilometres apart, making a cohesive infrastructure of corridors for plants elusive. It is argued that the best way to conserve endangered plant species that encounter dispersal barriers is to harvest seeds

from nearby source populations and introduce them at suitable habitats.

INTRODUCTION

The opportunities for wild plant species to persist in modern agricultural landscapes have declined sharply during this century (Falk 1992). Their original, widespread habitats have been fragmented into many small and isolated patches surrounded by uninhabitable farmed fields (Bunce and Howard 1990). In the Netherlands, the habitat quality of these remnant patches has deteriorated because of increasing eutrophication and acidification and falling water tables (Vos and Zonneveld 1993).

The plant species that disperse seeds over short distances are assumed to be particularly vulnerable to habitat fragmentation (Verkaar 1990). Such species with a short-range seed dispersal are unlikely to recolonize restored ecosystems, for two reasons. Firstly, seeds are dispersed up to several metres from the parent plant, with only very few seeds being deposited beyond this distance. Yet, these few long-range seeds may in fact recolonize the more remote habitat patches (Leishman et al. 1992). Secondly, the distances between habitat patches are usually many times the modal dispersal distance of seeds. A possible consequence of this limited recolonization capacity is that local extinction rates in occupied patches become greater than recolonization rates of empty patches and eventually the species dies out.

The measures used to increase the persistence of such plant species in fragmented landscapes include the conservation of the remaining core areas, the restoration of ecosystems on former agricultural land and the establishment of ecological corridors between core areas and restored habitats. In this study, we focused on the role of corridors as migration routes in fragmented landscapes and on the factors which determine the rate of migration by plants.

Corridors have been advocated by several authors because they would facilitate the interactions between spatially segregated populations, especially of animals and promote the recolonization of suitable patches by allowing a stepwise migration (Merriam 1984; Saunders and Hobbs 1991; Vermeulen 1994). The faster the organisms migrate through corridors, the greater the probability that empty patches will be recolonized and the greater the persistence of the metapopulation (Gilpin and Hanski 1991).

For plant species in fragmented landscapes, the role of linear landscape elements as corridors is not clear. Various authors have suggested that the long and narrow strips of land such as ditch banks, road verges, dikes and hedgerows in the Netherlands are potential corridors for wild plant species in agricultural landscapes (Nip-van der Voort et al. 1979; Melman et al. 1988; Verkaar 1990; Sykora et al. 1993). However, these linear elements are mostly ill-suited to function as corridors because they are usually very narrow and adversely affected by fertilizer inputs, herbicide drift, mulching and overgrazing (van Dorp and van Oeveren *submitted*; Chapter 2). In essence, landscape elements only function as corridors if they allow new plant populations to be recruited (van Groenendael and Kalkhoven 1990). Populations are likely to become established on patches where the growing conditions allow relatively high population growth rates. Given that there are large differences in the way linear landscape elements are managed, it can be expected that the percentage of such high quality habitat patches will vary considerably on the scale of an individual landscape element and in the landscape as a whole.

In the present study, the efficacy of linear landscape elements as corridors was investigated for perennial grassland species which grow on relatively fertile soils and disperse their seeds poorly. These species are fairly common in agricultural landscapes but are vulnerable to regional extinction as their habitat patches become smaller and more isolated. In such cases, they could become dependent on corridors for their persistence in agricutural landscapes. Three research questions were posed:

(i) How do habitat quality, corridor width and the dispersal capacity of plants affect the rate of migration along linear landscape elements?

(ii) Is a threshold percentage of high quality patches required within a corridor to trigger migration?

(iii) Do the few seeds dispersed long range contribute significantly to the rate of migration?

To answer these questions, a stochastic and spatially explicit model was constructed to simulate the migration of grassland species along corridors using actual field data to estimate the parameters of the model.

MATERIAL AND METHODS

The model

The model used is a cellular automaton model (Czárán and Bartha 1992, Silvertown et al. 1992) which treats the two major population processes, (i) the spatial dispersal of seeds from individual plants and (ii) the establishment and growth of plant populations in individual cells discretely (*see below*). The model was used to simulate the migration of plants with short-range and long-range dispersal of seeds along different types of corridors. The basic corridor was composed of grid cells measuring 1 m by 1 m which were treated as individual habitat patches. The width of a corridor was varied between 1 and 20 grid cells. The habitat quality of patches within a corridor was also varied, i.e. patches with low, medium and high population growth rates were distinguished. The model calculated migration rates (m/yr) which provided the basis for evaluating the efficacy of corridors for the species modelled. A simulation approach (*see* Fahrig 1991 for the approach) was chosen, because this allowed us to assess the significance to plant migration of very small probabilities of long-range dispersal and establishment.

I DISPERSAL OF SEEDS

Perennial grassland plants normally drop most of their seeds very close to the parent plant, with progressively fewer seeds being dispersed at increasing distances (McClanahan 1986; Willson 1992). The seed number to distance relationship can be fitted by a negative exponential function where the parameter α is the slope of the curve and reflects the seed dispersal capacity of a species. The shallower the slope, the further seeds are deposited from the seed source and the greater the dispersal capacity.

The pattern of seed deposition (*seed shadow*) around the periphery of the parent plant can be examined by mathematically integrating the area under the dispersal curve and then rotating it through 360° around the parent plant (Werner 1975). The resulting probability function per unit area is,

$$P(x,y) = \frac{\alpha^2}{2\pi} \cdot e^{\left(-\alpha \sqrt{x^2+y^2}\right)}$$

where P(x,y) is the probability of a single seed being dispersed to a grid cell at position (x,y), α the slope of the negative exponential function and $\alpha^2/2\pi$ the proportionality factor (Herben et al. 1991). This proportionality factor scales the area under the dispersal curve after mathematical integration to 1, in order to obtain the probability function. Using this probability function, the number of seeds dispersed to any grid cell (x,y) within the corridor can be calculated. Using N as the total number of dispersed seeds, the number of dispersed seeds to grid cell (x,y) from their point of release (0,0) was calculated as $N*P(x,y)$. During a simulation, the number of seeds dispersed to a grid cell, $N*P(x,y)$, was calculated deterministically if $N*P \geq 5$ [N*P seeds] and stochastically if $N*P < 5$ [0, 1, 2, 3 or 4 seeds].

II POPULATION DYNAMICS IN INDIVIDUAL CELLS

A transition matrix was used to model the growth of plant populations in individual grid cells (Van Groenendael et al. 1988). In the matrix, three different stages were distinguished: seeds (S), vegetative plants (V) and generative plants (G). Changes in the numbers of seeds and plants between years were obtained by multiplying the transition matrix by a stage vector which contained the number of seeds and/or plants in a particular year. The total number of seeds in a cell consists of seeds that are dispersed within the cell of origination and those that immigrate from other cells. The transition probabilities in the matrix were fixed at 0 and 0.4, but the number of seeds produced per plant (Q) and the probability of a seed becoming a vegetative adult (E) were varied as initial simulations indicated that the growth rate of individual populations (expressed as λ) was most sensitive to variation in precisely these two parameters Q and E (Table 1).

Table 1. Stages and transition probabilities in the transition matrix used in the simulations. The parameters seed production by generative adult plants (Q) and probability of establishment (E) were varied, all other transitions were kept constant.

STAGE	S	V	G
seed (S)	0	0	*Q*
vegetative adult (V)	*E*	0.4	0.4
generative adult (G)	0	0.4	0.4

The following set of conditions ("rules") was applied to the simulation of the population dynamics of individual cells:

- Delayed germination of seeds that survived adverse conditions (e.g. burial in the soil) was ignored P(S ⇨ S) = 0; it was assumed that the contribution of germinated seeds from the seed bank to the rate of migration was negligible.
- Germinated seeds became flowering plants in the second year following dispersal, hence P(S ⇨ G) = 0 and P(V ⇨ S) = 0; this is a common strategy of perennial grassland plants.
- Annual mortality of adult plants was set at 20%, both for vegetative (V) and generative (G) plants (p=0.2).
- Equal probability (p=0.4) of adult plants flowering or skipping flowering.
- Seed production (Q) and probability of establishment (E) decreased at a constant rate with habitat quality, thus the ratio of Q to E was made constant and independent of the population growth rate λ. The actual probability of establishment E was made linearly dependent on the number of established

plants per cell: for empty cells (no plants present) E was maximal, but for saturated cells with a maximum of 5 adult plants E was zero and cells were unavailable for additional plants. The long-term population growth rate λ of individual cells was calculated for different values of Q and E and was treated as an index of habitat quality; it forms a gradient of low (λ=0.8) to high (λ=2.5) quality patches, with three intermediate qualities (Table 2).

Table 2. Values of seed production (Q), probability of establishment (E) and calculated long-term growth rates (λ) that were used in the simulations on migration rate for corridors with five varying degrees of habitat quality ranging from low to high.

Habitat quality	**Q**	**E**	**λ**
LOW	50	0.0006	0.8
LOW-MEDIUM	333	0.004	1.2
MEDIUM	500	0.006	1.4
MEDIUM- HIGH	1000	0.012	2.0
HIGH	1500	0.018	2.5

PARAMETER ESTIMATION

dispersal capacity

Values of α (indicating the dispersal capacpity of plants) were derived from a wind tunnel experiment (van Dorp et al. *submitted;* Chapter 3), in which seeds of six perennial grassland species (all herbs) with different aerodynamic properties were released in a wind tunnel at various wind speeds (Table 3). Based on the results of this experiment, two levels for α were selected; $\alpha = -2.0$ which represents short-range dispersal of seeds up to 5 m at wind speeds of 3 to 6 m/s and $\alpha = -0.4$ which represents long-range dispersal of seeds up to 20 m at wind speeds of 6 to 10 m/s (Table 1). These two levels of α include the empirically derived values reported by Werner (1975) and Rabinowitz and Rapp (1981). Werner (1975) measured the pattern of seed dispersal in teasel *Dipsacus sylvestris* by using sticky traps up to 4 m from isolated plants and reported a value for α of -1.69. Rabinowitz and Rapp (1981) measured the seed dispersal of seven wind-dispersed prairie grass species. Linear regression of distance (m) against log-transformed number of seeds gave values for α varying between -0.47 and -1.58 for the seven grasses.

Table 3. Dispersal capacity (α) of six perennial grassland species differing in seed size (length in mm), weight (mg) and shape. Values for the parameter α were calculated for wind speeds of 3, 6 and 10 m/s using various empirical distributions of seed dispersal distances that were established in wind tunnel experiments.

	SEED ATTRIBUTE			WIND SPEED		
SPECIES	SIZE (mm)	WEIGHT (mg)	SHAPE	3 (m/s)	6	10
Lotus uliginosus	1.4	0.6	SPHERE	-8.8	-3.5	-0.6
Centaurea jacea	3.8	2.2	CYLINDER	-6.0	-1.4	-0.3
Hypericum quadrangulum	0.9	0.03	ROD	-5.5	-1.3	-0.4
Lychnis flos-cucli	1.0	0.15	SPHERE	-6.2	-0.8	-0.4
Thalictrum flavum	3.2	1.5	CYLINDER	-6.2	-0.5	-0.3
Peucedanum palustre	6.7	2.6	DISK	-3.3	-0.7	-0.2

To shorten the time needed to run a simulation, we truncated the dispersal function at 5 m for α= -2.0 and at 20 m for α= -0.4. The probability of an *individual seed* from a single source being dispersed beyond these limits becomes very small; 5.10^{-4} for α = -2.0 and 3.10^{-3} for α = -0.4. Given the range in seed production per plant (50 to 1500 seeds), the probability of an *individual cell* within the corridor and beyond these limits receiving a seed that will germinate and establish as an adult plant, was considered to be extremely small and was ignored. The effect of this truncation was addressed explicitly in a separate simulation about the contribution of long-range seeds to the rate of migration .

habitat quality

The transition probabilities and seed production values in the matrices were derived from an experimental study on the establishment of ten perennial grassland species on an experimental site near Wageningen (van Dorp *submitted*; Chapter 4). In an experiment in which seed was sown on bare soil or was sod seeded, the bare plots generally had a crop with a low biomass (< 500 g m^{-2}) after two years, a relatively high rate of establishment and high levels of reproduction of the introduced species, and are referred as *high quality* patches, whereas the plots with a closed turf generally had a crop with a high biomass (> 500 g m^{-2}), a low rate of establishment and reproduction, and are referred as *low quality* patches. The values for Q and E were derived from this study. The minimum and maximum values of both parameters vary by a factor of thirty, between 50 and 1500 seeds per plant for Q and between 0.0006 and 0.018 for E (Table 2).

width

Linear landscape elements in farmed landscapes in the Netherlands are usually narrow. In a sample of 90 ditch banks near Wageningen, the width (i.e. the stretch of the sloping talus from fence to ditch) was 1.8 m ± 0.1 s.e. with a maximum of 3.7 m. Other linear landscape elements such as road verges, hedges and wooded banks have similar values for width (van Dorp *unpubl. data*). The width in the simulations was varied between 1 and 20 m. We included corridors of 20 m wide to approximate the continuous non-corridor habitat for the selected plant species. Furthermore, corridors could consist of either a single habitat quality or a mixture of low and high habitat qualities, with different proportions of high quality patches. The percentage of high quality patches varied between 0 (all patches are of low quality) and 100 (all patches are of high quality) and can be regarded as an index of habitat hetereogeneity. The pattern of distribution of the high quality patches among the low quality ones was randomized.

III SIMULATIONS

Three simulation experiments were performed to answer the questions stated in the Introduction (Table 4). In the *first* simulation, the effect of varying the width (six levels) and habitat quality (three levels) of corridors on the migration rate for two seed dispersal classes (short-range and long-range) was studied. In the *second* simulation, the effect of different proportions of high quality patches within a corridor on the migration rate for two seed dispersal classes was examined. The high quality patches ($\lambda = 2.0$) were mixed with low quality patches ($\lambda = 0.8$) to give varying percentages (from 5 to 100%) of high quality patches in a corridor. The *third* simulation was concerned with the truncation of the dispersal functions. In this simulation, the seed shadows were truncated at 10, 15, 20 or 25 m from individual seed sources. If the total number of seeds covered by an infinitly large seed shadow is set at 100%, then the percentages for the truncated seed shadows with $\alpha = -0.4$ are 92.27 % , 98.50 % , 99.74 % and 99.96 % for 10, 15, 20 or 25 m respectively. By enlarging the seed shadows from 10 to 25 m, more long-range seeds could contribute to the rate of migration in corridors of varying habitat qualities and widths (Table 4).

The rate of migration was calculated by dividing the distance (m) between the initially occupied cells and the migration front after 30 time steps (i.e. years). The criterion for the position of the migration front was a mean density of established plants throughout the corridor (if > 1 cell wide) of at least 1.0 plant per cell. At the end of each simulation run the percentage of all seeds dispersed that landed in the corridor was calculated; 100 minus this percentage refers to seed losses to the surrounding uninhabitable habitat. Each simulation was replicated 3 times for corridors 10 and 20 m, 5 times for corridors of 5 m and 10 times for corridors ≤ 3 m to account for the larger variability in migration rates in narrow corridors due to stochasticity.

Table 4. Values of the various parameters used in the simulations with various factors. The factors of principal interest are in italics.

Effect of dispersal capacity, habitat quality and corridor width							
dispersal capacity	(α)	-0.4	-2.0				
habitat quality	(λ)	1.2	1.4	2.0			
width	(m)	1	2	3	5	10	20
Effect of heterogeneity							
dispersal capacity	(α)	-0.4	-2.0				
habitat quality	(λ)	0.8	2.0				
width	(m)	10					
heterogeneity	(%)	5	10	25	50	100	
Effect of tail length of seed shadow							
dispersal capacity	(α)	-0.4					
habitat quality	(λ)	1.2	1.4	2.0	2.5		
width	(m)	3	10				
tail length	(m)	10	15	20	25		

RESULTS

effects of dispersal capacity, habitat quality and corridor width

The results of the simulation on the effects of dispersal capacity and the habitat quality and width of corridors indicated that the migration rates of the imaginary species were always less than 5 m/year. The highest rates were recorded for the widest corridors consisting exclusively of high quality patches (width 20 m, $\lambda = 2.0$). Here, the rate was 0.9 m/year (± 0.1 s.e.) for plants with short-range dispersal ($\alpha = -2.0$), and 3.9 m/year (± 0.1 s.e.) for plants with long-range dispersal ($\alpha = -0.4$). In corridors that were narrow or consisted solely of low quality patches, migration rates were significantly lower (Figure 1).

A three-factor ANOVA on square-root transformed migration rates revealed that all three factors investigated (the extent of dispersal and the habitat quality and width of corridors) had highly significant and positive main effects (p<0.001). The interactions between dispersal x habitat quality and dispersal x width were very significant and positive (p<0.001; Table 5). These interactions indicate that the size of the effect of dispersal depended on the habitat quality and width of corridors, and that plants with short-range dispersal (α = -0.4) profit more from an increase in width and habitat quality of corridors, i.e. migrate at higher rates, than plants with long-range dispersal (α = -2.0).

Table 5. ANOVA on square-root transformed migration rates using the results of the simulation on the effects of dispersal capacity (α= -0.4 and -2.0) and habitat quality (λ= 1.2, 1.4 and 2.0) for narrow (<5 m) and wide (≥5 m) corridors.

Factor	df	SS	MS	F-value	P
Dispersal	1	8.227	8.227	170.584	<0.0001
Quality	2	20.906	10.453	216.753	<0.0001
Width	1	6.54	6.54	135.617	<0.0001
Dispersal x Quality	2	2.75	1.375	28.51	<0.0001
Dispersal x Width	1	1.992	1.992	41.305	<0.0001
Width x Quality	2	0.077	0.039	0.799	0.4512
Dispersal x Width x Quality	2	0.106	0.053	1.101	0.3343
Error	234	11.285	0.048		
Totals	245	51.883			

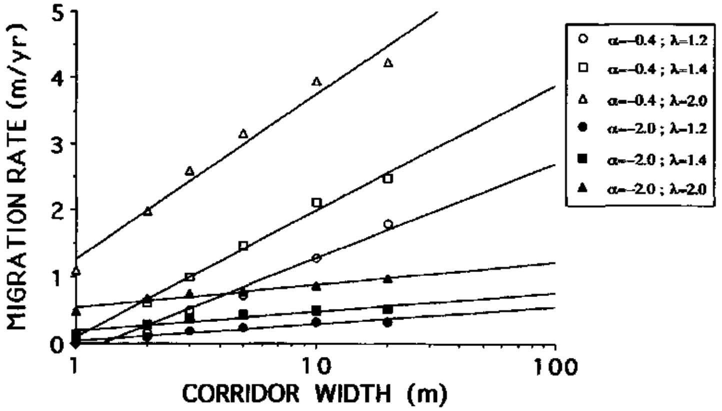

Figure 1. Relationship between corridor width (m) and migration rate (m/year) for short-distance (α= -2.0) and long-distance (α= -0.4) dispersal of seeds and three different habitat qualities of the corridor (λ = 1.2, 1.4 and 2.0).

These effects were largely due to the fact that plants growing in corridors lose a large percentage of the dispersed seeds to neighbouring cells outside the corridor, especially when corridors were narrow. The dispersal of seeds within the boundaries of the corridor was low for plants with long-range dispersal (α = -0.4) growing in narrow corridors (Figure 2). Extrapolation of log-transformed migration rates in figure 2 for α = -0.4 indicated that the necessary corridor width to retain 99% of all seeds produced during the entire simulation was 41.3 m (30.1 and 60.7 for upper and lower 95% confidence intervals respectively). For α = -2.0, no reliable widths could be calculated. In the study area however, the modal ditch bank is only 1.5 m wide. The seed losses for a corridor of modal width as calculated with the regression models are 37% for plants with short-range dispersal (α = -2.0) and 84% for plants with long-range dispersal (α = -0.4).

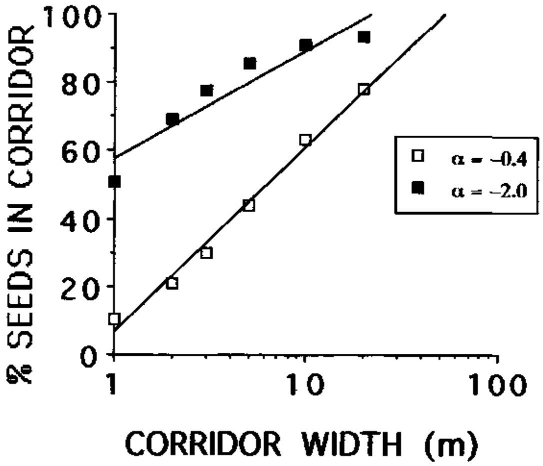

Figure 2. Relation between corridor width (m) and the percentage of seeds dispersed into the corridor, for short-range (α= -2.0) and long-range (α= -0.4) dispersal of seeds. Data were ln-transformed and fitted; the curves shown are Y= 57.8 + 31.9(ln width), R^2 = 0.89, df=5 for α= -2.0 and Y= 6.9 + 54.2(ln width), R^2 = 0.99, df=5 for α= -0.4.

effect of the percentage of high quality patches

The simulation on the effect of the percentage of high quality patches within a corridor revealed that this percentage significantly affected the migration rate. Below a certain threshold percentage of high quality patches in corridors, there was no migration from existing source populations. These threshold percentages were very similar for both dispersal classes: 5 % for plants with short-range dispersal (α = -2.0) and 6 % for plants with long-range dispersal (α = -0.4). Above this threshold, migration rates increased log-linearly, to a maximum migration rate when all patches in a corridor were of high quality (Figure 3).

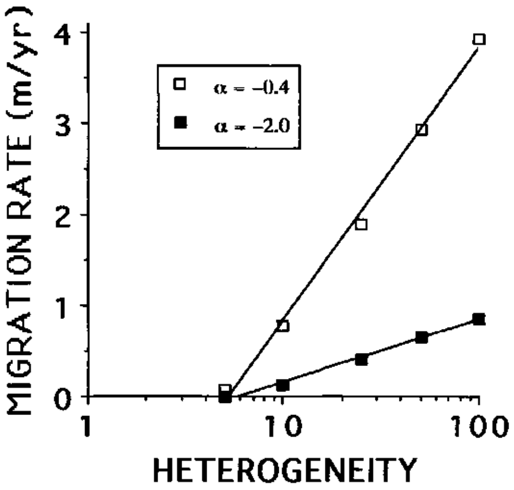

Figure 3. Relation between heterogeneity of a corridor [expressed as the percentage of high quality patches with λ = 2.0 in a corridor; other patches are low quality patches with λ = 0.8] and migration rate (m/year) for short-range (α= -2.0) and long-range (α= -0.4) seed dispersal. Corridor width was 10 m in all runs. Data were ln-transformed and fitted; the curves shown are Y= 0.29(ln HET) - 0.5, R^2 = 0.99, df=4 for α= -2.0 and Y= 1.30(ln HET) - 1.5, R^2 = 0.99, df=4 for α= -0.4.

effect of the length of tail of the seed shadow

The simulation on the effect of length of tail (i.e. attenuation with distance from seed source) on migration rates revealed positive and highly significant effects of habitat quality for 3 m wide corridors, but the effect of length of tail per se was not significant (p=0.13). For 10 m wide corridors, the effects of both habitat quality and the length of tail were positive and statistically highly significant (Table 6). The interaction between habitat quality and length of tail was statistically significant and positive for both 3 m and 10 m wide corridors (Table 6). The contribution of long-range seeds in the tail of a seed shadow to the migration rate was thus dependent upon the habitat qualtiy of corridors, but was most effective in wide, high quality corridors (width 10 m, $\lambda = 2.5$) (Figure 4).

Table 6. ANOVA on square root transformed migration rates using the results of the simulation on the effects of length of tail of seed shadow (10, 15, 20 and 25 m) and habitat quality (λ=1.2, 1.4, 2.0 and 2.5), separately for two corridor widths (3 and 10 m).

WIDTH = 3 m

Source	**df**	**SS**	**MS**	**F-value**	**P**
Tail length	3	0.146	0.049	1.905	0.1314
Quality	3	52.129	17.376	682.038	<0.0001
Tail length x quality	9	0.496	0.055	2.162	0.028
Error	144	3.669	0.025		
Totals	159	56.4			

WIDTH = 10 m

Source	**df**	**SS**	**MS**	**F-value**	**P**
Tail length	3	0.295	0.098	72.079	<0.0001
Quality	3	10.575	3.525	2582.13	<0.0001
Tail length x quality	9	0.049	0.005	4.025	0.0016
Error	32	0.044	0.001		
Totals	47	10.963			

Extending the radius of the seed shadow from 10 to 25 m resulted in 7.69% of the total number of dispersed seeds being added to the tail of the seed shadow, causing the migration rate to increase by 1.1 m/year (to 4.6 m/year); this represented a 31% faster migration rate in wide, high quality corridors (width 10 m, $\lambda = 2.5$). For wide, low quality corridors (width 10 m, $\lambda = 1.2$) the increase was 0.3 m/year (to 0.9 m/year) which represented a 54% faster rate. For narrow, high quality corridors (width 3 m, $\lambda = 2.5$) the increase was less in both absolute and relative terms: on average 24% faster (0.6 m/year). For narrow, low quality corridors (width 3 m, $\lambda = 1.2$), seeds with long-range dispersal had no effect on migration rates.

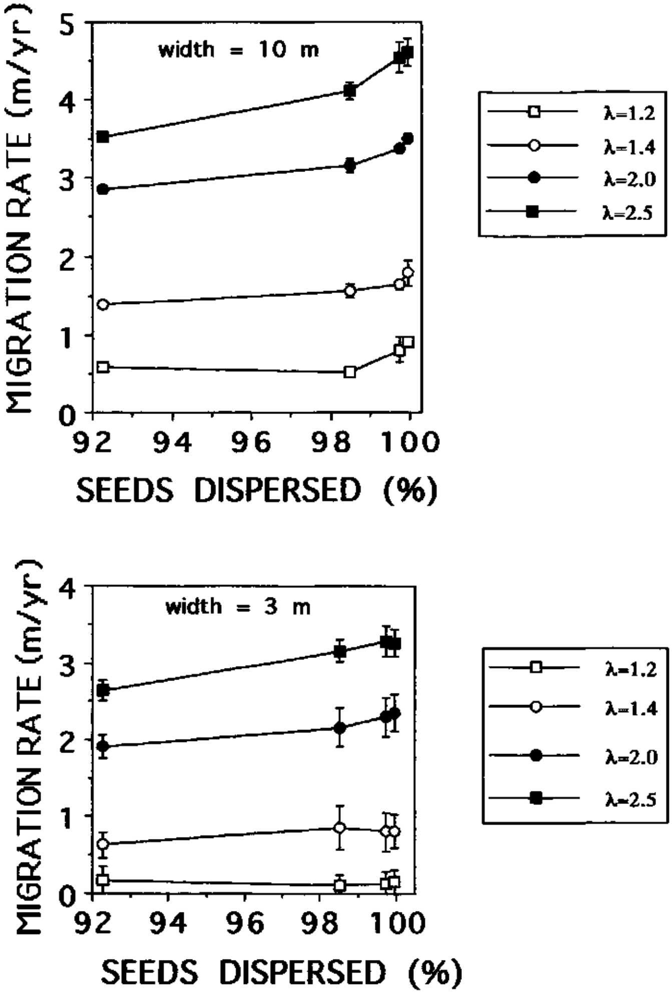

Figure 4a / 4b. Effect of tail length of seed shadow (expressed as a percentage of the total number of seeds dispersed, within a radius of 10, 15, 20 and 25 m from a seed source) on the migration rates of plants (m/year) for corridors of different habitat quality (λ = 1.2, 1.4, 2.0 and 2.5) and width (3 and 10 m). Plotted values are mean rates (± SD) of n=10 runs for corridors of 3 m wide and n=3 runs for corridors of 10 m. In both simulations, dispersal capacity α was -0.4.

DISCUSSION

As shown in the preceding section, the migration rates derived from the simulations varied from 0.1 to maximally 5.0 m/year, which suggests that even under optimal conditions (wide corridors, consisting exlusively of high quality patches), migration proceeds very slowly. We will now discuss the various factors that were included in the simulations and their possible implications for the preservation of plant species in fragmented landscapes.

dispersal capacity

It has been well established that dispersal in grassland species which lack the specific adaptations to wind dispersal is non-directional and for most seeds is limited to 1 to 10 m from the parent plant (Howe and Smallwood 1982, Willson 1992). Werner (1975) recorded that the dispersal of seeds in teasel (*Dipsacus sylvestris*) was limited to 1.5 m from the parent plants. Verkaar et al. (1983) observed that seed dispersal in short-lived forbs in chalk grasslands was restricted to 3.5 m. In populations of ragwort (*Senecio jacobaea*), McEvoy and Cox (1987) found that the majority of dimorphic wind-dispersed achenes were also dispersed over short distances: 31% travelled only 1 m, 89% travelled 5 m or less, and no seeds were collected more than 14 m from the source.

These studies indicate that extremely few seeds will be present in the tail of a frequency distribution at distances greater than 20 m. In our simulations with the model, we used ecologically relevant values of α which correspond well with the field observations mentioned above and make the estimates of migration rates credible for wind-dispersed species. Our findings imply that the contribution of long-range seeds to plant migration likely remains to be limited. This is largely because seeds dispersed long distances by the wind will be deposited on patches regardless of their habitat quality; they are not preferentially dispersed to high quality patches. Given the constraints of the model ($\lambda \leq 2.5$), long-range dispersal will rarely lead to the establishment of new populations.

However, the simulations also indiciated that migration rates were positively affected by habitat quality per se and by the density of high quality patches. This suggests that the conditions of *directional* dispersal of seeds to remote patches of very high quality ($\lambda > 2.5$) actually confer an advantage to migrating plants. We acknowledge that small proportions of the produced seeds are sometimes indiscriminately or accidentally dispersed by some unorthodox dispersal mechanism other than the wind. Examples of such dispersal mechanisms are grazing herbivores (Bullock and Primack 1977; Janzen 1984), humans via machinery, cars, boots etc. (Schmidt 1989) and overflowing rivers (Skoglund 1990).

Directional dispersal mechanisms which couple long-range dispersal of seeds with fine-scale soil disturbances (e.g. mole hills) particularly enhance the rate of establishment of new plants and could be important to plant migration. In that case, long-range dispersed seeds are preferentially deposited on bare (i.e. high quality) patches and are more likely to establish new populations than 'normally' wind-dispersed seeds. It is thus possible that we underestimated the importance of directed dispersal events and that in reality plant migration may proceed faster. In that case, the model used functions as a *null* model, valid for the dispersal of seeds by wind.

We must stress here that the importance of directional dispersal by agricultural machinery is limited to those plant species that are already present in linear elements in the fragmented landscape. We see no reason why regionally extinct species, species restricted to isolated nature reserves or even in refugia in linear landscape elements should benefit from this type of dispersal.

corridor width

The simulations also indicated that plants in narrow corridors migrate at lower rates than in wide corridors; this can be explained by the losses of seeds to non-habitat environments such as farmed fields, roads etc. In corridors that are *narrow* relative to the seed shadows of plants, a large proportion of the seeds produced by individual plants will be lost. Patches in narrow corridors will lose many seeds, but receive few. Wind-dispersed species with long-range dispersal (α = -0.4) and growing on narrow corridors (< 3 m) are particularly prone to heavy seed losses and more than half of their seed crop will be wasted. Such species would benefit from wider corridors, but there is little reason to make them wider than 5 m (Figure1).

In corridors that are *wide* relative to the seed shadows of plants, seed losses are small and have little or no effect on migration rates. Individual patches in the centre of wide corridors receive the seeds from many different reproductive neighbours and from various directions. Sufficient numbers of seeds are available to allow the recruitment of new plants which then further propel the migration of plants along corridors.

E.g., short autochorous plants with short-range dispersal of seeds (α = -2.0) growing on wide corridors (> 10 m) will experience little or no effects of seed losses. Plants on such wide corridors experience a continuous rather than a fragmented habitat. In wide corridors, the habitat quality and heterogeneity of corridors determine the migration rates.

habitat quality of patches

The simulations further suggested that the habitat quality of patches in a corridor is important. We characterized the habitat quality by the probability of establishment (E) and the seed production (Q); both factors can be manipulated by the management of the vegetation, as was demonstrated by the seed addition experiment (van Dorp *submitted*; Chapter 4). The percentage of high quality patches in a corridor also significantly affected the migration rate.

In linear landscape elements in fragmented landscapes, high quality patches for perennial grassland species are often not permanent and only available locally. This is because these linear elements are heavily influenced by management and the agricultural activities on the adjacent fields (van Strien et al. 1989). Only the more competitive and ruderal plant species are able to withstand the spill-over of nutrients, herbicide drift, fluctuating water tables, frequent disturbances by machinery, and trampling and overgrazing by live-stock. Landscape elements with a *high* percentage of *high* quality patches may function as corridors for competitive and ruderal species, but landscape elements with a *high* percentage of *low* quality patches are at best a refugium for plant species.

implications for nature conservation

The conservation of plant species with short-range dispersal of seeds in fragmented landscapes is problematic because these species do not establish easily in newly created and restored habitat patches or on patches from which the species have died out by chance (Primack and Miao 1992). Three alternative solutions to this problem exist: (1) to wait several years or even decades (depending on the size of a target site and the spatial distribution of source populations) for seeds to be deposited by rare and unpredictable dispersal events (*chance dispersal*), (2) to introduce seeds from nearby populations or (3) to enhance habitat connectivity in a landscape and to promote the migration of plants along ecological corridors. In this study, we specifically explored the third alternative.

It is doubtful that linear landscape elements in fragmented landscapes will provide the appropriate growing conditions necessary to function as corridors for a wide range of grassland species. Species of wet nutrient-poor ecosystems such as *Succisa pratensis, Gentiana pneumonanthe* and *Linum catharticum* are particularly unlikely to migrate along such elements because of the occurrence of patches of inferior habitat quality. Such species remain restricted to nature reserves and may run the risk of population extinction due to the loss of genetic variation (Ouborg 1993). The few remaining populations of such species in linear elements in fragmented landscapes run high risks of being eliminated successively.

The migration of herbaceous perennial grassland species of relatively fertile soils is also impeded and limited to maximally 5 m/year. The time needed to cover the distances between existing sources (refugia and core areas) and uncolonized appropriate habitats in fragmented landscapes (e.g. restored set-aside areas) on a local to regional scale may well be 100 to 1000 years. This finding is clearly unacceptable for those committed to the conservation of plant species diversity in fragmented landscapes. To maintain linear elements in fragmented landscapes as refugia for plant species, an *ecologically sound management* of these linear landscape elements is required. But to restore the former species-rich meadows on abandoned farmed fields, it will be necessary to harvest seeds from many species from nearby source populations and to introduce them into suitable habitats.

Acknowledgements

We thank F. van den Bosch (Wageningen Agricultural University) for his advice to use the formula describing the distribution of dispersed seeds around a source. F. Berendse critically reviewed earlier drafts of this paper.

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CHAPTER 6

Dispersal interactions between fleshy-fruited plants and fruit-eating birds in a Dutch agricultural landscape.

submitted to Vegetatio

Abstract

The dispersal interactions between fleshy-fruited plants and fruit-eating birds have been studied in a Dutch agricultural landscape (6,500 ha) consisting of small woodlots, wooded banks and farmed fields. The aim of this study was to relate the distribution of fruit-eating birds, fleshy-fruited plants and the bird-mediated seed rain to the landscape structure (i.e. the density of wooded landscape elements such as wooded banks and small woodlots).

In the study area, 26 fleshy-fruited plant species were recorded on 99 100-m transects of wooded banks. On average there were 7 fleshy-fruited plant species per 100-m transect (the range was 2 to 14 species). The number of fleshy-fruited species of the transects did not correlate statistically significantly with the density of wooded banks or of woodland within radii of 0.3, 0.9 or 1.5 km.

Eight fruit-eating passerine bird species were identied as the major avian seed dispersers in the study area: *Erithacus rubecula, Sylvia atricapilla, Turdus philomelos, Turdus merula, Turdus viscivorus, Turdus iliacus, Turdus pilaris* and *Sturnus vulgaris.* These species were divided into two ecologically distinct categories on the basis of differences in social and foraging behaviour, fruit and habitat selection: *longitudinal* (the first four species) and *transverse* dispersers (the last four species). Longitudinal dispersers carry the seeds of the majority of fleshy-fruited species over short (i.e. < 0.1 km) distances only. Hence, seed dispersal is limited to the network of wooded landscape elements. Transverse dispersers carry the seeds of species with conspicuous fruit crops over large(r) distances, and by so doing frequently disperse seeds to and from dissimilar landscape elements (wooded banks, open fields, forest edges etc.).

The bird-mediated seed rain on wooded banks was sampled in twelve transects using 120 seed collectors and by systematically collecting droppings from leaves, stones, poles etc. In one dispersal season (1987), 6434 seeds of eighteen fleshy-fruited plant species were retrieved from the seed collectors. The seed rain was dominated by the five plant species: *Rubus fruticosus, Sorbus aucuparia, Frangula alnus, Lonicera*

periclymenum and _Sambucus nigra_. The mean density of the seed rain was 215 ± 68 seeds m^{-2}, with values between 34 and 873 seeds m^{-2}. The phenology of fruiting was recorded simultaneously with the sampling of the seed rain, which allowed the seed rain to be split into three components: seeds mainly deposited on seed collectors during the fruiting period of the species involved (_component I_ seeds: 87.6%); relatively few seeds deposited when ripe fruits were no longer available (_component II_ seeds; 6.8%); seeds deposited on transects where fruiting adults were absent (_component III_ seeds; 5.6%).

Kendall's rank correlation coefficient τ indicated that seed rain _component I_ varied positively with size of fruit crop and number of longitudinal and transverse dispersers, but varied inversely with the density of wooded banks within 0.9 km. The seed rain _components II+III_ varied positively with size of fruit crop. In all other comparisons, no statistically significant correlations were detected.

The results of this study help to clarify the complex interactions between birds, plants and landscapes and their effects on the dynamics of plant populations in fragmented landscapes. The ecological differences between longitudinal and transverse dispersers deserve more attention in particular, in order to be able to predict the consequences of changes in the density of wooded landscape elements on the species richness and distribution of fleshy-fruited plants in fragmented landscapes.

INTRODUCTION

Various mutualistic relations between fruit-eating birds and fleshy-fruited plants have evolved in the temperate zones (Herrera 1984, Willson 1986, Snow and Snow 1988, Jordano 1992, Willson and Whelan 1993). Several passerine species ingest whole fruits, consume the pulp and then drop the seeds in a viable condition somewhere around the parent plant (Howe and Smallwood 1982). Fruit-eating birds generally consume the fruits of several fleshy-fruited plant species, while plants employ several fruit-eating bird species to disperse their seeds (Herrera 1985).

When foraging for fruits, fruit-eating birds constantly decide where to eat which type of fruit and for how long (Sallabanks 1993). These foraging decisions may be influenced by various factors at different hierarchical levels, i.e. at the level of individual fruits, plants, patches and perhaps even at the level of landscapes. Examples of such factors include the diameter, pulpiness and nutritional value of fruits (Herrera 1981), the accessibility of fruits to birds (Moermond and Denslow 1983), the size of fruit crops (Thiebaud and Debussche 1992), the number of fruiting plants (Sargent 1990), the presence of avian predators (Howe 1977) and the type of habitat (Hoppes 1988, Guitián et al. 1992, McClanahan and Wolfe 1993, Debussche and Isenmann 1994). McDonnell (1988) observed that for instance open fields affect the behaviour and distribution of fruit-eating birds that inhabit woodlands and will act as repulsion elements in a landscape. These decisions at multiple levels are likely to affect the seed shadows and distribution patterns of individual plant species in a landscape (Johnson et al. 1981). McDonnell (1988) suggests that the probability of seeds reaching a habitat patch is affected by the availability of food such as fruits and insects, the foraging and social behaviour of the seed-dispersing bird, the exposure and accessibility of a site to predators (*attractiveness*) and the occurrence of repulsion elements in a landscape.

Fleshy-fruited plants are common among shrubs and trees and occupy landscape elements such as wooded banks and small woodlots (van Ruremonde and Kalkhoven 1991). Fruit-eating birds commonly use these elements to feed, shelter and rest. In the Netherlands, landscape elements rich in fleshy-fruited plants such as "mature" wooded banks (*houtwallen*, i.e. banks with a layer of shrubs under trees that were planted) and hedges are disappearing from the rural landscape as the intensity of agricultural activities is stepped up. At the same time, "new" landscape elements with no fleshy-fruited plants are planted in other sites in the landscape (Vos and Zonneveld 1993).

Changing the overall structure of a landscape (i.e. the density of wooded landscape elements) is likely to affect the composition of communities of breeding woodland birds in small woodlots (e.g. van Dorp and Opdam 1987). The question is whether such changes also affect the number and distribution of fruit-eating birds outside the breeding season. It is important to know the answer to this question because the dispersal of seeds and hence the colonization of new landscape elements by fleshy-fruited plants may in turn be affected by the specific interactions between birds and plants. In the context of habitat fragmentation (Verboom et al. 1993), it is of particular interest to study which factors influence the dispersal interactions between landscape elements such as wooded banks, woodlots and fields. At the landscape level, little research has yet been done on the factors that affect the process of seed dispersal.

In this study, I investigated the interactions between fruit-eating birds and fleshy-fruited plants in a Dutch agricultural landscape in which the density of wooded landscape elements varied by more than one order of magnitude. The central aim of this study was to compare the distribution of fruit-eating birds and fleshy-fruited plant species and the implications of this for the dispersal of seeds in landscapes that vary in the density of wooded landscape elements (*connectivity*). The following questions were posed:

1. What are the major avian seed dispersers in the study area and what

are their characteristics, numbers and distribution?

2. Are the number of avian seed dispersers and fleshy-fruited plant species related to the density of wooded landscape elements?

3. Does the density of wooded landscape elements affect the seed rain on specific wooded banks ?

4. What consequences does a change in the density of wooded landscape elements have for the dispersal of seeds of fleshy-fruited species?

MATERIAL AND METHODS

The study area

The field data were collected in the summer and autumn of 1987 in the north-eastern part of the province of Overijssel in a rural landscape of 6500 ha (52° 27' N - 6° 50' E; 20 to 70 m a.s.l.). The landscape consists of mosaics of small (< 5 ha) and young (< 100 years) mixed deciduous woodlands (mainly *Quercus robur L., Alnus glutinosa (L.) Gaertner*and *Betula pendula Roth*), wooded banks, intensively exploited pastures and arable fields which are mostly planted with maize (*Zea mais L.*). Nomenclature of plants follows van der Meijden (1990).

Within the study area, twenty blocks of 0.5 km by 0.5 km (25 ha) were selected from a 1:25,000 topographic map and assigned to four density classes of woodland (< 1.0, 1.0-2.0, 2.0-3.0 and >3.0 ha woodland per 25 ha) and six density classes of wooded banks (< 0.4, 0.4-0.8, 0.8-1.2, 1.2-1.6, 1.6-2.0 and >2.0 km total length of wooded banks per 25 ha) (after Schotman 1988). Combining both attributes gave twenty-two combinations, two of which did not occur in the study area. These blocks form a gradient in connectivity from a relatively *open* (< 1.0 ha woods and < 0.4 km wooded banks) to a relatively *closed* (> 3.0 ha woods or > 2.0 km wooded banks) landscape. A total of 99 wooded banks was selected, with four to nine wooded banks per block. On each selected bank, a transect 100 m long and 2 to 6 m wide was laid out. The wooded banks had a well developed tree layer, but the shrub and herb layer varied both in cover and species composition.

Fruit-eating birds

During a preliminary study in 1986 (van Dorp 1987), the most important fruit-eating bird species in the study area were two small (<30 g) species, *Erithacus rubecula* (robin) and *Sylvia atricapilla* (blackcap) and six medium-sized (>60 g) species, *Turdus philomelos* (songthrush), *Turdus iliacus* (redwing), *Turdus merula* (blackbird), *Turdus viscivorus* (mistle thrush), *Turdus pilaris* (fieldfare) and *Sturnus vulgaris* (starling). These eight species are also regarded as the major avian seed dispersers because they feed heavily on fleshy fruits and deposit viable seeds away from the parent plant (Snow and Snow 1988). Large differences in foraging strategy, fruit and habitat selection, flocking and social behaviour were observed between these major seed dispersers (van Dorp 1987). From the plant's point of view, these major seed dispersers could be divided into two ecologically distinct categories, *longitudinal and transverse seed dispersers.*

Longitudinal seed dispersers (including *E. rubecula, S. atricapilla, T. philomelos* and *T. merula*) perform their activities (feeding, moving, hiding and resting) exclusively within the network of wooded banks. Hence, dispersal of seeds by longitudinal dispersers is essentially within-habitat and along the wooded bank. *Transverse* seed dispersers (including T. *viscivorus, T. iliacus, T. pilaris* and *S. vulgaris*) forage extensively on fruit in wooded landscape elements, but also on small invertebrates in open fields. They frequently commute between wooded banks, woodland edges and open fields to feed, shelter and rest. Hence, dispersal of seeds by transverse dispersers is essentially between-habitat and is directed away from the wooded bank to both suitable and unsuitable habitat patches (Appendix 1).

Other common bird species that regularly eat fruits such as *Columba palumbus* (wood pigeon), *Pica pica* (magpie), *Corvus corone* (carrion crow) and several *Parus* species act more as fruit thieves and seed predators than as seed dispersers (Snow and Snow 1988).

Fruit-eating birds

Censuses of the eight major fruit-eating bird species in the study area were conducted in 100-m transects of wooded banks from early July to late November 1987. Each census consisted of counting the number of birds *arriving at* (a), *departing from* (d) and *flying over* (o) the wooded bank in a five-minute period and was concluded with a count of the birds that were *present* (p) in the trees and shrubs within the transect. The number of birds present (p) may include those arriving (a) at the transect during the five-minute period. To demonstrate the differences in foraging behaviour between the bird species, a simple index of mobility was obtained by dividing the number of flying birds by the number of birds present. This ratio of flying to non-flying birds (a+d+o)/p varies between species from 0 (very sedentary) to > 5 (very nomadic) (*see* Results). A total of 682 bird censuses was carried out in all blocks of the study area, representing a total of 56.8 hours of observation. The number of fruit-eating birds in the twelve transects with seed collectors (*see below*) was recorded weekly during the entire study period, yielding 17 observations per transect. During the censuses, observations on the kinds of fruit taken by individual bird species were also recorded, to obtain local information on the type of fruit taken by birds.

Fleshy-fruited plants and availability of fruits

In June 1987, all fleshy-fruited plants including herbs, climbers, shrubs and trees taller than 1.0 m were mapped and counted on all 99 transects. The data provided an estimate of the *species richness*, i.e. the number of fleshy-fruited species per 100-m transect. From early August until late November 1987, the total number of ripe fruits for each plant species was estimated in seven censuses conducted at 2-weekly intervals for the twelve transects that had seed collectors.

Seed rain on wooded banks

The seed rain on wooded banks was sampled with seed collectors during seventeen weeks on twelve wooded banks from August 3 1987 until November 23 1987. The seed collectors measured 0.5 x 0.5 m and were made of cheese cloth stapled to a steel rectangle and placed 0.3 m above the ground. On each transect, ten seed collectors were put at 10 m intervals. The total sampling surface was 30.0 m^2. The twelve transects in wooded banks were stratified along a gradient in connectivity from an open to a closed landscape.

The seeds that had been deposited by seed-dispersing birds were collected weekly, yielding seventeen seed collections per collector. The contents of 2040 seed collections (i.e. 12 transects x 10 seed collectors x 17 weeks) were inspected. In addition, bird droppings with seeds were systematically collected from leaves, poles, stones and soil for each of the twelve transects throughout the observation period. The seeds were identified with the help of a reference collection.

A comparison between the composition of the seed rain and the availability of ripe fruits for each wooded bank allowed the seed rain to be split into three components: *component I*, comprising the seeds deposited when ripe fruits of the species involved were available on the transect; *component II*, the seeds deposited when ripe fruits were no longer available on the transect; and *component III*, the seeds deposited on the sampled wooded banks on which no fruiting adults of the species involved were growing. The first component of the seed rain included *local* seeds (i.e. from within a transect) and *immigrant* seeds (i.e. from outside a transect). The latter two components were composed exclusively of *immigrant* seeds since all seeds must have immigrated from seed sources outside the transect; their provenances were unknown.

Statistical analyses

The relation between the number of fleshy-fruited species and the landscape structure was examined by testing the differences in the number of fleshy-fruited species between the classes of the variables density of woodland and density of wooded banks with one-factor ANOVA Scheffé's F-test. The data from all 99 transects were used in the analysis.

Kendall's τ coefficient was used to test the correlation between the number of longitudinal and transverse dispersers and size of fruit crop (total sum of ripe fruits of all fleshy-fruited species per 100 m transect), species richness (number of reproductive fleshy-fruited plant species / 100 m transect), density of woodland (ha / 25 ha landscape) and density of wooded banks (km / 25 ha landscape) within radii of 0.3, 0.9 and 1.5 km from a selected transect. It was investigated whether the size of the seed rain (*components I* and *II+III*) correlated with the number of longitudinal and transverse dispersers and with the variables mentioned above. A non-parametric method was used instead of regression analyses because of the small sample size (n=12 transects) and the large variation in the values of the dependent variables, even after log or square root transformation of the data. Seed rain *components II+III* were pooled in the analysis because of the small numbers.

RESULTS

Longitudinal and transverse seed dispersers

The bird censuses indicated that *Sturnus vulgaris* was the most frequent fruit-eating bird species in the study area with *Turdus merula* ranking second (Table1). Three bird species are resident in the study area for part of the time; *Sylvia atricapilla* is a summer resident and was observed until late August, *Turdus pilaris* and *T. iliacus* are migrants and winter residents and were observed from early October onwards. In five species (*E. rubecula, S. atricapilla, T. philomelos, T. merula* and *T. viscivorus*) more nonflying than flying birds were observed in wooded banks during 56.8 hours of observation, in three species (*T. iliacus, T. pilaris* and *S. vulgaris*) more flying than nonflying birds were observed, hence the mobility indices of these two groups were <1 and >1, respectively.

On the basis of the mobility index and foraging behaviour (*see* Appendix 1), the first four species were characterized as longitudinal seed dispersers, and the last four as transverse seed dispersers. The difference in mean mobility of longitudinal birds (0.26, range 0.08-0.55) and of transverse birds (2.86, range 0.71-5.29) was one order of magnitude, indicating that longitudinal dispersers are basically sedentary birds whereas transverse dispersers are far more nomadic in their behaviour (Table 1).

Table 1. Results of bird censuses conducted on 99 transects (A; n=682 censuses) and the 12 transects with seed collectors (B; n=204 censuses) from July until November 1987, separated into longitudinal and transverse dispersers, with the total number of birds recorded, relative frequency (i.e. mean number of birds in a transect per census) and mobility index of bird species (ratio of the number of birds flying to number of birds present). N.d. means no data are available. Species are listed in order of increasing mobility index.

SPECIES	NUMBER OF BIRDS		RELATIVE FREQUENCY		MOBILITY INDEX
	A	B	A	B	A
LONGITUDINAL					
Erithacus rubecula	159	69	0.23	0.34	0.08
Sylvia atricapilla	95	n.d.	0.12	n.d.	0.12
Turdus philomelos	62	16	0.08	0.08	0.32
Turdus merula	406	122	0.60	0.60	0.55
Totals	722	207	1.03	1.02	1.07
TRANSVERSE					
Turdus viscivorus	274	101	0.35	0.50	0.71
Turdus iliacus	267	70	0.29	0.34	1.45
Turdus pilaris	35	9	0.03	0.04	4.00
Sturnus vulgaris	1645	481	2.31	2.36	5.29
Totals	2221	661	2.98	3.24	11.45

The mean number of transverse seed dispersers on a 100 m transect in 1987 was 2.9 times higher than the mean number of longitudinal dispersers (2.98 versus 1.03 birds, respectively). For the subset of twelve wooded banks with seed collectors that were censused more frequently (n=17), the overall density of transverse dispersers was 3.2 times higher than the overall density of longitudinal dispersers (3.24 versus 1.02 birds, respectively: Table 1). Rank correlation analyses showed that the number of longitudinal birds varied positively with the density of woodland within a radius of 1.5 km (Kendall's coefficient τ = .412, $p<0.025$, n=12). The number of transverse birds varied inversely with the density of woodland (τ = -.410, $p<0.025$) and wooded banks within a radius of 0.3 km (τ = -.422, $p<0.025$). In all other comparisons, no correlations were detected (Table 2).

Table 2. Kendall's statistic τ (corrected for ties) for the 12 transects with seed collectors on the correlation between the number of longitudinal and transverse seed dispersers with the size of fruit crop, number of fruiting plant species, density of woodland and density of wooded banks within radii of 0.3, 0.9 and 1.5 km from the transect. Independence between rankings (H_0) was tested with *a one-tailed probability and rejected in* 3 out of 16 cases (n=12). ** = $p<0.025$.

VARIABLE	LONGITUDINAL DISPERSERS	TRANSVERSE DISPERSERS
Size of fruit crop	.321	.046
Species number	.176	.112
Density of woodland		
r=0.3	-.016	-.410**
r=0.9	.260	-.137
r=1.5	.412**	-.107
Density of wooded banks		
r=0.3	-.141	-.422**
r=0.9	-.108	-.292
r=1.5	-.168	-.198

Fleshy-fruited plant species

In the study area, twenty-six fleshy-fruited plant species were recorded in 99 100-m transects, including nineteen tall shrubs, three herbs, three climbers and one dwarf shrub species. The five most frequent and abundant species on wooded banks were, in order of decreasing frequency/abundance *Rubus fruticosus L., s.l., Sorbus aucuparia L., Rhamnus frangula L., Lonicera periclymenum L.* and *Sambucus nigra L.*. The five rarest species were *Vaccinium myrtillus L., Sambucus racemosa*

L., Juniperus communis L., Cornus sanguinea L. and *Rhamnus catharticus L.*. The few senescent individuals of *Juniperus communis* and *Rhamnus catharticus* that were present did not bear fruits in 1987. The other fleshy-fruited species occurring in mature deciduous woods elswhere in the study area but not recorded in this sample were *Adoxa moschatellina L., Arum maculatum L., Bryonia cretica L., Convallaria majalis L., Paris quadrifolia L., Prunus padus L.* and *Taxus baccata L.*.

The mean number of fleshy-fruited plant species per 100-m transect was 7.0 ± 0.3, with a range of 2 to 14 species (Table 3). In one block of 25 ha in a relatively closed agricultural landscape (i.e. one not subjected to land consolidation: density of woodland: 1.2-1.6 ha, density of wooded banks: 2.0-3.0 km), the number of fleshy-fruited species was exceptionally high with 10, 12,13 and 14 species on four wooded banks with luxuriant undergrowth and mature oak (*Quercus robur*) trees. Statistical analysis showed that differences in the number of fleshy-fruited plant species between the six density classes of wooded banks (range 6.3 - 7.7 species per transect) and between the four density classes of density of woodland (range 6.5 - 8.4 species per transect) were not statistically significant, except in one case. The third class of density of woodland (1.3-1.6 ha woodland per 25 ha) with 8.4 ± 0.7 species was statistically significantly different from the first density class (< 1.0 ha woodland per 25 ha), with 6.0 ± 0.3 species ($p<0.05$) (Table 3). In general, the number of fleshy-fruited plant species on wooded banks in relatively open sections of the study area was not statistically significantly different from the number in relatively closed sections.

Table 3. Number of fleshy-fruited plant species in a sample of 99 transects distributed over four density classes of wood (density of woodland in ha per 25 ha) and six density classes of wooded bank (length of wooded banks in km per 25 ha) (values are means of four to nine 100-m transects). Dash means no transects could be selected. For each variable, menas with a different letter are significantly different at α=0.05 according to one-factor ANOVA Scheffé's F-tests. s.e. is standard error of the mean.

	WOODED BANK								
WOOD	**<0.4**	**0.4-0.8**	**0.8-1.2**	**1.2-1.6**	**1.6-2.0**	**>2.0**	**mean**	**s.e.**	**n**
< 1.0	6.8	7.3	6.2	5.7	5.9	8.5	6.5^{a}	0.3	33
1.0 - 2.0	8.5	5.0	6.3	7.3	7.9	4.0	6.6^{ab}	0.5	27
2.0 - 3.0	8.0	5.5.	7.0	12.3	9.3	-	8.4^{b}	0.7	20
>3.0	7.5	7.5	7.5	6.3	7.3	-	7.2^{ab}	0.4	19
mean	7.7^{a}	6.4^{a}	6.7^{a}	7.3^{a}	7.4^{a}	6.3^{a}	7.0	0.3	99
s.e.	0.6	0.5	0.4	0.5	0.5	0.9			
n	16	16	17	20	22	8			

Bird-mediated seed rain

In a single dispersal season, 6434 seeds were retrieved from the seed collectors. The mean density of seeds deposited by birds on wooded banks was 215 ± 68 seeds m^{-2} (n=12), the minimum and maximum densities being 34 and 873 seeds m^{-2}, respectively. The seeds of 18 out of 24 reproducing fleshy-fruited plant species occurring in the study area (75.0 %) were identified. The five most abundant seed species *Sorbus aucuparia, Rubus fruticosus, Sambucus nigra, Rhamnus frangula* and *Solanum nigrum L.* had mean densities of >10 seeds m^{-2} and together comprised 91.1% of the total seed rain. The ten least abundant seed species had densities of <1 seed m^{-2} and together comprised <1% of the total seed rain. Among these ten species, three species *Ribes rubrum L., Sambucus racemosa and Taxus baccata* had no fruiting plants on the twelve transects and were thus immigrants from elsewhere. One species, *Prunus serotina Ehrh.*, although fruiting on a transect, was not recorded in the seed rain (Table 4).

Table 4. Seed rain of 19 fleshy-fruited plant species on the 12 transects with seed collectors. Shown are (i) the total number of seeds collected from 120 collectors, (ii) seed density (i.e. mean number of deposited seeds m^{-2} ± s.e.), (iii) percentage of the three components of the total number of seeds per species and (iv) frequency of a species in the twelve transects as fruiting adults (Ad) and/or as seeds in three components of the seed rain - *component I:* during fruiting of conspecifics, *component II:* outside fruiting period of conspecifics and *component III* on wooded banks without fruiting adults (*see text*). Species are listed in order of increasing density of deposited seeds and divided into three groups with <1, 1-10 and >10 seeds m^{-2}.

SPECIES	TOTAL	DENSITY		PERCENTAGE			FREQUENCY			
	seeds	$\#m^{-2}$	s.e.	I	II	III	Ad	I	II	III
Prunus serotina	0	0	0	0	0	0	1	0	0	0
Rosa canina	1	0.03	0.03	100	0	0	5	1	0	0
Taxus baccata	1	0.03	0.03	0	0	100	0	0	0	1
Viburnum opulus	2	0.07	0.07	100	0	0	5	1	0	0
Prunus spinosa	3	0.1	0.1	100	0	0	1	1	0	0
Ribes ruburm	6	0.2	0.1	0	0	100	0	0	0	3
Ilex aquifolium	8	0.3	0.3	100	0	0	2	1	0	0
Prunus avium	12	0.4	0.2	8.3	0	91.7	1	1	0	3
Solanum dulcamara	22	0.7	0.4	86.4	0	13.6	3	3	0	2
Sambucus racemosa	27	0.9	0.5	0	0	100	0	0	0	5
Rubus idaeus	53	1.8	1.3	75.5	0	24.5	1	1	0	4
Crataegus monogyna	92	3.1	2.0	95.6	2.2	2.2	3	3	1	1
Amelanchier lamarckii	140	4.7	2.2	22.1	40.0	37.9	5	1	1	4
Lonicera periclymenum	206	6.9	2.0	84.9	14.6	0.1	9	9	8	1
Solanum nigrum	488	16.3	11.3	70.1	26.2	0.3	2	2	2	6
Rhamnus frangula	936	31.2	15.2	97.6	2.3	0.1	11	10	4	1
Sambucus nigra	1057	35.2	15.2	76.7	17.5	5.8	6	6	4	5
Rubus fruticosus	1430	47.7	19.7	91.7	7.8	4.8	11	11	6	1
Sorbus aucuparia	1950	65.0	39.1	96.9	0.8	2.3	11	11	5	1
Totals	6434	215	68	87.6	6.8	5.6	77	62	31	38

The depostion of seeds on wooded banks by fruit-eating birds was largely restricted to the fruiting period of the plant species present on a transect; *component I* of the seed rain comprised 87.6% of all seeds retrieved from the seed collectors. Relatively few seeds were deposited on transects at times when ripe fruits of the species involved were no longer available (*component II*; 6.8 % of all retrieved seeds) or on transects where fruiting adults were absent (*component III*; 5.6 % of all retrieved seeds) (Table 4). In terms of frequency of occurrence, the sum of the frequency of nineteen fleshy-fruited species with reproductive individuals was 77 (i.e. 33.8% of the maximum score, which is 19 species times 12 transects = 228): 62 (27.2%) for species with *component I* seeds, 31 (13.6%) for species with *component II* seeds and 38 (16.7%) for species with *component III* seeds.

The correlation between seed rain and density of landscape elements was investigated for *component I* and *components II+III* separately using the data from seed collectors (n=120) and bird droppings (n=681). The ranks of the seed rain on the twelve wooded banks were compared with the numbers of longitudinal and transverse dispersers, the size of fruit crops, number of species and the density of woodland and wooded banks within radii of 0.3 to 1.5 km of a transect. The data on the variables are summarized in Table 5, the results of the correlations are shown in Table 6.

Paris quadrifolia, a fleshy-fruited herb restricted to forest interiors (Photo IBN-DLO)

Table 5. Sum, mean (± s.e.), minimum and maximum of various variables for the 12 transects with seed collectors; *seed rain*: total number of seeds and number of seed species from seed collectors and bird droppings separated into local (component I) and immigrant (component II+III) seeds; *seed dispersers*: number of longitudinal and transverse birds; *size of fruit crop*: number of ripe fruits available to birds; *species number*: number of fruiting plant species; *density of woodland* (ha) and *length of wooded banks* (km) within radii of 0.3, 0.9 and 1.5 km from a transect.

VARIABLE		SUM	MEAN	MIN.	MAX.
Seed rain: local seeds					
- total number of seeds	collectors	5636	470 ± 149	56	1891
	droppings	7159	597 ± 252	26	3134
- species number	collectors	8	5.5 ± 0.4	4	8
	droppings	10	4.4 ± 0.3	3	6
Seed rain: immigrant seeds					
- total number of seeds	collectors	796	67 ± 22	6	291
	droppings	906	76 ± 26	0	227
- species number	collectors	15	6.0 ± 0.5	3	8
	droppings	13	2.8 ± 0.6	0	6
Seed dispersers	longitudinal	207	17.3 ± 4.9	1	62
	transverse	661	55.1 ± 20.0	0	232
Size of fruit crop	in 10^3 fruits	608.6	50.7 ± 17.1	6.4	222.3
Species number	fruiting ad.	16	6.0 ± 0.6	3	9
Density of woodland	0.3 km	-	1.7 ± 0.3	0.1	3.2
	0.9 km	-	14.6 ± 3.1	1.9	34.2
	1.5 km	-	44.6 ± 9.4	11.5	119.1
Density of wooded banks	0.3 km	-	1.4 ± 0.2	0.2	2.8
	0.9 km	-	8.5 ± 1.0	3.4	15.1
	1.5 km	-	18.7 ± 1.8	8.4	28.4

Table 6. Kendall's statistic τ (corrected for ties) for the 12 transects with seed collectors on the correlation between the seed rain components I (local and immigrant seeds) and II+III (exclusively immigrant seeds) with the number of longitudinal and transverse seed dispersers, size of fruit crop, species richness of fleshy fruited plants, density of woodland and density of wooded banks within radii of 0.3, 0.9 and 1.5 km from the transect. A distinction was made between seeds retrieved from seed collectors and those retrieved from bird droppings. Independence between rankings (H_0) was tested with a one-tailed probability and rejected in 6 out of 40 cases (n=12). * = p <0.05, ** = p<0.025, *** = p <0.005.

VARIABLE	COMPONENT I		COMPONENT II+III	
	collector	dropping	collector	dropping
Seed disperser				
Longitudinal	.458**	.458**	.275	.092
Transverse	.214	.397*	.031	-.214
Size of fruit crop	.576***	.333	.455**	.333
Species richness	.254	.127	.254	0
Density of woodland				
r=0.3	-.062	0	-.123	.185
r=0.9	0	.303	-.182	0
r=1.5	.030	.333	-.212	-.091
Density of wooded banks				
r=0.3	-.186	-.248	-.124	.248
r=0.9	-.214	-.397*	.031	.092
r=1.5	-.212	-.333	.030	-.091

DISCUSSION

In this study, the effects of birds eating the fruits and dispersing the seeds of various fleshy-fruited plants were studied in an agricultural landscape in which the density of wooded landscape elements varied by more than one order of magnitude. Other researchers (e.g. Snow and Snow 1988) have observed large differences between bird species with respect to selection and processing of fruits similar to those observed qualitatively during this study. Birds that disperse the ingested seeds unharmed ("seed dispersers") can be distinguised from those that eat the pulp or the seeds but do not disperse the seeds ("pulp and seed predators") (Herrera 1984). Willson and Whelan (1993) divided seed dispersers into major and minor dispersers on the basis of their efficiency of dispersal and overall abundance. My distinction into longitudinal and transverse seed dispersers reflects the large differences in fruit and habitat selection, in behaviour and distribution of fruit-eating bird species in an agricultural landscape.

In this study, the longitudinal and transverse dispersers selected fleshy-fruited plant species that are also consumed by fruit-eating birds in southern England (Snow and Snow 1988). According to Snow and Snow, the four longitudinal bird species identified in *this* study consume the fruits of significantly more fleshy-fruited plant species from the regional flora than the four transverse bird species (53-77% versus 28-42%; t-test, $p<0.05$) (Appendix 1). These observations have been confirmed by my study, though it should be noted that several fleshy-fruited plant species that are important food plants in England are unimportant or even absent in the study area; *Cornus sanguinea*, *Evonymus europaeus L.*, *Rhamnus catharticus* (rare in the area), *Lonicera caprifolium L.*, *Sorbus aria (L.) Crantz* and *Viscum album L.* (absent from the area).

Longitudinal dispersers do not appear to have strong preferences for particular types of fruit or growth form but consume the fruit of any tree, shrub, climber and herb species. Passerines such as *E. rubecula* and *S. atricapilla* take fruit smaller than 9 mm, whereas the larger *T. philomelos* and *T. merula* take almost any type of fruit available, regardless of its size. Seeds of the climber *Lonicera periclymenum* are probably dispersed exclusively by longitudinal dispersers as they are more willing or able to sally for the less accessible fruits than transverse dispersers. Species with small crops and/or low abundances such as *Maianthemum bifolia (L.) F.W. Schmidt*, *Rubus idaeus L.*, *Solanum dulcamara L.* and *Vaccinium myrtillus* are probably also exclusively dispersed by longitudinal birds in the study area. By contrast, transverse seed dispersers concentrate on the abundant shrub and tree species which have attractive conspicuous crops with masses of fruit. In the study area, starlings avidly ate the fruit of *Hedera helix L.* in spring and *Prunus avium (L.) L.*, *Amelanchier lamarckii F.G. Schroeder*, *Rhamnus frangula*, *Sambucus nigra* and *Sorbus aucuparia* in summer, whereas the three thrush species in particular ate the fruits of *Prunus spinosa L.*, *Crataegus spp.*, *Ilex aquifolium L.* and *Rosa canina L., s.l.* in autumn and winter. However, extensive field work is required to quantify the differences between these two categories of seed dispersers.

The differences in the number of longitudinal and transverse birds were partly related to the landscape structure. The rankings between bird numbers and density of wooded banks or the density of woodland were not independent in a few cases; longitudinal dispersers are more frequent and abundant in the relatively closed sections of the study area, the transverse dispersers more frequent and abundant in the relatively open sections.

Fleshy-fruited plants

Established individuals of twenty-six fleshy-fruited plant species were recorded in this study on nearly ten kilometres of wooded banks in an agricultural landscape. In the same region, van Ruremonde and Kalkhoven (1991) recorded the presence of 25 fleshy-fruited species in small woodlots. The two studies together identified the presence of 29 species, which is 45% of the entire flora of fleshy-fruited plant species in the Netherlands (van der Meijden 1990). Twenty-two species were common to both wooded banks and small woodlots and the frequencies of fleshy-fruited plant species on both types of landscape elements were correlated statistically significantly. Such a close similarity suggests that the environmental conditions in both landscape elements generally resemble those of their natural habitats, being forest gaps and ecotones between forests and grasslands. Only a few species occurred more frequently on wooded banks (e.g., *Rosa canina* and *Lonicera periclymenum*) or in woodlots (e.g., *Maianthemum bifolia* and *Prunus serotina*). Disparities can be explained by a variety of factors such as differences in parent material (soil conditions), time since disturbance, management (selective cutting and introduction of species) and isolation (distance from source populations). For most species, woodlots will function as stepping stones and wooded banks function as corridors, together forming an ecological network.

One category of fleshy-fruited species was consistently absent from the wooded elements investigated: the shade-tolerant geophyte herbs of forest-interiors such as *Adoxa moschatellina, Arum maculatum, Convallaria majalis* and *Paris quadrifolia*. These species were probably absent due to a lack of seed dispersed by fruit-eating birds to patches outside the few relict populations and/or a poor habitat quality (no mesic conditions sustained for growing plants). Neither woodlots nor wooded banks are likely to facilitate the dispersal of such species within agricultural landscapes. Dzwonko and Loster (1988) also recorded fewer fleshy-fruited herb species in the small woods in the western Carpathian foothills (Poland) that had been more disturbed by man and had been isolated for longer periods.

The evidence that isolation is an important factor affecting the number of fleshy-fruited species in wooded landscape elements is scanty. In their study on woodlots with only minor variation in soils and vegetation structure van Ruremonde and Kalkhoven (1991) could not derive strong evidence that isolated woodlots had fewer fleshy-fruited plant species than non-isolated woodlots. In the analysis of single species, honeysuckle (*Lonicera periclymenum*) was the only species for which a statistically significant inverse relationship was found between the probability of occurrence and the degree of isolation. In the present study, the number of fleshy-fruited species of wooded banks did not correlate statistically significantly with the density of wooded banks and density of woodland within a certain radius (two relevant aspects of isolation) either. These results suggest that despite the differences in density of landscape elements between open and closed sections of the study area, the process of colonization of wooded banks is unlikely to be affected by the landscape structure either. However, it could be erroneous to derive conclusions about the working of a process from the analysis of a pattern. In the present case, the present-day number of fleshy-fruited species of wooded banks may well correlate with the structure of the historical landscape of several decades ago due to the long life-spans of most fleshy-fruited species (tens to hundreds of years). Perhaps more time is needed for the number of fleshy-fruited species to reach equilibrium with the present-day landscape structure (*relaxation effect*).

Seed dispersal by birds in agricultural landscapes

The seed shadows created by various assemblages of fruit-eating birds in agricultural landscapes have been sampled in a few other studies. McDonnell and Stiles (1983) studied the deposition of seeds by fruit-eating birds on two oldfields differing in structural complexity of the vegetation. Holthijzen and Sharik (1985) recorded the seed shadow of red cedar (*Juniperus virginiana L.*) from a forest edge to a grassland along a fenceline. Guevara et al. (1986) studied isolated primary forest trees in tropical grasslands which attract many seed-dispersing birds and bats. Such isolated trees act as recruitment foci and considerably accelerate forest succession. Other researchers (e.g. Debussche et al. 1982) deduced the role of seed-dispersing birds from surveys of seedlings and saplings.

The seed rain on wooded banks in my study area was directly related to the frequencies and abundances of the reproducing fleshy-fruited plant species and was dominated by the five most frequent and abundant plant species. Their high dispersal success can be explained by a combination of several fruit attributes such as smallness of fruits (< 9 mm in diameter), high pulp-to-seed ratio of fresh weights and small seeds that are defecated in clumps rather than regurgitated individually. Moreover, these five species provide ripe fruits from summer to mid-autumn when local resident birds with their offspring mix with numerous migrant and winter resident birds. In the Netherlands as a whole (33,000 km^2), tens of millions of longitudinal and transverse birds are present each year and consume the fruits of many fleshy-fruited plant species and disperse their seeds (Appendix 1). This large pool of avian seed dispersers is likely to reduce the negative effects of distance and barriers on the dispersal interactions between landscape elements.

Few or no seeds of plant species with a low frequency and abundance in the study area were recorded in the seed rain. The total collector surface of 30 m^2 meant that only a tiny proportion of the total seed rain created by seed-dispersing birds was sampled. Fruits of these sparse fleshy-fruited plant species were probably consumed by birds but escaped detection by this method. The positive relations found between the availability of fruits, dispersers and the density of wooded landscape elements on the total volume of the seed rain suggest that wooded banks with large supplies of fruit attract many dispersers which deposit many seeds, including seeds from distant seed sources. The relatively large proportion of immigrant seeds in the seed rain (12.4%) was only statistically significantly related to the availability of fruits, but not to the density of landscape elements nor to the availability of dispersers. This result suggests that for the five most abundant plant species at least, the distances between sources and targets in the study area did not significantly affect the between-habitat dispersal of seeds.

Dispersal of seeds to new sites

The findings of this study suggest that the probability of seed dispersal to new landscape elements in agricultural landscapes is basically governed by (1) the local frequency and abundance of fleshy-fruited plant species, (2) the preferences and mobility of seed dispersers and (3) plant attributes such as crop size, seed size and seed number of single fruits.

With respect to the changes in the landscape structure, I expect for a new landscape element at a certain distance from local seed sources that (i) plant species dispersed by transverse birds will arrive *sooner, more frequently and in larger numbers of seeds* than species dispersed by longitudinal dispersers. The reason is that longitudinal birds generally move only short distances through the network of wooded banks or occasionally use woodlots as stepping stones if wooded banks are absent. Transverse birds are not confined to such a network and move freely between wooded banks, woodlots and the open fields. The plant species that primarily depend on longitudinal birds migrate slowly in a stepwise fashion through the corridor network if the patches posses a sufficient habitat quality to allow recruitment. Plant species that are also dispersed by transverse birds will also arrive on wooded landscape elements that are poorly connected within a network or are isolated from other similar elements.

If the distances between patches or the resistance to bird movements are increased, then a threshold distance will be exceeded where the probability of seed dispersal by longitudinal dispersers becomes close to zero and then immigrant seeds are dispersed solely by transverse birds. This threshold distance is not fixed but varies with the availability of fruits (periods of fruit scarcity) and seed dispersers (invasions). I also expect this threshold distance to be shorter for plants with large and heavy seeds than for plants with small and light seeds.

In relatively *closed* landscapes, the new landscape elements are more or less connected to seed source populations, interpatch distances will be short and both longitudinal and transverse dispersers will visit these new elements. Diversity of fleshy-fruited plants will be 'high' and will consist of species dispersed by both transverse and longitudinal dispersers.

In relatively *open* landscapes, the new landscape elements will remain relatively isolated and will be visited mostly by transverse dispersers, because longitudinal dispersers will be faced by increased travel times and the presence of repulsion elements. Diversity of fleshy-fruited plants will initially be 'low' and will consist of species dispersed by transverse dispersers. Gradually, more plant species will immigrate to a patch via chance dispersal.

Concluding remark

The ecological differences between longitudinal and transverse seed dispersers seem large and meaningful. The transverse birds are more mobile and are able to more frequently bridge larger distances between habitat patches and in larger numbers than longitudinal birds. Moreover, they are less affected by repulsion elements such as open fields, roads and built-up areas in the landscape. Yet, many interactions between birds and plants on the landscape scale remain poorly understood and require further study, especially, the differences between bird species in terms of the selection of fruits, the number of fruits ingested per feeding bout (Snow and Snow 1988), the retention times of seeds in the digestive tract of dispersers (Levey 1986), the duration and frequency of visits, group size (social and flocking behavior), flying patterns within a landscape, and changes in abundance of dispersers in different landscapes (mobility). Such observations will further clarify the many complex interactions between birds, plants and landscapes and their influence on plant population dynamics in fragmented landscapes.

Acknowledgements

I thank the Research Institute for Nature Management for allowing me to study the interactions between fruit-eating birds and fleshy-fruited plants. R. van Hiele and F. Verstappen assisted with the field work. The interpreations of my observations advanced after discussions with J. Armesto, C. Bokdam, M.J. McDonnell, J. Kalkhoven and P. Opdam. F. Berendse and J.M. van Groenendael critically reviewed earlier drafts of this paper.

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Appendix 1 (*see* p. 154)

Characteristics of longitudinal and transverse seed dispersers. Information on fruit selection and foraging behaviour of bird species has been adapted from field studies in England by Snow and Snow (1988) [1], information on the sociability and mobility of eight bird species is from van Hiele (1988) [2], and the general distribution and abundance in the Netherlands has been derived from data in the Atlas of Birds by Sovon (1987) [3]. D and ND indicate whether or not bird species defend fruit sources, D= defended, ND=non-defended, ? = no data.

LONGITUDINAL

SOLITARY
SEDENTARY
SPECIALIZED FEEDERS

VARIABLE				
Fruit-eating bird species Scientific name	Robin *Erithacus rubecula*	Blackcap *Sylvia atricapilla*	Songthrush *Turdus philomelos*	Blackbird *Turdus merula*
Body weight bird (g) [1]	20-22	19	86	96 - 114
Gape-width beak (mm) [1]	7	7.5	10.5	11
Principal foraging method [1]	sally	perch & pluck	perch & pluck	perch & pluck
% of time sallying [1]	68.0%	3.0%	16.9%	9.0%
Defence of fruit sources [1]	no, but territorial	no	no	occasionally
Largest meal size (g) [1]	0.4 - 1.5	0.8 - 1.7	4.6 - 9.8	6.3 - 13.3
as a % of body weight [1]	2 - 8%	4 - 9%	5 - 12%	6 - 12%
Interval between feeding bouts [1] (mean and range; in minutes)	12 (5-25)	12 (6-21)	15 (9-19)	18 (9-28)
Number of spp. consumed [1] (as % of total number = 43 spp.)	29 (67%)	23 (53%)	27 (63%)	33 (77%)
Number of spp. consumed [1] (only species with >5% of all records)	4 (n=629)	7 (n=540)	5 (n=1984)	7 (n=6869)
Species names of latter category [1] (diameter of fruit in mm)	E. europeaus (4.5) Sambucus nigra (6.2) Hedera helix (8.8) Cornus sanguinea (7.3)	Hedera helix (8.8) Sambucus nigra (6.2) Ilex aquifolium (9.3) S. dulcamara (8.6) L. caprifolium (6.1) E. europeaus (4.5) Bryonia dioica (8.4)	Taxus baccata (10.3) Hedera helix (8.8) Prunus spinosa (14.3) Sambucus nigra (6.2) Crataegus spp.(10.7)	Crataegus spp. (10.7) Hedera helix (8.8) Ilex aquifolium (9.3) Rosa canina (12.8) Taxus baccata (10.3) Prunus avium (11.8) Sorbus aucuparia (8.6)
Number of flying/non-flying birds [2]	12/158	9/74	15/47	151/275
Mobility index (N=682)[2]	0.08	0.12	0.32	0.55
Group size: mean (max) [2]	1.2 (3)	?	1.4 (5)	1.8 (9)
Presence in the Netherlands [3]	all year	April-October	all year	all year
as % of all 5x5 km blocks [3]	76-90%	39-83%	66 -90%	87 -90%
Size population (in M=million birds) [3]	0.1 - 1 M	0.2 - 0.5 M	1 - 3 M	5 - 15 M

TRANSVERSE

GREGARIOUS
NOMADIC
OPPORTUNISTIC FEEDERS

VARIABLE				
Fruit-eating bird species Scientific name	Mistle thrush *Turdus viscivorus*	Redwing *Turdus iliacus*	Fieldfare *Turdus pilaris*	Starling *Sturnus vulgaris*
Body weight bird (g) [1]	129 -144	65	118	92
Gape-width beak (mm) [1]	12	9.5	12	9
Principal foraging method [1]	perch & pluck	perch & pluck	perch & pluck	perch & pluck
% of time sallying [1]	12.3%	7.7%	1.2%	<0.1%
Defence of fruit sources [1]	yes	no	occasionally	no
Largest meal size (g) [1]	4.1 - 13.0	2.0 - 5.7	6.3 - 7.2	2.5 - 6.6
as a % of body weight [1]	3 - 9%	3 - 8%	6 - 7%	3 - 7%
Interval between feeding bouts [1] (mean and range; in minutes)	?	?	14 (7-20) ND 21 (17-26) D	?
Number of spp. consumed [1] (as % of total number = 43 spp.)	18 (42%)	14 (33%)	12 (28%)	15 (35%)
Number of spp. consumed [1] (only species with >5% of all record:	5 (n=1450)	6 (n=1819)	4 (n=1676)	5 (n=4621)
Species names of latter category [1] (diameter of fruit in mm)	Ilex aquifolium (9.3) Viscum album (8.3) Taxus baccata (10.3) Hedera helix (8.8) Crataegus spp.(10.7)	Ilex aquifolium (9.3) Crataegus spp.(10.7) Hedera helix (8.8) Sorbus aria (11.0) R. catharticus (8.6) Cornus sanguinea (7.3)	Crataegus spp.(10.7) Rosa canina (12.8) Hedera helix (8.8) Ilex aquifolium (9.3)	Cornus sanguin. (7.3) Taxus baccata (10.3) Sambucus nigra(6.2) Rubus fruticosus - Hedera helix (8.8)
Number of flying/non-flying birds [2]	114/160	158/109	28/7	1396/264
Mobility index (N=682)[2]	0.71	1.45	4.00	5.29
Group size: mean (max) [2]	4.7 (26)	8.7 (49)	4.7 (26)	14.7 (75)
Presence in the Netherlands [3]	all year	September-April	August-May	all year
as % of all 5x5 km blocks [3]	54-75%	29-90%	61-91%	91-93%
Size population (in M=million birds) [3]	0.01 - 0.1 M	1 - 10 M	1 - 10 M	10 - 25 M

MANAGEMENT IMPLICATIONS

For the first time in recent history, there are great opportunities to give nature more space and to restore the ecosystems that have become endangered during this century. The results in this thesis however, suggest that restoration processes cannot completely undo the decline in plant species diversity that has taken place and that long time periods can be lapsed before the desirable species have recolonized the target areas.

Although most restoration projects in the Netherlands are quite recent, they can already be classified into relatively "successful" and "unsuccessful" ones. The factors that critically determine success or failure in the restoration of ecosystems are the presence of gaps in the vegetation, the availability of plant propagules and associated dispersal vectors and the performance of species to germinate, grow and compete (Pickett et al. 1987). These factors fit into the concepts of accessibility and suitability. *Accessibility* is concerned with the spatial configuration of seed sources and gaps in the vegetation with respect to the dispersal capacity of plants. *Suitability* is concerned with the habitat quality of gaps with respect to the germination and establishment requirements of desirable species and its neighbours (van Groenendael 1995).

If we focus on those areas where the restoration of wet nutrient-poor ecosystems has been attempted, the "successful" examples include the meadows in the upper reaches of small streams in the catchment-area of the *Drentse A* (Bakker 1989, Grootjans et al. 1993). Here, successes of the restoration of wet nutrient-poor ecosystems on set-aside land can be attributed to the relatively high density of semi-natural areas of great ecological value, easily to restore geohydrological factors conducive to wet nutrient-poor growing conditions and the presence of active dispersal vectors in the landscape such as free-ranging large herbivores and inundating small streams. Thus, the conditions to increase both the accessibility and suitability of particular areas in this landscape suffice the restoration of species-rich meadows.

The "unsuccessful" examples include the meadows undergoing restoration in heavily exploited agricultural landscapes such as the Veenkampen in the *Binnenveld* area (*this thesis*). Here, the principal *factors impeding a full restoration* include the difficulty to restore the upwelling of base-rich groundwater to the root zone of the soil, the isolated position of the experimental set-aside area *Veenkampen* relative to the few fragmented nature reserves, the few remaining refugia on the banks of ditches in a heavily exploited agricultural landscape and the absence of actively operating dispersal vectors such as those present in the *Drentse A*-area. The measures to increase both the accessibility and suitability of habitat patches in this landscape did not up till now suffice for a complete restoration of the former species-rich meadows.

A landscape ecological comparison regarding the accessibility and suitability aspects of both systems could reveal their relative importance to the restoration of wet nutrient-poor ecosystems in each landscape. The case of the Veenkampen is an interesting one because as it has shown the two fundamental problems which arise when former heavily exploited agricultural fields are to be transformed into specific types of nature. These problems were:

1. improvement of the site *accessibility* to diaspores which is determined by :
    - contents of seed banks in the soil
    - numbers and distribution of refugia in surroundings
    - presence and efficacy of various dispersal vectors
    - seed production of populations in refugia
    - properties of seeds of the species involved

2. improvement of the site *suitability* for the selected species is determined by:
    - soil fertility, soil pH, soil calcium content, groundwater level
    - productivity and structure of the vegetation
    - presence and dynamics of gaps
    - germination and establishment requirements of species

Both the accessibility and the suitability of a target area need to be improved if the main management or policy goal has to be achieved. In the past, the attention of ecologists and planners has been focused on the second aspect, thereby assuming that the propagules of desirable species are everywhere and that once the habitat of species is realized, the species will be present almost instantaneously. The results in this thesis show that this assumption is not valid for the *Veenkampen* site, and probably in many other cases as well.

Both problems will be discussed briefly below and conclusions and recommendations for management and research derived from this thesis, will be given as well.

SITE ACCESSIBILITY

The first question concerning the accessibility of a target area is *"where are the desirable species in the landscape"?*

The **first** option would be to look for remnant seeds in the soil of the desirable species once present. It has been well established that soils may contain significant numbers of seeds of species that are not part of the vegetation. Chapter 1 shows that several species typical of wet nutrient-poor conditions (especially *Carex* spp.) reappeared almost exclusively on sod-stripped plots, most likely through the recruitment from old buried seeds. The soil seed bank is thus a vital asset in the restoration of species-rich meadows. Historical records of the botanical composition of fields could help to select the desirable plant species that were present in the former species-rich fields, but were still absent from the fields undergoing restoration.

Surprisingly, a species such as *Gentiana pneumonanthe* which is known to have a transient seed bank, was also recruited on a sod-stripped plot. As this species is regionally extinct, its reappearance strongly suggests that a minute fraction of the seed pool was buried in the deeper layers of the soil and remained viable until sod stripping provided the appropriate germination and establishment conditions for this species.

The results of the burial experiment of Chapter 4 corroborates this supposition as it indicates that long-term survival of seeds is probable once seeds have entered the deeper soil layers. It is important that information will be collected on the decay rates of buried seeds of wild plant species in relation to varying levels of the moisture content of the soil (i.e. different groundwater levels), the type and frequency of soil disturbances as a result of different cultivating practices and the level of supply of inorganic fertilizers. This information can be used in combination with historical land-use data to select those fields which have preserved the original topography best and which may still contain (some) seeds of the desirable species.

Moreover, this information could be used by planners and reserve managers who want to restore community types on the so-called *nature restoration areas.* These areas have low actual ecological values due to previous agricultural practices such as ploughing and reseeding of fields, but presumably have high potential ecological values. Because soil seed banks will be depleted in many such nature restoration areas, the restoration of specifically those fields with undisturbed soil profiles deserves a higher priority.

The **second** option would be to look for desirable species in refugia in the surroundings of a target area. Especially when the soil seed bank has been depleted, recolonization can only result from the immigration of seeds from neighbouring sources. Moreover, not all species do form persistent seed banks (Chapter 1).

It was clearly shown that many plant species typical of the former species-rich plant communities were still present in the landscape in refugia on ditch banks (Chapter 1 and 2) and wooded banks (Chapter 6). Actually, we discovered the refugia on ditch banks of more plant species than was expected originally: 106 out of 145 (73%) species have survived fifty years of intensive agricultural farming, including 21 species (14%) that were missing from the target area but were still present on ditch banks in the surrounding landscape.

Although vegetation types such as the ecologically highly indicative *Cirsio-Molinietum* and the associated landscape of the *Binnenveld* of 50 years ago have gone, it seems that the majority of plant species has survived in spite of the high pressures of the agricultural practices. The species that did become regionally extinct were stress-tolerators (*sensu* Grime) that are typical of wet nutrient-poor conditions, that have transient seed banks and depend on seasonal regeneration in vegetation gaps. I expect that among the regionally and locally extinct species, those species with a long-range dispersal of seeds and/or a permanent seed bank should be able to recolonize the lost habitat patches, either through the direct input of long-range dispersed seeds or through the recruitment of old buried, dormant seeds from the soil seed bank. The species with a short-range dispersal of seeds and/or transient seed banks may recolonize lost patches only through a stepwise migration along linear landscape elements or through a deliberate re-introduction of seeds.

The second related question then is *"by which vector and how far are seeds dispersed from their sources"* ?

The answer to this question is important when species have become locally or regionally extinct and their soil seed banks have been depleted. In that case, seeds have to be dispersed from more remote seed sources.

Dispersal of seeds occurs via different vectors such as water, wind, animals and humans. Dispersal by water (*hydrochory*) is a powerful vector to bring back the seeds of the desired species to a target area. Many wet meadow species have evolved specific adaptations such as air sacs (e.g. the utricles of various species of *Carex*) to disperse their seeds via water, owing to their origin as species of river flood plains. In areas undergoing restoration, the question often is whether this dispersal vector can be reactivated at all, e.g. by allowing streams to shape their own meandering course and riverbeds to become flooded. The result of such a policy would be that the riverbed will become more frequently inundated and that seeds will be deposited across the entire gradient of inundation. Another strategy would be to preserve autochtonous rainwater and upwelling groundwater in order to create areas that are attractive to seed dispersing waterfowl.

If the role of water as a dispersal vector cannot be reactivated as in the case of the Veenkampen, then dispersal by wind (*anemochory*) is the most important dispersal vector. To determine its efficacy as a dispersal vector, a wind tunnel was used to estimate the dispersal distances of various seed forms under varying release heights and wind speeds (Chapter 3). In a wind tunnel, beyond relatively small distances from a seed source (say >10 m), the probability of seed deposition becomes effectively close to zero, in the order of 1 seed per ha which is no doubt beyond the detection limit in the field.

The wind tunnel experiment also revealed that the tail of frequency distributions is potentially much longer than is estimated from exponential decay models, in the order of tens of metres rather than in metres. Although strong winds in the dispersal season of most plant species are quite rare, the importance of such erratic events cannot be ignored. Populations of long-lived perennial plant species may in fact be less isolated than is believed and consequently, metapopulations may be structured on larger spatial scales.

The wind tunnel can further be used to determine effectively the importance of relevant aerodynamic properties of seeds such as diameter, mass, shape and specific mass. Other biological relevant factors include the height of the surrounding vegetation, the phenology of fruiting and the strength of the bondage between seed and parent which determines the biologically meaningful minimal release speeds which are necessary to dislodge the seeds. These factors together determine the seed shadow around an individual source.

In reality, seeds will be dispersed not by just a single dispersal vector but by various vectors in concert (*polychory*). Wind-dispersed seeds in a farmed landscape are also likely to be transported by animals (both externally and internally) as well as by running water (e.g. small streams, ditches) and by man (e.g. agricultural machinery). If one studies the dispersal aspects of recolonization of an area, ideally the entire spectrum of dispersal vectors should be taken into consideration and one should not solely study the dispersal by one particular vector.

It is fair to say that our knowledge of seed dispersal mechanisms of plant species is still very limited. The precise data and models to accurately predict the number and types of seeds a target area will receive are not yet available. Although dispersal studies have a great significance to e.g. succession and metapopulation theory, few ecologists seriously study the seed dispersal ecology of plants. This is especially problematic with respect to the restoration of ecosystems.

SITE SUITABILITY

We have concluded that seeds can enter an area undergoing restoration through emergence from the soil seed bank and/or through dispersal of seeds from neighbouring seed sources via various dispersal vectors. If seed banks have been depleted and dispersal vectors cannot be reactivated, then seeds of the desirable species have to be introduced deliberately. If one declines deliberate introduction of seeds, then one accepts that restoration of the former species-rich meadows remains incomplete. In all other cases, the next question regards the suitability of an area: *"what is the fate of naturally deposited and buried seeds"* ?

In the Veenkampen with a clay-on-peat soil, a large buffer of organic material ensures that monocotyledonous species of relatively nutrient-rich sites will dominate the vegetation for the time being. In the dense sward, gaps are very few and competition with grasses is intense. The management measures applied since 1978 have been directed at reducing the soil fertility and raising the groundwater level in order to restore the wet nutrient-poor growing conditions, but have been only partially successful. Moreover, very few seeds appear to reach the site naturally and very few opportunities arise for the immigrated seeds to germinate and establish in the intact sod.

In the intact sod, whether mown or grazed, the probability to establish was very small. Seeds did not germinate in the intact vegetation, probably because of unfavourable red/far-red ratios and insufficient temperature fluctuations to break the dormancy of seeds. If seeds did germinate, seedlings died, because of the intense above-ground competition for light and below-ground competition for water and *nutrients, with the dominant (grass) species.*

The findings of the seed addition experiment show that all selected species depended on regeneration in vegetation gaps; only species with large seeds were able to establish in the intact vegetation but at much lower densities and with lower reproductive output than on sod-stripped plots. More research should be directed towards quantifying the environmental attributes of different types of vegetation gaps, i.e. the levels of red and far-red light and temperature fluctuations within gaps, in combination with the germination requirements of the plant species of interest.

MIGRATION OF SPECIES ALONG CORRIDORS

If a site is suitable for germination and establishment, but seeds are not present in the seedbank or only available from remote sources, then the next question becomes *"are landscape elements such as ditch banks in a fragmented farmed landscape, effective corridors which enhance the recolonization of regionally and locally extinct plant species"* ?

The mapping of several plant species indicated that on a landscape scale, populations appeared to be truely isolated because their short-range dispersed seeds will not be capable to recolonize the remote sites that experienced extinctions in the past.

From simulation experiments in Chapter 5, it became clear that linear landscape elements are not effective corridors for plants with short-range seed dispersal in fragmented landscapes, because the calculated migration rates were very low (<5 m/yr). Moreover, landscape elements are likely to have low proportions of high quality patches, while refugia and suitable habitat patches are often located kilometres apart. These circumstances make a cohesive infrastructure for plants with restricted dispersal of seeds rather elusive. Especially for regionally extinct species that have short range dispersal of seeds (with closest sources kilometers away) and/or a limited viability of seeds once buried in the soil, very little possibilities exist for those species to recolonize lost sites without help.

INTRODUCTION OF SPECIES

If migration is not a likely scenario, then deliberate introduction is a final option. In order to decide when introduction of seeds of desirable species should be advocated, 8 possible cases are presented which follow from combining three criteria: presence of (i) seedbanks in the soil, (ii) refugia in the surroundings and (iii) effective corridors in the landscape (Table 1). This assumes that suitability of a habitat for the target species can be restored by appropriate management which provides colonizable gaps at the right moment and reduces the competition from resident species by mowing and removal of the harvested biomass.

Cases 1 and 2 unfortunately appear to be the most frequent in agricultural landscapes (as in the case of the Veenkampen). Cases 3 and 6 also occur in agricultural landscapes but are not relevant in the case of ecosystem restoration. In cases 4 and 8, individual populations are effectively structured as a metapopulation and the latter situation could be regarded as the ideal situation. In case 7, ecologically sound management of ditch banks by farmers could improve the growing conditions for the less critical plant species. In case 5, sod stripping may stimulate that buried seeds in the soil seed bank start to germinate and establish.

Table 1. Eight cases which follow from combining three criteria: presence of (i) seedbank (-: seed bank absent; + seed bank present), (ii) refugia (-: regionally extinct; + reproductive populations in refugia) and (iii) corridors (-: landscape elements ineffective as corridors, barriers to migration; +: elements effective as corridors). The cases apply to plant species with dispersal problems that recolonize sites undergoing restoration..

CASE	SEEDBANK	REFUGIA	CORRIDORS	INTRO- DUCTION
1	-	-	-	yes
2	-	+	-	yes
3	-	-	+	yes
4	-	+	+	no
5	+	-	-	no
6	+	-	+	no
7	+	+	-	no
8	+	+	+	no

It can be argued from this table that if restoring *biodiversity* is the primary goal, the best way (in 2 out of 8 theoretical cases) to preserve endangered plant species with dispersal problems would be to harvest *seeds from local seed sources and to introduce them at suitable habitat* patches. If restoring biodiversity is *not* the primary goal, then the development of plant communities demanding less critical growing conditions is to be preferred and deliberate introduction of seeds is not an option.

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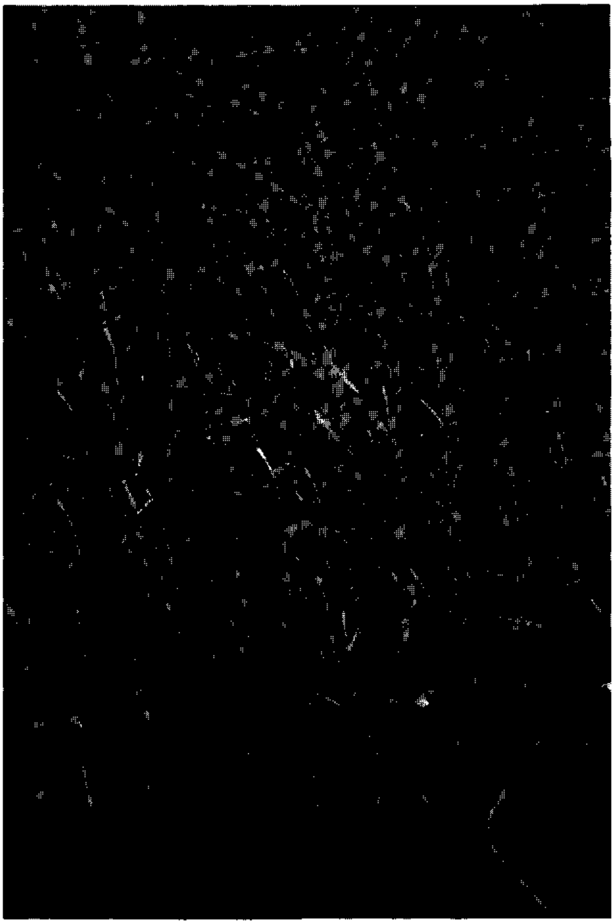


Wet nutrient-poor meadow rich in plant species such as Cirsium dissectum and Sanguisorba officinalis (Veerslootslanden)

SUMMARY

The restoration of species-rich meadows on former agricultural land in the Netherlands has a high priority, because these ecosystems have been disappearing rapidly due to eutrophication and acidification and falling water tables. In order to be able to restore such ecosystems on wet nutrient-poor soils, the *suitability* and *accessibility* of target sites have to be improved.

The starting point for the restoration of species-rich meadows is frequently a soil that has been drained and enriched with fertilizers and polluted with pesticides for decades. Increasing the suitability of a site then involves ameliorating the habitat quality for the selected plant species by rewetting the soil, by reducing the availability of nutrients to plants through cutting and grazing and by removing the enriched topsoil, so that new individuals can establish. It is generally assumed that seeds are still available or will soon become available. This is not necessarily always the case. There are two alternative strategies by which plants may (re)colonize new sites; either through the germination of seeds buried in the soil or through the dispersal of seeds.

In situations where soil seed banks have been depleted, dispersal of seeds from neighbouring sources via water, wind, animals and humans is the only natural option to restock a site with seeds. Since most grassland species have a limited dispersal capacity, the distances between seed sources and target sites become crucial. Ecological corridors could facilitate the dispersal of species in agricultural habitats if they satisfy the habitat requirements of the selected species.

This thesis deals with a few aspects of the regeneration ecology of several meadow plant species (Chapters 1-5). Two questions are raised in particular: is it possible to restore species-rich meadows on previously farmed fields? and do ditch banks function as ecological corridors for species that are absent from a site undergoing restoration? To provide a contrast with typical grassland species, fleshy-fruited plant species and their specific dispersal characteristics have also been studied (Chapter 6).

Chapter 1 describes the first phase of the restoration of species-rich meadows on former agricultural land in an intensively farmed landscape in the centre of the Netherlands. A comparison between the species pools of the former (pre-1950) species-rich meadows, a set-aside area undergoing restoration and the ditch banks in the surrounding farmed landscape, revealed that 106 out of the 145 meadow species of the former species-rich meadows were still present in refugia on ditch banks. Eighty-five out of these 145 meadow species have survived or already recolonized the set-aside area, but another 60 species has not yet recolonized the site due to insufficient seed dispersal, depleted soil seed banks and/or too few appropriate microsites in the vegetation for germination and establishment.

An increase in the number of meadow species would be attainable if the accessibility and suitability of the site can be maximized. The effectiveness of the dispersal vectors water, humans and animals is extremely limited in the study area, leaving wind as the principal dispersal vector. Although some of the missing (extinct) species with long-range dispersal or permanent seed banks will reach the site without help, most species will not re-establish without being introduced deliberately.

Chapter 2 analyses the dynamic distribution of ten perennial plant species typical of species-rich meadows in a Dutch agricultural landscape (220 ha). Mapping in 1990, 1991 and 1992 showed that ditch banks in the study area (comprising a set-aside area and the surrounding farmed landscape) form an important refugium for the selected species. Ditch banks were managed by regular mowing plus removal of the harvested biomass in the set-aside area and by grazing, mulching and dredging in the farmed landscape. In the set-aside area, seven species were more frequent, whereas two species were less frequent. One species did not differ in frequency between the two areas.

The distribution of the selected species varied greatly between years, suggesting frequent extinction and colonization events. This type of variation was expressed as E/C, i.e. the mean ratio of the number of extinctions and colonizations. The overall E/C index for all species and all years was 0.99. Four species appeared to be decreasing in distribution in the study area ($E/C>1.0$), six species appeared to be stable ($E/C=1.0$) or even increasing ($E/C<1.0$). A related index used was the proportion of cells that was occupied permanently ($P/(T+P)$).

For the the selected plant species, the variation in the indices E/C and $P/(T+P)$ was related to five life-history attributes (seed weight, dispersal mechanism, dispersal distance, ability to vegetatively spread and seed bank type) and proved to be not significantly associated. It is concluded that different combinations of life-history attributes (i.e. regeneration strategies) lead to species stability in this type of agricultural landscape.

Chapter 3 explores the effects of five wind speeds (variable V: 2-13.5 m/s) and five release heights (variable H: 0.2-0.6 m) on the dispersal distances of seeds of six barochorous grassland perennials in a wind tunnel. The variation in dispersal distances within a seed population and between species with different aerodynamic attributes was expressed as 1-percentile, mode and 99-percentile values. Regression analyses showed that a model with three terms (V, $V*H$ and V^2) best explained the variance in the dispersal distances across all species. According to the regression models, the dispersal distances of seeds in the tail of a frequency distribution (99-percentile values) increased exponentially with wind speed. At wind speeds of 14 m/s, predicted maximum distances were 10 to 15 m for small and relatively heavy spherical seeds and 20 to 30 m for large and relatively light cylindrical or disk-like seeds.

A review of meteorological data showed that wind gusts >10 m/s at plant height occur at least annually. The long life-spans of plants of the selected species (up to several decades) suggests a large potential for long-range dispersal during their life-time. Individual populations appeared to be less isolated from other populations than can be inferred from distribution patterns of seed sources.

Chapter 4 reports on the success of establishment after adding seeds of ten selected perennial plant species to a grassland undergoing restoration. The recolonization of former agricultural grasslands by perennial grassland species is assumed to be delayed or even prevented by a lack of seeds, by a lack of microsites offering opportunities for germination and establishment, or by both.

Sampling the seed rain with sticky traps recorded the seeds of resident species and ubiquitous wind-dispersed species of the genera *Betula*, *Cirsium* and *Epilobium*. Given the spatial distribution of seed sources in the surrounding agricultural landscape and the limited dispersal capacity of the selected species, the fields of the restoration site are largely inaccessible. Lack of seeds was a major cause of their absence.

Seeds of ten plant species were also added to a sward that was mown, clipped or from which the sod had been stripped. Established plants were allowed to grow for two years and then harvested. The establishment success of the selected species on sod-stripped plots was significantly higher than on mown or clipped plots. Differences between these treatments can be explained by the low density and short duration of gaps in the intact (mown and clipped) vegetation. Differences between species were related to seed weight; species with large heavy seeds had a significantly higher establishment success than species with small and light seeds. The lack of appropriate microsites, especially for species with small seeds, was another cause of their absence.

Recruitment from old buried seeds is another recolonization route. Burial of seeds for two years revealed very low mortality rates in species with small, spherical and hard-coated seeds, and moderate mortality rates in species with seeds of high area/content ratios and direct germination. Species of the first group are expected to be frequently recruited from seeds buried in the soil when sod stripping has been applied.

Chapter 5 explores the importance of linear landscape elements as ecological corridors. A cellular automaton model was built in order to determine the relative importance of the principal factors which determine the rate of migration of plants through corridors: the width and habitat quality of patches within a corridor (expressed as the population growth rate λ) and the dispersal capacity of plants (expressed as the slope α of the relationship between seed number and log-distance).

Simulations with the model using different levels of the principal factors indicated highly significant and positive main effects of dispersal capacity, habitat quality and width of corridors on the rate of migration. Significant interactions existed for dispersal capacity x width and dispersal capacity x habitat quality, indicating that the effects of width and habitat quality depended on the dispersal capacity. In narrow corridors most of the dispersed seeds were deposited outside the corridor, which significantly reduced migration rates, especially for species with long-range dispersal of seeds. In wide corridors (up to 20 m), seed losses were much smaller and migration rates approximated those of continuous habitats. The contribution of the few long-range dispersed seeds to the rate of migration was significant when the quality of habitat patches was high. In all simulations, migration rates were <5 m/yr.

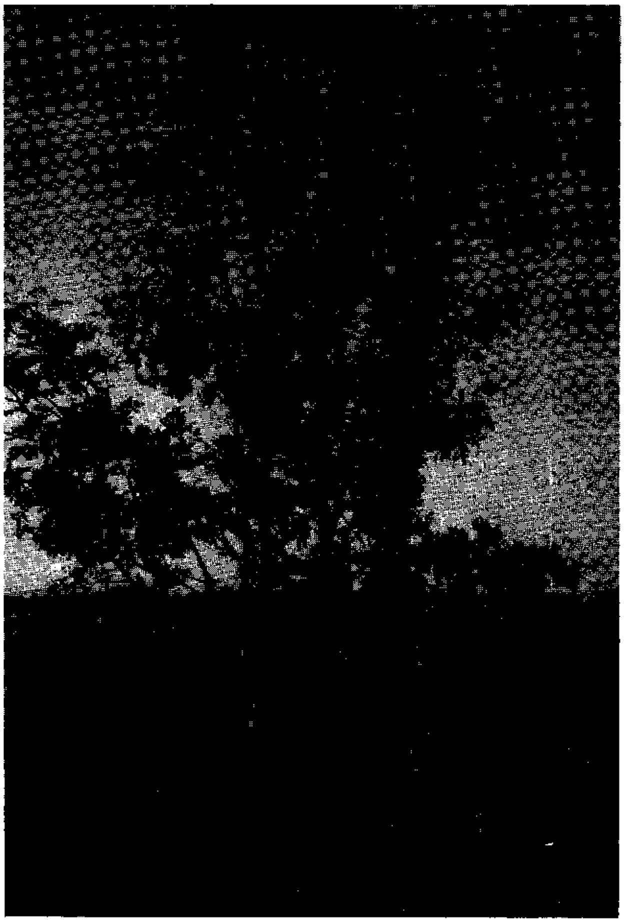
Linear landscape elements are not effective corridors for plants with short-range dispersal of seeds, because migration rates are low (<5 m/yr), high quality patches are few, and refugia and suitable habitat patches are frequently several kilometres apart, making a cohesive infrastructure for plants elusive.

Chapter 6 deals with the dispersal interactions between fruit-eating birds and fleshy-fruited plants that grow on wooded banks in an agricultural landscape in Twenthe, Overijssel province, the Netherlands. Wooded banks are a characteristic feature of the landscape, but their density in the landscape is changing, i.e. in some areas wooded banks have been removed whereas new banks are being planted elsewhere. On average, there were 7 fleshy-fruited plant species per 100-m transect (the range was 2 to 14 species). The number of fleshy-fruited species of the transects did not correlate with the density of wooded banks or of woodland.

Eight fruit-eating passerine bird species were regarded as the major avian seed dispersers. They were divided into *longitudinal* dispersers which carry the seeds of the majority of fleshy-fruited species over short (<0.1 km) distances only and *transverse* dispersers which carry the seeds of species with conspicuous fruit crops over larger distances (>0.1 km). Seed dispersal by longitudinal dispersers is limited to the network of wooded landscape elements whereas transverse dispersers frequently disperse seeds to and from dissimilar landscape elements.

The bird-mediated seed rain on wooded banks was sampled in twelve transects by using 120 seed collectors and by systematically collecting bird droppings. The seed rain was dominated by *Rubus fruticosus, Sorbus aucuparia, Rhamnus frangula, Lonicera periclymenum* and *Sambucus nigra.* The density of the seed rain was 215 ± 68 seeds m^{-2}. Most seeds (87.6%) were deposited during the fruiting period of the plant species involved; the rest (12.4%) was deposited when ripe fruits were no longer available or was deposited on transects where fruiting adults were absent and should be regarded as immigrants.

In order to clarify the complex interactions between birds, plants and landscapes, the ecological differences between longitudinal and transverse dispersers deserve more attention. It will help to better predict the consequences of changing the density of wooded landscape elements on the species richness and distribution of fleshy-fruited plants in fragmented landscapes.



Berries of Sorbus aucuparia are avidly eaten by fruit-eating birds

SAMENVATTING

In dit proefschrift wordt verslag gedaan van een onderzoek naar de mogelijkheden voor het herstel van soortenrijke graslanden op voormalige landbouwgronden. Daarbij is in het bijzonder aandacht besteed aan de rol van zaaddispersie. Soortenrijke graslanden in Nederland zijn sterk in natuurwaarden achteruit gegaan als gevolg van ontwatering en bemesting van deze ecosystemen. Het herstel van met name natte schraallanden heeft een hoge prioriteit in het natuurbeleid van de overheid.

Bij het herstel van natte schraallanden spelen twee begrippen een belangrijke rol, te weten *toegankelijkheid* en *bereikbaarheid*. Om een ontregeld ecosysteem weer toegankelijk te maken voor plantesoorten van natte, voedselarme standplaatsen is het allereerst noodzakelijk bepaalde inrichtings- en beheermaatregelen te nemen. Hieronder vallen het verhogen van.de grondwaterstand en het verminderen van de bodemvruchtbaarheid. Een geschikt milieu voor de nieuwe of verdwenen plantesoorten kan bevorderd worden door respectievelijk het vasthouden van gebiedseigen water en het maaien en afvoeren van de geproduceerde plantenbiomassa dan wel door het afplaggen van de bodem. Daarbij moeten er voldoende open plekken in de bestaande vegetatie beschikbaar zijn die kieming en groei mogelijk maken. Deze ontstaan doordat er kleine of grote verstoringen van de bodem optreden, waardoor lokaal planten kunnen doodgaan.

Het herstel van soortenrijke graslanden kan echter niet beperkt blijven tot het terugbrengen van de oorspronkelijke abiotische condities. Het terrein moet ook bereikbaar zijn voor de gewenst maar nog ontbrekende plantesoorten. In een sterk versnipperd cultuurlandschap kan de beschikbaarheid van zaden een beperkende factor zijn. De vraag is óf er in de bodem nog kiemkrachtige zaden van de oorspronkelijk aanwezige plantesoorten bewaard zijn gebleven. Indien dit niet het geval is, is het de vraag óf zich in de omgeving van een terrein nog effectieve zaadbronnen bevinden en óf de geproduceerde zaden het terrein kunnen bereiken. Indien het antwoord op alle drie vragen negatief is, is het vervolgens de vraag óf slootkanten als corridors voor plantesoorten met een beperkt dispersievermogen kunnen fungeren. Wanneer blijkt dat ook dat niet het geval is, kan het gewenst of noodzakelijk zijn om plantesoorten door middel van zaaien te herintroduceren.

In dit proefschrift zijn enkele facetten van het herstelproces van natte schraallanden op de Veenkampen in het Wageningse Binnenveld onderzocht (Hoofdstuk 1-5). In Noordoost Twente is een ander aspect van bereikbaarheid bestudeerd, namelijk de verbreiding van besdragende struiken door vogels in relatie tot de landschapsstructuur (Hoofdstuk 6).

In **Hoofdstuk 1** wordt de eerste fase van het herstel van natte schraallanden op de Veenkampen beschreven. De Veenkampen is een proefaccomodatie (13.2 ha) in het open cultuurlandschap van het *Binnenveld* dat door de overheid grotendeels is aangewezen als natuurontwikkelingsgebied. De vernatte graslandpercelen zijn sinds 1978 niet meer bemest en aangenomen wordt dat deze toegankelijk zijn voor een reeks van soorten die tot op heden nog ontbreken.

Een vergelijking tussen de flora van de percelen van vóór 1950, en die van de huidige Veenkampen en van de slootkanten in de omgeving laat zien, dat 106 van de 145 plantesoorten van de blauwgraslanden verrassend genoeg nog langs slootkanten in de directe omgeving van de Veenkampen aanwezig *waren, 39 soorten waren regionaal of lokaal uitgestorven.* Van deze 106 soorten hebben 85 soorten zich inmiddels weer op de Veenkampen gevestigd of stand gehouden. Dit betekent dat 60 soorten (145-85) het doelgebied nog niet hebben bereikt als gevolg van het ontbreken van kiemkrachtig zaad in de bodem, het ontbreken van refugia in de directe omgeving of een onvoldoende vermogen het terrein door middel van zaaddispersie te bereiken.

In een cultuurlandschap als het Binnenveld is de wind de belangrijkste vector in de verbreiding van gewenste nog ontbrekende plantesoorten. Aangezien het herstel van overige vectoren (dieren, water) niet aan de orde is, zal het herstel van natte schraallanden beperkt blijven. Veel soorten zullen het gebied niet te weten te bereiken of pas na zeer lange tijd; herintroductie kan dan worden overwogen.

In **Hoofdstuk 2** wordt de verspreiding van tien overblijvende plantesoorten van soortenrijke graslanden in een gebied van 220 ha rondom de Veenkampen geanalyseerd. Gedurende drie jaar is de verspreiding langs slootkanten gekarteerd en in verband gebracht met het gevoerde slootkantenbeheer en met eigenschappen van de plantesoorten zelf.

De kaarten laten grote verschuivingen in de verspreiding zien en suggereren dat op landschapsschaal lokale extinctie en kolonisatie frequente gebeurtenissen zijn. Een index om deze veranderingen weer te geven is de ratio van het aantal extincties en kolonisaties (E/C). Voor vier soorten was deze ratio <1.0 (de soort gaat achteruit), voor zes soorten was deze gelijk aan 1.0 (de soort is stabiel) of >1.0 (de soort gaat vooruit). Een andere gebruikte index (P/(T+P)) betrof de verhouding tussen het aantal permanente bezette plekken (P) en tijdelijk bezette plekken (T); deze index varieerde van .15 (*Thalictrum*) tot .51 (*Hypericum*).

Beide indices werden voor elke soort in verband gebracht met de kenmerken zaadgewicht, dispersie-mechanisme, dispersie-afstand, vermogen tot vegetatieve verbreiding en het type zaadbank. In géén van de gevallen waren de verbanden statistisch significant. De conclusie luidt dat met name de soorten met aanvullende regeneratie-kenmerken kunnen overleven in een cultuurlandschap.

In **Hoofdstuk 3** wordt het vermogen van zaden om door de wind te worden verplaatst experimenteel onderzocht in een windtunnel. Zaden van zes soorten die sterk verschillen in vorm, gewicht en grootte werden op verschillende hoogten (H: tussen 0.2 en 0.6 m) en bij verschillende windsnelheden (V: tussen 2.0 en 13.5 m/s) losgelaten en op plakstroken weer opgevangen. Uit de statistische analyse bleek een algemeen model met drie termen (V, $V*H$ en V^2) de variatie in dispersie-afstanden het best te beschrijven. De dispersieafstanden van zaden in de staart van de frequentie-verdeling ("*99-percentiel*") namen exponentieel toe met de snelheid van de wind. Voor relatief kleine en zware zaden varieerden de geschatte afstanden bij een windsnelheid van 14 m/s tussen de 10 en 15 m; voor lichte, ronde en afgeplatte zaden tussen de 20 en 30 m.

Dergelijke dispersieafstanden zijn groter dan doorgaans in het veld kunnen worden vastgesteld. Het dispersievermogen van vooral lang-levende planten wordt dan ook sterk onderschat. Voor lang-levende soorten kunnen stormen in het dispersie-seizoen met een (zeer) lage frequentie (bijv. eens per 25 jaar) extra belangrijk zijn voor het kunnen herbezetten van lege geschikte plekken in het landschap.

In **Hoofdstuk 4** worden de factoren onderzocht die het succes van introductie van soorten bepalen. Het uitblijven van vestiging van de 10 plantesoorten van Hoofdstuk 2 op de Veenkampen kan te wijten zijn aan het ontbreken van zaad, aan de afwezigheid van geschikte kiem- en vestigingsplekjes of aan beide.

De zaadregen werd bemonsterd met behulp van plakbakjes. De opgevangen zaden waren voornamelijk afkomstig van windverspreiders (*Betula, Cirsium, Epilobium*) en ter plekke reeds aanwezige soorten (*Juncus*). Uit de positie van de zaadbronnen in het omringende landschap, hun zaadproductie en het dispersievermogen van zaden kon worden afgeleid dat de bereikbaarheid van de Veenkampen voor de meeste soorten onvoldoende is. Het ontbreken van zaad is dus een belangrijke oorzaak voor het ontbreken van soorten in de vegetatie.

De toegankelijkheid van de Veenkampen werd vervolgens getoetst door zaden te zaaien in veldjes van 0.25 m^2 die (i) 2x per jaar werden gemaaid, (ii) regelmatig geknipt of (iii) waarvan aan het begin van de veldproef de bovenste 5 cm werd afgeplagd. Na twee groeiseizoenen werden alle opgekomen planten geoogst. Het bleek dat in de intacte vegetatie de kans op vestiging en bloei voor alle soorten significant kleiner is dan in de afgeplagde veldjes. Blijkbaar zijn er in de intacte vegetatie, als gevolg van de hoge bodemvruchtbaarheid, nog steeds te weinig open plekjes beschikbaar, die geschikt zijn voor succesvolle kieming en vestiging. Blijkbaar is het ontbreken van voldoende geschikte kiem- en vestigingsplekjes is een tweede belangrijke oorzaak voor het ontbreken van de gewenste soorten.

Als immigratie van zaden nagenoeg uitgesloten is, dan vormt de kieming van slapende zaden die bewaard zijn gebleven in de bodem een alternatief. Een experiment waarbij begraven zaden op regelmatige tijdstippen werden opgegraven, liet zien dat gedurende 2 jaar de mortaliteit onder kleine, ronde zaden met een harde zaadhuid kleiner dan 10% bedroeg. Voor soorten met grote, platte zaden zonder strikte kiemingsvoorwaarden bedroeg de mortaliteit maximaal 60%. Met name van soorten uit de eerste groep (bijv. *Carex, Luzula, Viola*) kan worden verwacht dat ze zich kunnen hervestigen uit bewaarde slapende zaden.

In **Hoofdstuk 5** is onderzocht hoe snel planten kunnen migreren langs lijnvormige elementen in het landschap zoals slootkanten. In het geval de zaadvoorraad in de bodem van een natuurontwikkelingsgebied is uitgeput, zijn slootkanten mogelijke belangrijke corridors voor plantesoorten met een beperkt dispersievermogen. Met een ruimtelijk verbreidingsmodel is nagegaan hoe snel planten langs corridors migreren, afhankelijk van drie factoren: het dispersievermogen van planten, de breedte van corridors en de kwaliteit van habitatplekken in corridors. Uit simulaties bleek dat de migratiesnelheid voor soorten met een beperkte zaadverspreiding (tot 20 m) maximaal 5 m/jaar bedroeg. Met name planten met een groot dispersie-vermogen bleken zich slecht langs smalle corridors te verplaatsen, omdat zij veel zaad aan de omgeving van een corridor verloren. De bijdrage van zaden uit de staart van de frequentieverdeling aan de migratiesnelheid was alleen van betekenis wanneer een corridor bestond uit habitatplekken van uitsluitend hoge kwaliteit.

De conclusie van deze studie is dat slootkanten voor lokaal of regionaal uitgestorven plantesoorten met een beperkt dispersievermogen geen rol van betekenis kunnen spelen bij de hervestiging in natuurontwikkelingsgebieden. De belangrijkste redenen hiervoor zijn dat de migratiesnelheid te gering is, de afstanden tussen refugia en geschikte habitatplekken vaak te groot zijn en de kwaliteit van plekken in lijnvormige elementen als gevolg van het gevoerde beheer onvoldoende is. Een ecologische infrastruktuur voor juist deze soorten is dan ook illusoir.

In **Hoofdstuk 6** wordt aandacht besteed aan de zaaddispersie van besdragende planten door vruchtenetende vogels in een Twents houtwallenlandschap. Als gevolg van herinrichting zijn op vele plaatsen in het landschap houtwallen verdwenen, terwijl elders nieuwe houtwallen zijn aangeplant. De vraag is of de dichtheid van houtwallen in het landschap (*landschapsstruktuur*) effect heeft op de aantallen aanwezige vruchtenetende vogels en derhalve op de verbreiding van zaden.

Uit waarnemingen van vruchtenetende vogels bleek dat 8 vogelsoorten als de belangrijkste zaadverbreiders kunnen worden beschouwd. Deze zijn in twee groepen te verdelen, namelijk de *longitudinale* en *transversale* zaadverbreiders. Het verschil tussen beide groepen heeft vooral te maken met de voorkeursrichting waarin de zaden door vogels worden getransporteerd, respectievelijk in de lengte-richting of dwars op het landschapselement. Verder verspreiden longitudinale verbreiders de zaden van nagenoeg alle in een landschap aanwezige besdragende plantesoorten en meestal over korte afstanden (<0.1 km), terwijl transversale verbreiders de zaden van met name de reeds algemene en goed bereikbare plantesoorten verspreiden en meestal over lange(re) afstanden (>0.1 km).

De zaadregen van besdragende planten werd tevens bemonsterd in 12 houtwal-transecten welke zich bevonden in zowel de open als gesloten delen van het Twentse landschap. Hieruit bleek dat de dichtheid van zaden in houtwallen gemiddeld 215 zaden per m^2 bedroeg en dat 5 soorten (*Gewone braam, Lijsterbes, Sporkenhout, Kamperfoelie* en *Vlier*) de zaadregen domineerden. Een gering deel van de zaadregen (12.4%) betrof met zekerheid zaden van buiten het element (*immigranten*). Dergelijke zaden werden gedeponeerd in houtwallen op een moment dat er geen vruchten van deze soorten (meer) aanwezig waren. Er zijn geen aanwijzingen dat de grootte of samenstelling van de zaadregen enig verband hielden met de verschillen in landschapsstructuur.

CURRICULUM VITAE

Dirk van Dorp werd op 30 oktober 1957 geboren te Zuidwolde (Dr.). In 1976 deed hij examen atheneum aan de Nijmeegse Scholengemeenschap te Nijmegen, waarna hij begon met de studie Biologie aan de Universiteit van Nijmegen. In het kader van deze studie deed hij onderzoek naar de plantengroei van de Duinen van Oostvoorne, naar de relatie tussen de vogelbevolking en struktuur van rivierbossen en naar de dispersie van zaden door vruchtenetende vogels in een Mexicaans regenbos. In mei 1984 sloot hij deze studie af met het doctoraalexamen.

Van maart 1985 tot juni 1986 was hij via ZWO-SRO aangesteld als onderzoeker bij de afdeling Landschapsecologie van het Rijksinstituut voor Natuurbeheer, Leersum, alwaar hij de ecologische infrastructuur voor de avifauna als toetssteen voor de inrichting van cultuurlandschappen onderzocht. Aansluitend deed hij tot mei 1988 zijn vervangende dienstplicht op hetzelfde instituut en verrichtte onderzoek naar de dispersie van besdragende planten in cultuurlandschappen op de hogere zandgronden.

Van juli 1988 tot augustus 1989 was hij werkzaam als Research Assistant bij het Institute of Ecosystem Studies van de New York Botanical Garden in een onderzoek naar successie-mechanismen in bossen.

Van september 1989 tot december 1992 was hij door NWO-SRO (Stichting voor Sociaal-Ruimtelijk Wetenschappelijk Onderzoek) als onderzoeker aangesteld bij de voormalige vakgroep Vegetatiekunde, Plantenoecologie en Onkruidkunde (thans de vakgroep Terrestrische Oecologie en Natuurbeheer) van de Landbouwuniversiteit Wageningen. De resultaten van dit onderzoek vormen de kern van dit proefschrift.

Sedert april 1993 is hij als docent landschapsecologie verbonden aan de Internationale Agrarische Hogeschool Larenstein, opleiding Tuin- en landschapsinrichting te Velp.

Met ingang van december 1995 is hij tevens hoofdredacteur van het wetenschappelijk tijdschrift voor landschapsecologie en milieukunde Landschap van de Werkgemeenschap voor Landschapsecologisch Onderzoek (WLO).

Hij is getrouwd met Alice Zwaan en vader van twee zonen, Jan en Maarten.

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