Plant survival in dynamic habitat networks in agricultural landscapes

Willemien Geertsema

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Abstract

The research described in this thesis aims at better understanding the relation between survival of plant species and the fragmentation and dynamics of habitat in networks of linear landscape elements in agricultural landscapes. This knowledge can be used to increase the effectiveness of management agreements that aim at better protection of botanical diversity of agricultural landscapes. Herbaceous perennial plant species were studied in a network of ditches with fragmented and dynamic habitat.

Field studies in an agricultural area in the north of the Netherlands showed that the occupation and colonization probabilities decreased and the extinction probabilities increased with increasing spatial isolation of habitat patches. These results did not differ considerably between species with contrasting dispersal or seed bank characteristics. The results of a simulation model were consistent with these observations on the short term (5 years). Long term simulations (250 years) clearly showed that the effect of landscape fragmentation and dynamics on the survival probability of plant species differed considerably between species with contrasting colonization strategies.

Three alternative scenarios for increasing the effectiveness of conventional management agreements were compared using the simulation model. A further increase of the habitat quality created by the management agreements was not effective, but longer contract times for management agreements were advantegeous for the survival of species on the landscape scale. By far the strongest positive effect was found when management agreements were spatially clustered in one part of the landscape instead of distributed randomly over the landscape.

Key words: agricultural landscapes, colonization, ditches, extinction, field experiments, habitat fragmentation, habitat dynamics, herbaceous plant species, management agreements, metapopulations, linear landscape elements, population dynamics, seed bank, seed dispersal, simulation model

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Voorwoord

Dit proefschrift is het resultaat van vijf jaar onderzoek. In die vijf jaar heb ik me bezig gehouden met de vraag of er een relatie te vinden was tussen de overlevingskansen van planten en eigenschappen van landschappen waarin ze groeien. Een complexe vraag, maar ook een relevante vraag, omdat inzicht in die relatie gebruikt kan worden voor de bescherming van de flora. M'n belangstelling voor dit onderwerp werd vooral gewekt toen ik na m'n afstuderen een jaar lang bij de afdeling Landschapsecologie van het DLO-Instituut voor Bos- en Natuuronderzoek m'n tanden kon zetten in gegevens over verspreidingspatronen van bosplanten en allerlei informatie over leeftijd en verspreiding van bosjes. Dat werk heeft me enthousiast gemaakt voor het onderzoek naar de relaties tussen planten en landschappen. Daarbij vind ik het vooral interessant om te achterhalen hoe planten van de ene in de andere groeiplek kunnen komen, hoe lang ze als zaad in de grond betere tijden kunnen afwachten en wat daarvan het effect is op de overlevingskansen van plantenpopulaties. Ik heb dan ook met veel plezier gewerkt aan het onderzoek waarvan dit proefschrift het resultaat is.

Het onderzoek begon in januari 1997 op de afdeling Landschapsecologie van het Instituut voor Bos- en Natuuronderzoek in samenwerking met de leerstoelgroep Theoretische Productie Ecologie van de Landbouwuniversiteit. Het eindigde in januari 2002 op de afdeling Ecologie en Ruimte van Alterra in samenwerking met de leerstoelgroep Gewas- en Onkruidecologie van Wageningen Universiteit. De namen van de afdeling, groepen, instituut en universiteit zijn veranderd, maar de mensen met wie ik samenwerkte bleven hetzelfde. Een aantal van die mensen wil ik graag bedanken, want zonder hen was het niet mogelijk geweest om het allemaal af te ronden.

Allereerst wil ik mijn promotoren Paul Opdam en Martin Kropff bedanken voor hun stimulerende begeleiding. Jullie hebben me enorm geholpen en ik heb er veel van geleerd. Het begon met het afbakenen van het onderzoek en het doorhakken van vele knopen en het eindigde bij het schrijven van artikelen en uiteindelijk het proefschrift.

De uitvoering van het werk werd mogelijk gemaakt door nog veel meer mensen. Zonder Jolanda Dirksen zou het veldwerk nooit zijn gelukt. We hebben samen vele tientallen kilometers in weer en wind afgelegd. Ik hou er goede herinneringen aan over. Ook wil ik de boeren in Bovensmilde bedanken

chapter 1

Introduction

Nature and agriculture: a love-hate relationship

Species rich vegetations in North Western Europe have evolved from agricultural activities in the past. Vegetation types that are nowadays highly valued for their botanical richness, such as heathland, calcareous grasslands and wet grasslands, resulted from low-intensity farming systems, which are disappearing from the farm landscape (Bignal & McCracken 1996; Poschlod & Bonn 1998). Without the impact of man, large areas of these vegetation types could not exist and would have changed into shrub- or woodland (Bakker 1989; Falinska 1991; Barbaro *et al.* 2001). Grazing of sheep and cattle and hay-making prevented the establishment of woody species and the productivity of the soil was high enough to support many species and low enough to prevent a few dominant species suppressing the less competitive species (Bakker 1989; Bakker & Berendse 1999).

In the second half of the 20th century a historical change took place in agriculture in North Western Europe, parts of North America and Australia. The application of artificial fertilizers and mechanisation made it possible to cultivate the low productivity areas that were once only suitable for hay making or as grazing areas for sheep and cattle (Vos & Zonneveld 1993). The productivity of agriculture increased as the intensity of management increased. This management implied not only an increased use of fertilizers and herbicides on individual fields or the use of more productive crop varieties (both arable crops and grassland species), but the landscape itself changed (McLaughlin & Mineau 1995). New techniques required larger fields. The development of large-scale farms inevitably led to the removal of many landscape elements that were not used for agricultural production (Vos & Zonneveld 1993; Hobbs & Saunders 1991). Many kilometres of hedgerows were removed and ditches were filled up because improved water management techniques made them unnecessary. The change in agricultural practices resulted not only in the above mentioned intensification but also in abandonment of traditional use by livestock (Meeus 1993; Burel & Baudry 1995; Barbaro *et al*, 2001). Abandonment leads to spontaneous succession and a loss of species of open fields, but it may also lead to more habitat for species of forest habitat (Burel & Baudry 1995). The consequences of land abandonment are not included in this thesis.

The intensification of production methods was very important for producing enough food and increasing the economic value of the agricultural

landscape. However, the diversity of plants and animals decreased with this increased agricultural productivity (Vermeer & Berendse 1983). The landscape elements that were not used for agricultural production such as crop edges (Marshall 1989; Boatman 1994; Fry 1994; Kleijn *et al.* 1997), ditches (Melman *et al.* 1988; Van Strien *et al.* 1989) and hedgerows or woodlots (Middleton & Merriam 1983; Grashof-Bokdam 1997; Corbit *et al.* 1999) became a refuge for many species (Opdam *et al.* 2000). The supporting function of agriculture to biodiversity had turned into a competing relationship. Both land use functions needed space that was getting increasingly scarce.

To date, at the beginning of the 21st century, the relation between agriculture and nature conservation functions is changing again. In North Western Europe, but also in parts of Australia and North America, other interests compete for space in agricultural landscapes, such as infrastructure, recreation, water conservation, house building, etc. These are often economically more powerful functions than agriculture and nature. Because of their weaker economic value, agriculture and nature are threatened in many regions around the world.

At the same time, the value of agricultural landscapes for the conservation of plants and animals as well as the cultural values of agricultural landscapes receive more attention, from politicians as well as scientists and the society, indicated by the so called 'countryside goods' (Hodge 2001) or 'societal values' (Hess *et al.* 2000). The agricultural and nature policies of the European Union and the Dutch government emphasize the protection of species and landscapes in agricultural areas (Anonymous 1998; Ministry of Agriculture, Nature Conservation and Fisheries 2000a, 200b). The network of semi-natural landscape elements that are not primarily used for agricultural production is a focal issue in this policy. This network is called the *green-blue veining* (Opdam *et al.* 2000), as it includes woody vegetations (hedgerows, small woodlots), grasslands (road verges, field edges) as well as aquatic elements (streams, ditches, pools). The strength of green-blue veining is its support of multiple functions (Opdam *et al.* 2000). First of all it is the habitat for many plants and animals in agricultural landscapes and may also function as dispersal corridors between larger nature areas (Merriam 1988; Fry 1994; Marshall & Arnold 1995). They contribute to pest control in adjacent fields, as they are (winter-) habitat for natural enemies of pest organisms (Thies & Tscharntke 1999). They also have socio-cultural value as they visualize the identity of regions: closed small-scale landscapes with hedgerows versus open

landscapes with ditches (Meeus 1993; Goossen *et al.* 1997). Farmers receive extra income from the management of the green-blue veining on their farms (Kleijn *et al.* 2001). The competing relation between agriculture and nature is turning into a mutually supportive relation.

Green-blue veining and the protection of botanical diversity

The survival of plants in the green-blue veining is the subject of this thesis. While many plant species disappeared from the fields, many are still present in the network of semi-natural landscape elements. Still, the habitat of plants in this network needs to be protected from the often deteriorating effect of agricultural activities on the adjacent fields (Marshall 1989; Van Strien *et al.* 1989; Mountford *et al.* 1994; Kleijn *et al.* 1997). In many regions, the green-blue veining is fragmented in space as well as in time and the environmental conditions of parts of the remaining network are insufficient to support viable plant populations. Measures are taken to prevent a further decrease of the diversity and to restore species rich vegetation. Farmers can enter into contracts with the government to adjust the management of fields and other landscape elements in order to protect the biodiversity of agricultural landscapes (Anonymous 1998; Potter 1998). The protection of botanical diversity in these contracts is mainly aiming at increasing the local habitat quality. In a survey of the botanical diversity no effect of management agreements was found (Kleijn *et al.* 2001). A reason for the lack of effect may be that the allocation of management agreements in the landscape does not enable plants to (re)colonize the restored habitats. The research described in this thesis aims at understanding the relation between the spatial arrangement and dynamics of habitat in agricultural landscapes and the survival of plant species.

Spatio-temporal strategies of plants

Landscape ecological research has indicated the importance of the spatial arrangement of habitat for plants and animals for the persistence of species on the landscape scale (Opdam 1990; Bakker *et al.* 1996; Prins *et al.* 1998; Van Groenendael *et al.* 2000). The survival of species in fragmented and dynamic

landscapes is possible if the rate of local recolonization equals the rate of local extinction. Key factors in determining the colonization ability of plant species are the seed dispersal capacity and the seed bank persistence (Opdam 1990; Bakker *et al.* 1996). Seed dispersal enables plants to cross unsuitable habitat in space, whereas a persistent seed bank can be considered an adaptation for dispersal in time. The dispersal distance is determined by plant (e.g. plant height) and seed characteristics (e.g. plumes, wings, spiny structures) and the presence of dispersal vectors in the landscape (e.g. wind, animals, water) (Van der Pijl 1982; Willson *et al*. 1990). There are estimations of dispersal distances for different dispersal mechanisms available, but it remains unclear how to translate the dispersal characteristics of a plant species into realized dispersal distances. The extensive database of Thompson *et al.* (1997) gives an overview of the seed bank persistence of a large number of plant species in North Western Europe. The combination of seed dispersal and seed bank persistence determines the persistence of plant species in fragmented and dynamic landscapes. However, the knowledge of the implication of the two strategies of plant species to disperse in space and time for landscape management is still very limited.

Central questions

With this thesis I seek to improve our understanding of the interaction between habitat fragmentation and spatial dynamics in the habitat network as a condition for the survival of plant species with different spatio-temporal strategies. Thereby I want to help increasing the effectiveness of measures to protect the botanical diversity of agricultural landscapes.

> The main questions of this thesis are:
> • Is the survival probability of plant populations in agricultural landscapes influenced by the spatial arrangement of habitat and the dynamics of this habitat?
> • Does the impact of spatial fragmentation and dynamics of the habitat differ between species with contrasting dispersal and seed bank strategies?

• Can the effectiveness of measures to protect the botanical diversity be improved by including rules for spatial and temporal arrangement of habitat?
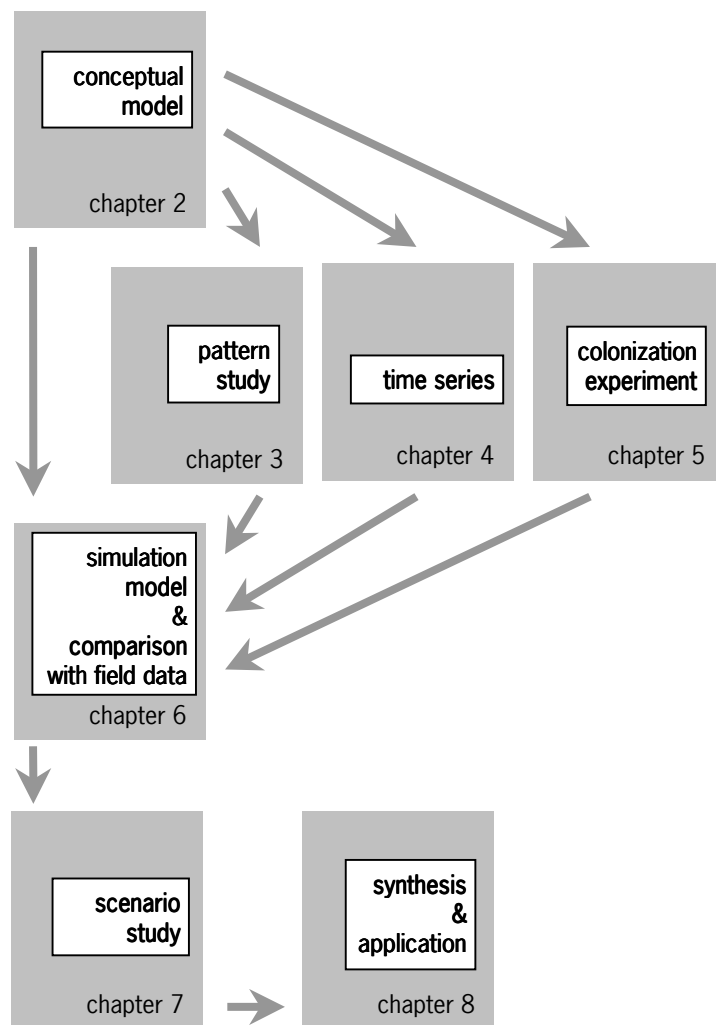
Figure 1.1 Structure of the thesis and relation between the different chapters.

Structure of the thesis

Both theoretical and empirical research was conducted to answer the questions. I chose this combined approach, because the approaches complement each other. An experimental approach would require large scale and very long term experiments. This approach was impossible to perform in the field because of the limited period of this study and because of the high financial cost. Methodologically an experimental approach is also extremely complex because it requires replicate landscapes, which are very hard to find. Modelling studies can solve this problem. With a simulation model different landscape alternatives can be compared. The weak point of a modelling approach is of course that it is based on a number of assumptions and simplifies the real world; therefore I combined the modelling approach with empirical studies. The different parts of the thesis are described below and the relation between the different parts is illustrated in figure 1.1.

First I developed a conceptual model that describes the relation between plant population dynamics and landscape dynamics (chapter 2). The conceptual model was the basis for the design of the field studies (chapters 3-5) and for the development of a spatially explicit simulation model (chapter 6). In the field studies, I focussed on thirteen herbaceous plant species with contrasting dispersal and seed bank characteristics. In the model, the population dynamics of four model species with contrasting dispersal and seed bank characteristics were simulated. The field studies were done in one study area, but the modelling studies in landscapes with different combinations of spatial and temporal habitat continuity.

I have described the field surveys in chapters 3 and 4. The study area was located in the province of Drenthe in the north of the Netherlands. The area consisted of a network of ditches and arable fields. The field studies described in the thesis are limited to species in this network of ditch banks. The area was suitable for the studies as the habitat quality of the ditch banks showed a large variation. It varied from very species poor to very species rich grassland vegetation types. In a pattern study the distribution of the thirteen focal plant species was related to habitat quality, habitat dynamics and spatial arrangement of the habitat (chapter 3). The distribution patterns were monitored over three years, which provided information on the rate and spatial patterns of population turnover as well as differences between the spatial dynamics of species with contrasting colonization strategies (chapter 4). The

colonization events that were observed in chapter 4 resulted from establishment from either seed dispersal or the seed bank. In chapter 5 experiments are described that explored the separate role of dispersal and seed bank in the colonization of ditch banks.

In the simulation model (chapter 6) I related the long-term survival of the four model species to the spatial and temporal continuity of habitat in a number of simulations. The model was parameterized with data from literature. I used the results of field surveys to evaluate results of the simulation model.

The question whether the effectiveness of measures to protect the botanical diversity could be improved by taking into account rules for spatial and temporal arrangement of habitat, was explored in a scenario study with the simulation model as a tool (chapter 7). The standard scenario simulated the current practice of management agreements in the Netherlands: they have a limited contract time and are distributed randomly over the landscape. Three alternative scenarios were tested for their effectiveness: the habitat quality was further increased, the contract time was doubled or the agreements were clustered in one part of the landscape.

The field studies and the model together resulted in new insight in the relation between survival of plants with different colonization strategies and the landscape that they live in. In the general discussion of this thesis I give a synthesis of the results of the different parts of the study and present directions for further study (chapter 8).

Nomenclature throughout the thesis follows Van der Meijden (1996).

chapter 2

Plant strategies and agricultural landscapes: survival in spatially and temporally fragmented habitat

W. Geertsema, P.F.M. Opdam and M.J. Kropff

Abstract

In agricultural landscapes many plant species are limited to the network of landscape elements that are not used for agricultural production. This habitat is fragmented in space and time due to anthropogenic, biotic and abiotic factors. Therefore, plant populations are spatially sub-divided and their persistence might be dependent on the spatial dynamics in the network of local populations. Dispersal characteristics and seed bank persistence are main determinants of colonization ability which in turn is a key determinant of metapopulation viability.

We propose a conceptual model that relates plant population dynamics to habitat quality, configuration and dynamics. In this model, the habitat is arranged as a network of suitable and unsuitable patches, the distribution of the patches is assumed to be dynamic in time.

Based on dispersal and seed bank characteristics four plant strategies are distinguished: species having either long (>100 m) or short (< 100 m) distance dispersal and either a long (> 5 yr) or short (< 5 yr) term persistent seed bank. We expect that species with contrasting strategies have different survival probabilities in landscapes with contrasting habitat arrangement in space and time.

We found few empirical studies for testing the hypotheses based on the model. Therefore the relation between landscapes and plant survival needs to be further explored, especially the quantitative aspects. We propose an iterative process of empirical and modelling research to determine this relation and to define management options for multifunctional farms in which biodiversity is one of the land use aims.

Key words: biodiversity, conceptual model, dispersal, landscape planning, metapopulation, seed bank

Plant diversity in agricultural landscapes

The botanical diversity of modern agricultural landscapes in North Western Europe has decreased during the last decades. The abundance of common species has increased and rare species have become even more rare (CBS 1993; Joenje & Kleijn 1994; Hodgson *et al*. 1995). A decrease of both quality and

quantity of habitat for the wild flora has caused this decline of biodiversity. The decline in the quality of habitat has been caused by increased nutrient and pesticide pressure (McLaughlin & Mineau 1995), whereas the up-scaling of farming systems resulted in the removal and fragmentation of habitat. Most wild plant species in modern agricultural landscapes occur in landscape elements that are not used for agricultural production such as crop edges (Marshall 1989; Boatman 1994; Fry 1994; Kleijn *et al.* 1997), ditches (Melman *et al.* 1988; Van Strien *et al.* 1989) and hedgerows or woodlots (Middleton & Merriam 1983; Grashof-Bokdam 1997). Weeding, tillage and the use of herbicides and fertilizers make the fields virtually unsuitable for wild plant species. Only a limited number of weedy species can survive in this harsh environment.

Today, the pressure on land is continuing to increase in agricultural landscapes of North Western Europe. Agricultural production, as well as expanding cities, industry and infrastructure claim land in the agricultural landscapes. The solution to this space-conflict can be the integration of different functions in multifunctional farming systems. For example agricultural production functions can be combined with nature and landscape conservation (Brandt *et al*. 2000). This trend to integrate functions can be considered a chance to improve the ecological quality of agricultural landscapes: nature conservation motives are combined with motives for recreation, cultural heritage and water storage to balance the claim for space by agricultural functions. Most of the non-agricultural functions coincide with the network of landscape elements that are not used for food production (Opdam *et al.* 2000). The development of multifunctional landscapes requires insight into the relationship between the spatial structure and network-dynamics of landscape elements and the distribution and persistence of populations of wild organisms. In this chapter we will propose a conceptual model that describes this relation for plant populations in agricultural landscapes.

The majority of studies on botanical values in agricultural landscapes have focused on the relationship between the environmental quality of a site and the composition of the present vegetation (e.g. Marshall 1989; Van Strien *et al*. 1989; Mountford *et al*. 1994; Kleijn *et al*. 1997). Nutrient availability was one of the key-parameters explaining the vegetation composition and the performance of individual species. Recent studies also suggest that the history of a site and the spatial relation with the surrounding landscape co-determine the vegetation composition of a patch (Bakker *et al.* 1996; Prins *et al*. 1998;

Van Groenendael *et al.* 2000). Therefore we argue that in studies of plant species survival and landscape structure and dynamics it is not enough to look only at the local conditions, but that the spatial structure of the disjunct habitat network has to be included, as well as the dynamics of this network. Table 2.1 gives a summary of a number of studies that demonstrated this relation between the diversity and distribution of species and the spatial arrangement and dynamics of habitats.

We will use the metapopulation theory as a theoretical framework to describe plant population dynamics in fragmented and dynamic agricultural landscapes. It is however not a goal of this chapter to demonstrate that plants really function as metapopulations. A spatially structured population of local populations that are linked by dispersing propagules can be described as a metapopulation (Levins 1970; Hanski 1985; Merriam 1988; Opdam 1990; Eriksson 1996; Husband & Barrett 1996). Metapopulations are characterized firstly by the turnover of local populations, secondly by the higher extinction chances and the lower recolonization chances in the smallest and most isolated local populations (isolation effect) and thirdly by the different spatial dynamics shown by different species (species effect) (Opdam 1990). A metapopulation can persist if extinction rates of local populations do not exceed colonization rates, provided that enough patches constitute a coherent network (Verboom *et al.* 1993). Local disturbances that frequently occur in agricultural landscapes, but also in more natural landscape types, can cause habitat patches to disappear (causing local extinction) or reappear; management and succession may cause habitat patches to reappear as well. Unoccupied patches of habitat can become (re)colonized by immigrating seeds from the seed rain or by germination of seeds from the soil seed bank. The ability of certain plant species to reproduce vegetatively, their potential longevity and the possession of persistent seed banks may influence the plants' metapopulation dynamics (Eriksson 1996). Although the criteria for the characterisation of metapopulations were developed for the study of metapopulations of animal species, several studies have shown that these criteria also apply to plant species. Turnover of populations was observed by e.g. Van der Meijden *et al.* (1992), Ouborg (1993), Antonovics *et al.* 1994, Fröborg & Eriksson (1997), Valverde & Silvertown (1997) and Harrison *et al.* (1998); the isolation effect was found by e.g. Ouborg (1993), Antonovics *et al.* (1994), Quintana-Ascencio & Menges (1996), Grashof-Bokdam (1997), Grashof-Bokdam & Geertsema (1998), Harrison *et al.* (1998) and Sarlöv Herlin & Fry (2000); differences in spatial

dynamics of species' responses were observed by e.g. Nip-Van der Voort *et al.* (1979), Dzwonko (1993), Grashof-Bokdam (1997), Fröborg & Eriksson (1997) and Harvey (2000). These studies encompass a wide variety of spatial scales, habitat types and regions, but they confirm our assumption that the metapopulation approach is a suitable theoretical background to study plant population dynamics in fragmented landscapes.

Species differ in their response to changes in the spatial structure of the landscape network because they differ in life strategies and dispersal strategies. This difference in response is problematic in landscape planning that is based on ecological principles. Vos *et al.* (2001) presented a strategy to bridge the gap between species level and landscape level. They stressed the need for developing ecological groups of species with similar responses to landscape structure and spatial scale. The conceptual model that we present in this chapter is based on this idea. We use colonization strategies of plant species to compose species groups. Although the approach that we use may be applicable to non-agricultural systems as well, we focus on agricultural landscapes, because of the higher frequency of disturbance that is related to human activities as compared to more natural systems. In agricultural systems the species in semi-natural landscape elements may be more susceptible for spatial fragmentation because of the higher disturbance frequency.

In this chapter we offer a conceptual model which structures the range of species responses to landscape structure and dynamics. With the model we intend to offer a tool that can be used to:

a) bridge the gap between species level information and ecology-inclusive landscape planning,

b) identify gaps in the knowledge of plant population dynamics in agricultural landscapes and structure the need for further research,

c) develop management guidelines for multifunctional agricultural landscapes that aim at improving ecological conditions for wild flora.

Table 2.1 Overview of studies concerning the relation between plant diversity or distribution patterns (including colonization and extinction) and spatial parameters measured at the landscape scale. The table shows some characteristics of the studies such as habitat type, spatial scale, types of explanatory parameters and the main conclusions.

habitat type	response parameter	spatial scale	explantory parameters - species -	explanatory parameters - site -
road verges in new polder	colonization of species in road verges	$\pm$ 2500 km^2	dispersal ability	-
forest fragments, hedgerows	colonization individual species in young forest	total area: $\pm$ 9 km^2	dispersal ability	-
various	diversity of sites	40 ha, with sites of 12.5 m^2	forest vs old-field species	-
rosemary scrub	species diversity and incidence of individual species	1075 ha, with scrub patches of 0.03-3.6 ha	habitat specialism, life form, regeneration mechanism	-
forest fragments	distribution pattern all species	zone up to 1 km around patches of $\pm$ 2 ha	interior vs edge and dispersal ability	-
recent forest adjacent to old forest	colonization of species in young forest	old forests: 0.6-11.8 ha + adjoining young forest	dispersal ability	light intensity
road verges	colonization and extinction	40 m segments along 150 km road	-	presence of herbivorous insect
grass land	change in vegetation composition and colonization/extinction individual species	national scale, sites: 0.1-35 ha.	-	environmental situation (Ellenberg)
hedge rows	diversity in margins	50 m margin length	-	margin structure and management
various	diversity in landscapes	3 landscapes 455-641 ha	-	margin stucture, adjacent land use and others

explanatory parameters - dynamics -	explanatory parameters - spatial -	main conclusion(s)	source
age of roads	distance to mainland	colonization depends on dispersal capacity of species, on the age of road verge and distance to mainland	Nip-Van der Voort *et al.* 1979
age forest patches and former land use	distance to nearest seed source	seed sources in old forests appear to be most important colonization sources, older forest patches are more often colonised than younger ones	Grashof-Bokdam & Geertsema 1998
land use change over 100 yr	connections between landscape elements and heterogeneity	diversity at the site level is correlated to landscape pattern and change, immediate neighborhood is more influential than distant one	Baudry & Tatoni 1993
time since fire	spatial isolation and patch area	presence of many habitat specialists related to isolation, patch area and time since fire	Quintana-Ascencio & Menges 1996
-	area and amount of forest habitat around patches	number of species and occurence of target species increase with area and (interior) zoochorous species are affected by isolation	Grashof-Bokdam 1997
-	distance to old forest	in 70-yr-old forest, vegetation composition depends on distance to old forest; animal (bird)- and wind-dispersed species are relatively quick colonisers	Dzwonko 1993
-	distance to conspecific patches	herbivory and spatial isolation increase extinction chances and isolation decreases colonization chances	Antonovics *et al.* 1994
-	area and isolation of sites	isolation affects colonization/extinction rates of individual species; little evidence of isolation effect on momentaneous distribution pattern of total species number	Ouborg 1993
-	distance from woodland	margin flora is correlated with margin structure and diverstiy is positively correlated with decreasing distance to woodland	Marshall & Arnold 1995
-	amount of hedgerows relative to other land use	margin structure and amount of hedgerows in the landscapes affect species composition more than site parameters (e.g. management)	Le Ceour *et al.* 1997

The conceptual model

The conceptual model that describes the habitat and population dynamics is visualised in figures 2.1 and 2.2. Figure 2.1A shows the relevant spatial scales in the model: a landscape consisting of agricultural fields intersected by linear landscape elements, which in their turn consist of patches with different habitat qualities. The potential habitat is limited to linear landscape elements because elements that are of importance to wild flora in agricultural landscapes are typically linear (ditches, hedgerows, field boundaries). The linear landscape elements constitute to some extent a continuous network of habitat but are heterogeneous lengthwise (Fry 1994). Consequently, a species' habitat will be divided into more or less isolated patches, thus dividing the plant species into local populations. Although in reality there is a gradient of suitable to unsuitable habitat, we have limited habitat suitability to the extremes of 'suitable' and 'unsuitable' (figure 2.1). The state of local populations is determined by the presence or absence of a soil seed bank and of plants. We make no distinction between seedlings, vegetative or flowering plants. Thus, the state of a patch is determined (for individual plant species) by habitat suitability, the presence of plants and the presence of a soil seed bank, resulting in six possible states (figure 2.1B). The change of the state of a patch to a different state is caused either by population dynamics (plants or seed bank) or by habitat dynamics. We will consider patches with plants as occupied and patches without plants as unoccupied, regardless of the state of the soil seed bank. Colonization implies the transition of an unoccupied patch to the occupied state and extinction the reverse process (figure 2.1B). Sources of colonization are either seeds dispersed from other patches or the soil seed bank. The soil seed bank dynamics consist of the appearance or disappearance of a viable soil seed bank.

Figure 2.2 shows the population dynamics within the patches in more detail. The majority of these demographic processes are influenced by the habitat quality of a patch (survival and mortality of plants, number of seeds produced, germination, mortality of seedlings, etc). The survival of plants at the patch scale includes survival of individual plants as well as vegetative reproduction which is mostly a local process and not a process at the landscape scale. Both habitat configuration in the landscape and the dispersal characteristics of the species determine the probability that seeds will be dispersed amongst other patches. Whether a patch is really colonized depends

also on the habitat quality. The probability that the soil seed bank is a source of colonization depends on the seed persistence of the species and the age of the soil seed bank. The age and consequently the viability of the soil seed bank are expected to be influenced by the temporal dynamics of the habitat quality; the longer a patch has been unsuitable, the fewer seeds will have preserved viability.

It must be recognized that both patch quality and patch configuration contribute to the spatial cohesion of the habitat network for a species. Habitat quality determines the size of local populations; the size of local populations influences the seed rain density. The more patches available, the higher the potential density of seed producing local populations, which causes an increase in the dispersal and gene flow through the landscape. Hence, processes at the patch level influence the spatial cohesion of the local populations at the landscape level.

In the next two sections, we will discuss the landscape and species characteristics that are used in the conceptual model.

Habitat dynamics in agricultural landscapes

We consider the habitat quality and spatial arrangement of the patches in linear landscape elements to be determined at three levels of spatial scale: within and between the landscape elements and at the landscape level (figure 2.1A). The spatial arrangement of suitable and unsuitable patches in the network of landscape elements determines the spatial isolation of habitat patches. The dynamics determine the temporal isolation of habitat patches.

The quality of habitat patches influences different demographic parameters that determine the local population dynamics (figure 2.2). We consider the pattern of suitable and unsuitable patches to be dynamic in time (figure 2.1B). The term dynamics includes any change in quality, spatial arrangement and size of the habitat patches in a landscape. The dynamics occur at different temporal scales (Merriam 1988; Baudry & Burel 1997). Small-scale spatial dynamics occur in general more frequently than large-scale dynamics. The background of the patterns and processes that lead to the fragmentation and dynamics of plant habitats at the three spatial scales in agricultural landscapes are described below.

A. landscape

suitable
patches

unsuitable patches

B. dynamics of patch states:

Plants
Seed bank
(suitable)

Seed bank
(suitable)

Seed bank
(unsuitable)

colonisation & extinction
(local plant population)

appearance & disappearance
(seed bank population)

habitat dynamics

Plants

(suitable)

(suitable)
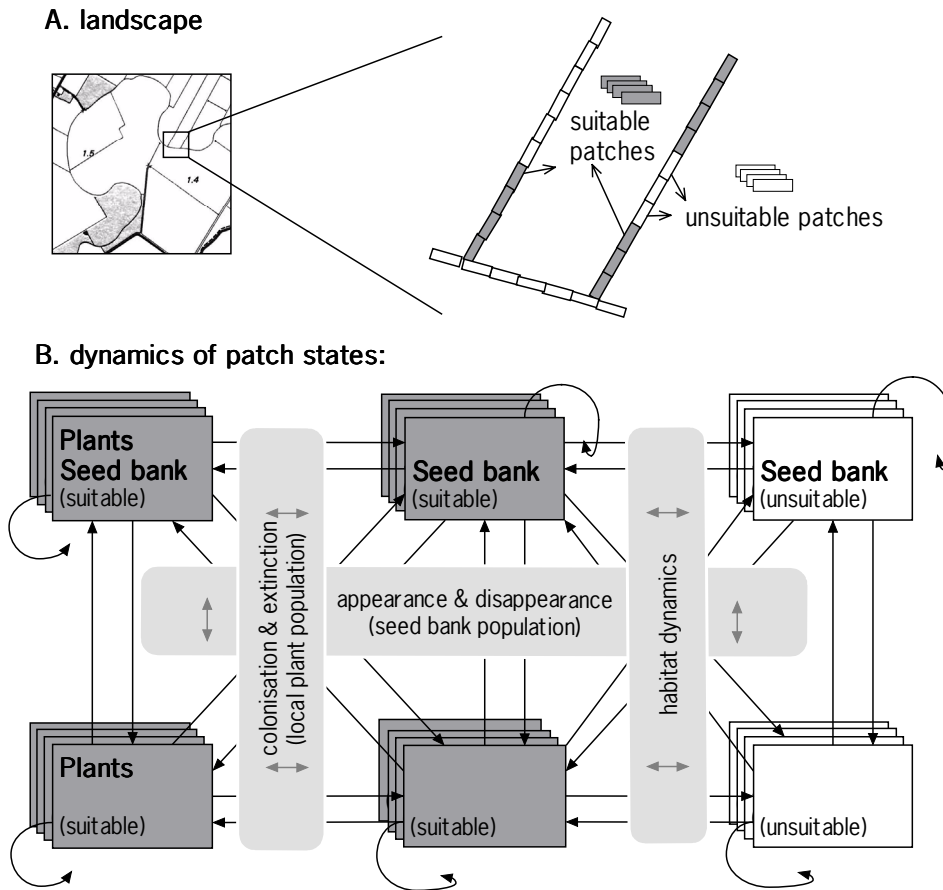
(unsuitable)

Figure 2.1 Conceptual model of the habitat and population dynamics in linear landscape elements. A: (hypothesised) location of suitable and unsuitable habitat patches in linear landscape elements in an agricultural landscape. B: six possible states of patches (dark grey and white boxes), based on habitat suitability and presence or absence of seed bank and local populations of plants. The arrows indicate dynamics of the patches which concern both habitat and population dynamics. The transition between the states of the patches is determined by the factors in the pale grey boxes: habitat dynamics, colonization and extinction of local populations of plants and appearance or disappearance of seed banks.
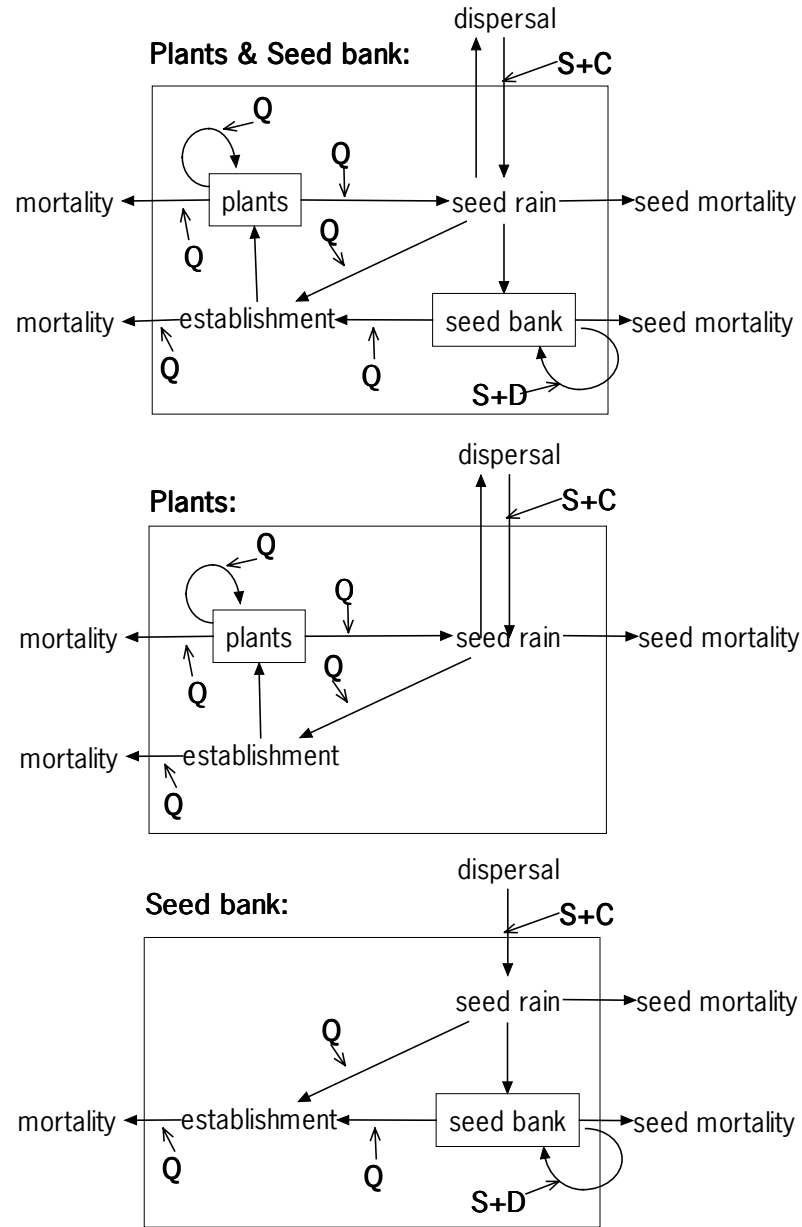
Figure 2.2 Conceptual model of the population dynamics within patches that are occupied by plants and/or with a soil seed bank present. Arrows indicate demographic processes, small arrows indicate by which factors the processes of the demographic processes are influenced (Q = habitat quality, D = habitat dynamics, C = habitat configuration, S = species characteristics).

i. within the landscape element: A landscape element can be considered as a 'linear mosaic' of suitable and unsuitable habitat patches (figure 2.1A). The heterogeneity in space and time of habitat quality within a landscape element is caused by a variety of factors, such as soil heterogeneity, vegetation succession, the distribution of competing species, the outbreak of pathogens or the presence of animals (herbivores, soil dwelling animals, etc). The heterogeneity can also be caused by agricultural practices, like herbicide drift or soil disturbance.

ii. the landscape element: At the scale of the landscape element, management of the element itself and the use of the adjacent fields result in a degree of similarity of habitat quality within one landscape element (figure 2.1A). For most herbaceous species management that prevents the surrounding vegetation becoming too dense or too competitive is favourable, e.g. mowing with removal of the hay (Parr & Way 1988). Different crops are associated with different nutrient and herbicide applications (Kleijn & Verbeek 2000), which has consequences for the habitat quality of the adjacent non-productive elements (De Snoo & Van der Poll 1999). Trampling by cattle has a negative impact on the habitat quality as it can destroy the above ground vegetation. The negative influence of the adjacent land use on landscape elements can be buffered by a strip without application of herbicides and fertilizers between the crop and the landscape element (Haughton *et al.* 1998; Moonen & Marshall 2001).

iii. the farm and landscape level: Farming systems play a key role in determining the spatial organisation of a landscape (Deffontaines *et al.* 1995). The layout of the fields (size, shape) determines the grid size of the network of landscape elements around the fields (figure 2.1A). This layout is closely related to the geomorphologic characteristics of the region, the history and regional planning in the region (Barends 1989). The dynamics at a farm and landscape level are a result of changes in farming systems due to farmers' response to the socio-economic environment, technical development or political decisions at a regional, national or international level. Changes in farming systems that frequently occurred during the last decades are the change from small-scale to large-scale farming systems and the conversion of conventional to ecological farming. The development of farmers' co-operatives,

which aim at environmentally benign farming, can increase the biodiversity of the landscape (Horlings 1996).

Plant population dynamics and strategies

Plant strategies in agricultural landscapes

Whether or not the isolation of habitat in space and time hampers the population dynamics of a species on the landscape scale, depends on individual species characteristics. A classification based on species characteristics that are related to landscape features could help us understand the spatial conditions that allow plant species persistence in the agricultural landscape (Vos *et al.* 2001). We will focus on those characteristics that determine the response of the species to spatial configuration and dynamics of habitat.

Several existing classifications used the response to disturbance events (Grime & Hillier 1992; Noble & Gitay 1996; Lavorel *et al.* 1998). Grime & Hillier (1992) describe the relation between regeneration strategies and the spatial and temporal predictability of disturbance. They expect that widely dispersed seeds will be advantageous when spatial predictability of disturbance is low and temporal predictability of disturbance is high, while a persistent seed bank will be advantageous when spatial predictability is high and temporal predictability of disturbance is low. We will use this classification as a starting point for a classification that can be used to generate general principles on the relationship between population survival and landscape structure and dynamics. In doing so, we assume that dispersal ability and seed bank persistence are the key traits in the survival of plants in fragmented, dynamic landscapes. Because the availability of seeds is often the bottleneck for colonization (Bakker *et al.* 1996; Bakker & Berendse 1999), we think that this assumption is justified. Other characteristics of importance for survival in disturbed environments are vegetative reproduction and longevity of species. The latter characteristics are of relevance for the local survival in response to deteriorated local conditions or small-scale disturbances. Vegetative reproduction is a means for the spread of plants on small spatial scales but it is not an effective strategy to bridge large distances between habitat patches. It does not play an important role in the response to the arrangement of habitat in space and time. Therefore these characteristics will not be considered in the classification of plant strategies.

Colonization rates should exceed extinction rates in order to allow persistence of species in fragmented landscapes. Therefore we will first discuss local extinction and persistence and which factors determine the extinction probability of local populations.

Local extinction and persistence

Frequent occurrence of extinction of local populations is reported in several empirical studies (e.g. Van der Meijden *et al*. 1992; Ouborg 1993; Antonovics *et al.* 1994; Van Dorp 1996; Fischer & Stöcklin 1997; Husband & Barret 1998). The extinction probability of local populations was influenced by habitat quality (Van der Meijden *et al.* 1992), increased with isolation of the patches (Ouborg 1993; Antonovics *et al*. 1994) and decreased with the size of habitat patches and populations (Ouborg 1993; Antonovics *et al*. 1994; Fischer & Stöcklin 1997). However, Husband & Barrett (1998) found no relation between extinction probability and population size.

The influx of seeds from other populations (figure 2.2) can be advantageous for the survival of local populations by adding more seeds and thus the potential for a larger population (rescue effect). Evidence of this was found by Ouborg (1993) and Antonovics *et al.* (1994) who observed smaller extinction risks for small populations that are close to other populations compared to small isolated populations. A persistent seed bank also adds seeds to the local population and thus can increase the persistence of a population. Influx of seeds as well as pollen into extant local populations can increase the genetic diversity of the local populations (Richards 2000). Isolated patches which do not receive genetic material from other populations, either by seed or pollen dispersal, risk inbreeding depression resulting in strongly reduced germination success which may result again in higher extinction probabilities (Richards 2000). Lamont & Klinkhamer (1993) showed decreasing seed production with declining population size due to reduced pollination or due to pollination between siblings.

In addition to habitat quality, patch size and patch isolation, destruction of habitat inevitably causes the extinction of local populations. Habitat in agricultural landscapes is characterized by frequent disturbances by agricultural practices and by a relatively small area available for populations in non-productive landscape elements (McLaughlin & Mineau 1995). Therefore environmental factors will be the major determinants of local extinction in agricultural landscapes. In ditch banks along arable fields we found high

extinction rates (on average: 0.30) for local populations which may indeed be a result of the frequent disturbance from the adjacent intensively cultivated arable fields (chapter 4).

Extinction frequency varies among plant species. In stable conditions the extinction risk is expected to be lower for perennial species and for species with the ability for vegetative reproduction and spread than for annual species. In frequently disturbed vegetations a short life cycle and high investments in regeneration are advantageous. Indeed, annuals, often with a persistent seed bank, are found more often in frequently disturbed environments, such as arable fields, whereas perennial species with the ability for vegetative spread, are more often in more stable environments, such as grasslands and hedgerows (CBS 1993; Hodgson *et al.* 1995) (figure 2.3). Vegetative reproduction enables a plant to survive for many years, resulting in a nearly immortal state, even if it is the only individual left at a certain site.

Because of the frequent occurrence of disturbance in agricultural landscapes, species can only survive when high extinction risks are counterbalanced by high colonization rates. Therefore, we focus the definition of plant strategies on the colonization ability of the plant species, which will be discussed in the next section.
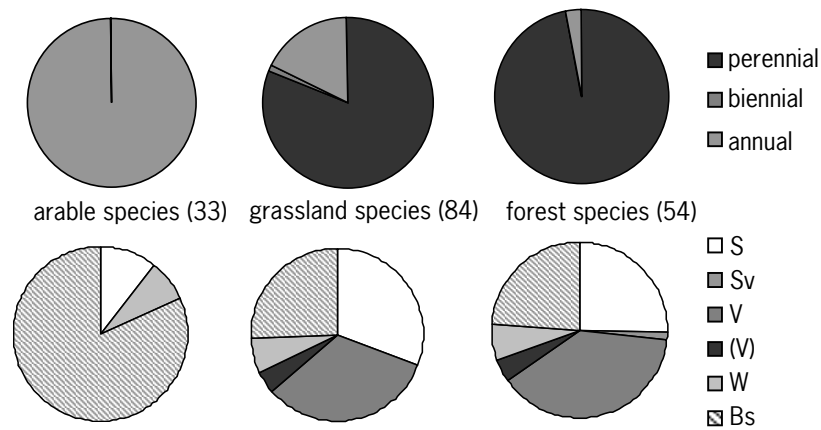
Figure 2.3 Distribution of life history (upper half) and regenerative strategies (lower half) in ecological groups: arable, grassland and forest species. Number of species in each group is given in parentheses. Regenerative strategies: S = seasonal regeneration by seed, Sv = seasonal regeneration by vegetative means, V = lateral vegetative spread, (V) = intermediate between V and Sv, W = regeneration involving numerous widely-dispersed seeds, Bs = persistent seed bank (Data from CBS 1993; Hodgson *et al.* 1995).

Colonization

Seed dispersal: Plants disperse seeds in such a manner that some may encounter a favourable situation for establishment (Howe & Smallwood 1982). This is crucial for survival in fragmented and dynamic habitats. Many species have morphologically adapted seeds for dispersal by a particular agent. Adaptations are known for dispersal by wind, vertebrates (seeds ingested with fruit or adhered to the skin), ants, water or by the plant itself (Van der Pijl 1982; Willson *et al.* 1990). Some species have adaptations for dispersal by more than one vector. The morphological adaptation to specific dispersal agents gives insight in the potential dispersal distances. The other important indication for dispersal distances is the presence of the dispersal agents themselves (Poschlod & Bonn 1998). Besides wind and water, animals and agricultural machinery may be important dispersal agents in agricultural landscapes. Water in ditches is a potentially important dispersal agent for long distance dispersal but a problem may be the frequent absence of flowing water due to water management in agricultural areas (Bulle *et al.* 1994).

Table 2.2 Estimates of dispersal distances for seeds with or without morphological adaptations for dispersal.

	dispersed by:	distance mean	max
short (< 100 m)	no adaptations	< 1 [1]	2-3 [1]
	ants	± 2 [1]	± 20 [2]
	wind[7]	1-10 [2]	> 100 [2]
long (> 100 m)	vertebrates		> 500 [3]
	water		> 3000 [4]
	machinery[8]		2-10 km [5,6]

[1]: Willson 1993; [2]: Hughes *et al.* 1994; [3]: Fischer *et al.* 1996; [4]: Danvind & Nilsson 1997; [5]: Bakker & De Vries 1988; [6]: Strykstra *et al.* 1996; [7]: wind dispersal can reach distances > 100 m in arable land and grassland (= long distance), in forest habitat it will generally be < 100 m (= short distance); [8]: No morphological adaptations involved, efficiency depends on the presence and timing of the machinery, not on morphological traits.

Although dispersal distances crossed in the field are hard to measure (Bakker *et al.* 1996), comparative data on dispersal distances for the different adaptations are available. In table 2.2 rough estimates are given for dispersal distances for different dispersal agents. Presuming the average length of a field margin (approximating the length of most linear landscape elements) to be ca 100 m, species dispersed by ants and species without adaptations and those

with heavier seeds dispersed by wind can be classified as short distance
dispersers. Species dispersed by vertebrates, wind, water or machinery are
classified as long distance dispersers. Cain *et al*. (2000) also classified dispersal
distances that exceed 100 m as long distance dispersal. The relative importance
of long and short distance dispersal characteristics for species from different
ecosystems is shown in figure 2.4 for groups that constitute the majority of the
vegetations in non-productive landscape elements in agricultural landscapes.
The majority of forest vegetations (56%) consists of species with short distance
dispersal, while the majority of arable and grassland vegetations (67% and 74%
respectively) consists of species adapted to long distance dispersal. More than
half of the arable plant species that are adapted to long distance dispersal
consist of species that are dispersed by agricultural machines (36% of the total
number of species) (Hodgson *et al*. 1995).
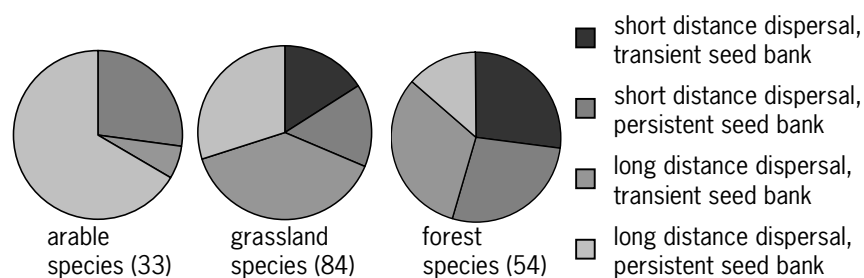
Figure 2.4 Relative abundance of species with contrasting dispersal and seed bank
strategies for groups of herbaceous plant species of arable land, grassland or forest habitat.
Number of species in each group is given in parenthesis. Short distance dispersal: species
with seed adapted for dispersal by ants or seeds without adaptations for dispersal; long
distance dispersal: dispersal by water or vertebrates. Wind dispersal: long distance in arable
and grassland habitat, short distance in forest habitat. Transient seed bank = species with
short-term persistent seed banks (< 5 years); persistent seed bank: species with long-term
persistent seed banks (> 5 years). Data from CBS (1993), Hodgson *et al*. (1995) and
Thompson *et al*. (1997).

Seed bank persistence: The potential of the seed bank as a source of
colonization depends on the persistence of the seeds in the soil, the age of the
seeds and the conditions of the soil (humidity etc) (Ter Heerdt *et al.* 1999). The
soil seed bank originates either from seeds produced by plants in the same
patch or from other populations in the landscape and that have been dispersed
over larger distances. Local populations that existed in the past but have long
disappeared, can also have been a source of seeds in the seed bank. Thus, the

local soil seed bank reflects not only the existing above ground vegetation, but also the past local vegetation and the past and present vegetation in the surrounding landscape.

Thompson *et al.* (1997) divided species into three groups that were based on the average longevity of seeds in the soil: transient (seeds that are persistent for less than one year), short-term persistent (seeds persistent for at least one but less than five years) and long-term persistent (seeds persistent for at least five years). We divided the group of species with short-term persistent seed banks between transient and persistent species. Depending on the number of observations of transient and long-term persistent seed banks that were found for a species in Thompson *et al.* (1997), we classified them either as transient or persistent. We divided the seed bank strategies in two groups because the two groups cover the extremes, which is sufficient for this chapter.

The potential of the soil seed bank as a source of colonization differs between vegetations of arable land, grassland or forest habitats (figures 2.3 and 2.4). Species of habitats that are regularly disturbed, like arable fields, very often have a persistent seed bank (87%), whereas fewer species of relatively undisturbed habitats, like grass lands and forested habitat have a persistent seed bank (46% and 41% respectively, figure 2.4).

Synthesis: strategies: When colonization ability is defined by dispersal capacity (high and low) and seed bank persistence (transient and persistent), we can divide species roughly into four strategies: i. Species with high dispersal capacity and persistent seed bank, ii. Species with high dispersal capacity and transient seed bank, iii. Species with low dispersal capacity and persistent seed bank, iv. Species with low dispersal capacity and transient seed bank.

Dispersal enables species to cross hostile environment in space ('*jumpers*'), while seed bank persistence enables it to overcome hostile environment in time ('*waiters*'). Other species cannot jump nor wait, probably because they evolved in stable environments where they did not have to adapt to (re)colonize empty patches and where the threat of extinction is also low because of the stability of the environment. All four strategies occur in nature (figure 2.4); examples of species are given in table 2.3.

Table 2.3 Some examples of herbaceous species for the 4 strategies.

		seed dispersal long distance	short distance	
seed bank	persistent	*Linaria vulgaris*	*Conium maculatum*	
		Senecio jacobaea	*Plantago lanceolata*	
		Lychnis flos-cuculi	*Silene latifolia*	→ waiters
		Typha latifolia	*Stachys palustris*	
		Tripleurospermum maritimum	*Medicago lupulina*	
	transient	*Achillea millefolium*	*Rhinantus angustifolius*	
		Cirsium vulgare	*Lysimachia vulgaris*	
		Cirsium pallustre	*Daucus carrota*	
		Heracleum sphondylium	*Vicia cracca*	
		Valeriana officinalis	*Galium verum*	

↓

jumpers

The link between landscapes and plant strategies

In this section we will formulate the expected qualitative output of the model and compare it with empirical data. Survival probabilities of species in the model are driven by the interplay of habitat dynamics, spatial arrangement and species characteristics.

With little continuity of habitat in both space and time, we expect survival probabilities to be low in all strategies, because extinction rates exceed colonization rates, either by dispersal or seed bank (figure 2.5). We expect that populations of *jumpers,* the species with a well-developed dispersal capacity (such as wind dispersers) have higher survival probabilities than species lacking such traits in landscapes with a low spatial cohesion (i.e. highly fragmented). This difference is most obvious when the distribution of habitat becomes more continuous in time. If, however, habitat becomes more variable in the temporal dimension, populations of *waiters*, the species with a long-term persistent seed bank, will have the highest survival probabilities. This difference is most obvious when the distribution of habitat is relatively continuous in space. With high continuity of habitat in both space and time, we expect high survival probabilities in all strategies, because extinction probabilities will be low enough to compensate by colonization, even for species with short distance dispersal and a transient seed bank.
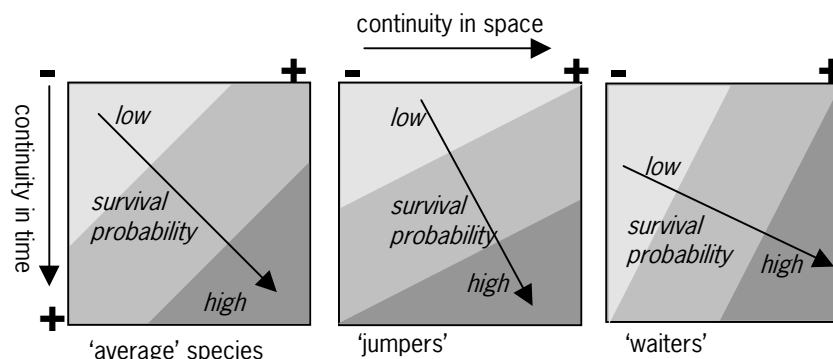
Figure 2.5 Expected relations between survival probability of 'average' species, 'jumpers' and 'waiters' and the spatial and temporal cohesion. The boxes represent combinations of low to high spatial (x-axis) and low to high temporal continuity (y-axis). Shading intensity indicates survival probability (light = low, dark = high).

The hypotheses produced by the conceptual model can be tested with empirical studies that compared the presence of species with contrasting strategies in one landscape or studies that compared the presence of a specific strategy in contrasting landscapes.

First we present some studies that focused on the contrasts between *jumpers* and *non-jumpers*. Van Dorp (1996) related the population turnover of ten herbaceous plant species in ditch banks to five life-history traits (including dispersal class). They didn't find a significant relation between life-history traits and the found variation, but concluded that the combination of life history traits could lead to species stability. Kleijn *et al.* (1998) found that common and mobile, perennial species are very successful colonizers of 3-year old herbaceous strips along arable fields, whereas woodland species and annual species were poor colonizers. Grime & Hillier (1992) found species with widely dispersed seeds to play a more significant role in early successional habitats than species lacking this trait. Our qualitative prediction on the survival of *jumpers* is supported by these finding, but Grime & Hillier (1992) nor Kleijn e*t al.* (1998) give quantitative data of the distances that could have been crossed. The predicted low survival of *non-jumping* species in highly fragmented landscapes is supported by data of species of forest habitats (e.g. hedgerows). Colonization probabilities of forest plants dropped to less than 0.5 at a distance of more than 100 m from source patches (Grashof-Bokdam & Geertsema 1998).

Next, we present some studies that focused on the contrasts between *waiters* and *non-waiters*. The higher the discontinuity of habitat in time, the

longer the period of unsuitability will be. Species with a long-term persistent seed bank can still germinate when a patch becomes suitable again after more than five years of unsuitability. When periods of unsuitability become longer than the duration of persistence, the survival of the species becomes dependent on the presence of stable source patches. Some field studies support the predicted relation between *waiting*-strategies and landscape characteristics. Grime & Hillier (1992) found species with a persistent seed bank to be present in both stable and disturbed habitat types but still they were relatively more present in disturbed habitats than species lacking this trait. The value of stable source patches has been found in a study of colonization patterns of forest plants with transient seed banks (Grashof-Bokdam & Geertsema 1998). In a study of the distribution of grassland species in ditch banks, species with persistent seeds were more abundant in young ditch banks (2-5 years old) than species with transient seeds. The latter species group was more strictly limited to the older (more than 10 years old), more stable ditch banks (chapter 3).

Few studies that compare the presence or survival of strategies in contrasting landscapes exist. Le Coeur *et al.* (1997) compared species richness in hedgerow networks of different grain size and found a clear landscape effect, but they made no remarks on the species composition or the strategies present. Grime & Hillier (1992) compared regenerative strategies in contrasting habitat types on a large scale, but gave no data on the presence of strategies of one habitat type in contrasting landscapes. A preliminary comparison of the density of ditches and the number of grassland species in km^2 grids revealed that almost 30% of the variation of species number was explained by ditch density; poorly dispersing species were found more often in areas with high ditch densities whereas they were missing in areas with a low ditch density, *jumpers* were equally abundant in the landscapes with high or low ditch densities (Schipperijn, unpublished data).

The predictions of the model may not be surprising. It does predict what one would expect, but this can be considered a confirmation of the value of the approach. New in the approach is that species with different strategies need different spatial and temporal configuration of habitat and this knowledge should be used in management plans and design of agricultural landscapes.

Conclusions

The value of the conceptual model

We showed that previous studies in farmland landscapes so far highlighted three separate aspects of the relationship of landscape pattern to plant biodiversity. Much attention has been paid to the local environmental conditions of field margins for plants and how to keep these in an adequate state by adaptive management. Also, the number of studies that focus on the spatial conditions for plant persistence is growing, but most of these studies are restricted to specific plant species in more or less isolated remnants of nature in an unsuitable surrounding. Plant species strategies were proposed in relation to vegetation dynamics before, but they focus mainly on the presence of strategies in contrasting vegetation types, often on small scales (several m^2) and hardly on the presence of the strategies in landscapes with contrasting spatial and temporal habitat arrangement. We offer a conceptual model that integrates all of these elements that, we believe, are crucial to the survival of plant species in spatially and temporally discontinuous habitat networks, which are so typical for farmland landscapes. We claim that this attempt is new, which explains why we could not find strong pieces of evidence to validate the model predictions, neither qualitatively nor quantitatively. Consequently, it is not possible to scale axes of the model and find thresholds of spatial cohesion in relation with a variable amount of patch disturbance.

Our model is developed with the Western and Central European farmland as our mental map. Most of the research we could find also applies to this type of landscape. However, we see no reason why the model would not apply to eastern North American farmland, or to farmland landscapes in southeastern Australia. We believe that it is applicable in landscapes used for intensive agriculture and being carried out in parcels, which are embedded in a structure of linear landscape elements (like road verges and field margins) that constitute a more or less continuous network, and are liable to frequent disturbances by management practices for other land use functions.

Ecological profiles of species

Seed dispersal and a viable soil seed bank are key sources for (re)colonization of empty patches in a landscape and thus key parameters for the survival in a fragmented and dynamic landscape. Combining these two adaptations, four plant strategies emerge which differ in the adaptation to long distance dispersal

and to persistence of the soil seed bank. We hypothesized that, firstly, the differences between survival probabilities of species with contrasting jumping strategies are governed by the spatial structure in the landscape and secondly, that the differences between survival probabilities of species with contrasting waiting strategies are governed by the variation in time at the patch level. These findings can help bring back the variation in species-landscape relations and serve as a basis for management and research.

Management implications

Our model predicts that spatial structure and the dynamics of the habitat on the landscape scale matter to the survival of plant species in agricultural landscapes. Given the limited amount of quantitative data, it is not possible to test the assumptions and determine critical thresholds for survival. Therefore, only qualitative management rules can be defined.

Management domains at two spatial scales control the botanical diversity in modern agricultural landscapes, where most species are restricted to the non-productive landscape elements. Firstly the domain of the management of the landscape elements: the quality of the landscape elements as patches for local populations. Secondly the domain of the landscape management: the spatial cohesion of the habitat network and the dynamics in the network determine the quality of the landscape network for metapopulations. The network cohesion is affected by changes in the use of the landscape by man. We recommend that measures to improve the ecological quality of farm landscapes be focussed on the landscape level rather than on the level of the landscape element or the field. These measures should be adapted to the desired vegetation. Vegetations with many species with poor dispersal capacities need a network as coherent in space as possible. Vegetations with many species with transient seed banks need a stable habitat network; at least part of the network should be made stable in time, to allow plant species to build up local populations and effectively disperse to newly developed elements.

In the Netherlands, subsidies to increase the botanical diversity of farm landscapes are paid to individual farmers, often at the level of individual fields or field margins. We predict that such measures will be much more successful if subsidies are paid to groups of farmers to restore landscapes rather than individual landscape elements. The effectiveness of such conservation contracts could be explored with the help of alternative landscape scenarios and dynamic models based on our conceptual model.

Table 2.4 Research approaches needed for landscape planning for plant biodiversity.

study type	priority	contents/purpose	result type
pattern studies	high	effect landscape structure + dynamics (Grashof-Bokdam & Geertsema 1998)	explorative, validation of models
time series	high	quantifying colonization and extinction probabilities, effect of landscape structure + dynamics (Ouborg 1993; Van Dorp 1996)	quantifying, parameterisation models
dispersal experiments	high	quantifying dispersal distances and seed rain density (Strykstra *et al*.1996; Van Dorp *et al*. 1996); special attention for role of field margins as corridors needed	quantifying, parameterisation models
seed bank experiments	moderate	Quantifying seed bank persistence, presence in an area (Bekker 1998; Falinska 1999)	parameterisation models
establishment experiments	moderate	Quantifying establishment probabilities (Kleijn *et al*. 1997; Tilman 1997)	parameterisation models
genetic studies	high	relating geographic distance with genetic distance (Grashof-Bokdam *et al*. 1998; Ouborg *et al.* 1999)	quantifying potential and actual dispersal distances
modelling studies	high	Integrating, generalizing and extrapolating different studies (Valverde & Silvertown 1997; Frank & Wissel 1998)	integrating, generalising, extrapolating

Further research

We have shown that few empirical studies are available to underpin and quantify our theory. There is a need for quantitative studies that track the history of spatial distribution of plant populations in dynamic landscapes and analyse the spatial dynamics in the context of spatial structure of the landscape and the patch dynamics. Also the combined effect of spatial arrangement and temporal dynamics of habitat rather than their separate effects on species survival should be investigated. Such data should be generalized and extrapolated by means of computer modelling. A further urgent step is to quantify the scales of figure 2.5 and determine the critical thresholds on them.

This would help to develop a tool (e.g. a decision support model) to distinguish between sustainable and unsustainable landscape scenarios for the survival of specific species groups. An example of such a tool is a spatially

explicit rule based model, the output of which is properly related to commonly used biodiversity measures (Opdam in press; Opdam *et al.* in press). The approaches in case studies and modelling studies we recommend are summarised in table 2.4. Empirical and modelling work should be integrated in an iterative process of defining and testing hypotheses wherein models replace experiments that are hard to design in practice.

One of the unresolved problems is the translation of a dispersal curve (for instance measured in a wind tunnel or inferred from terminal dropping velocity) into a rule for the minimal distance between patches that is needed in order to keep colonization probabilities in line with extinction probabilities. Especially the role of long distance dispersal in the survival of plant populations in fragmented landscapes needs further attention (Cain *et al.* 2000).

Also the role of the seed bank in metapopulation dynamics in fragmented dynamic landscapes should be studied more specifically in different areas.

Since agricultural landscapes have multifunctional purposes, it is often not enough to base the landscape planning on nature conservation values only. In such cases, scenario studies of alternative spatial configurations and dynamics are helpful to look for the type of landscape that allows an optimal combination of agricultural dynamics and plant diversity. A simplified spatially explicit model system based on metapopulation knowledge may then be developed as a tool to assess the conservation value of alternative landscape scenarios.

chapter 3

Plant distribution patterns related to species characteristics and spatial and temporal habitat heterogeneity in a network of ditch banks

W. Geertsema and J.T.C.M. Sprangers

Abstract

In this chapter we investigated the relationship between the distribution patterns of a number of herbaceous plant species and the isolation and age of habitat patches. The study was conducted for a network of ditch banks in an agricultural landscape in The Netherlands. Thirteen plant species were selected representing contrasting dispersal and seed bank characteristics. Isolation of habitat patches was determined by the distance to the nearest occupied patch and by the number of occupied patches in circles of increasing radius around the patches. Age was the number of years since the creation of the ditches. The separate effects of age of the habitat and the spatial variables were analyzed in a multiple logistic regression model. A number of habitat variables were used to correct the effect of habitat quality.

We concluded that distribution patterns of plant species were mainly determined by habitat quality and the presence of seed sources at short distances (< 25 m). This conclusion was independent of the dispersal characteristics of the species. Most species had higher occupation frequencies in older than younger ditch banks. Only species with persistent seeds had comparable occupation probabilities in older and younger habitat patches, indicating the importance of the soil seed bank as a source of colonization after large-scale disturbances. The effect of age and management on the occupation probabilities of the species was often diminished in the regression model, probably due to correlation between some habitat variables and the age of the patches.

Key words: agricultural landscape, dispersal, ditch bank, habitat fragmentation, metapopulation, seed bank

Introduction

The maintenance of plant diversity of agricultural landscapes has received increasing attention in the past two decades (Merriam 1988; Bunce *et al*. 1993). Non-productive landscape elements such as ditches, hedgerows, field margins and road verges, are of major importance for the survival of wild plants in these landscapes (Bunce & Hallam 1993). Adjacent agricultural activities strongly influence the quality of the habitat of those elements (Kleijn & Verbeek 2000).

Their often linear shape makes them especially sensitive to adjacent land use. The plant diversity is influenced by the application of fertilizers and pesticides on the adjacent fields and by the amount of drift (Perry *et al*. 1996; De Snoo & Van der Poll 1999). The presence of a strip where no herbicides and fertilizers are applied between the crop and the landscape element can increase the botanical value of the landscape elements (Kleijn *et al*. 1997). The management of the landscape elements themselves may also influence the biodiversity (Parr & Way 1988).

The non-productive landscape elements seldom provide a continuous network of suitable habitats (Fry 1994). The network is often fragmented as a result of large scale modern farming systems. The habitat quality for specific plant species within the landscape element varies in space and time due to abiotic factors, the activities of soil dwelling organisms, the distribution of competing plant species and activities that are related to agricultural practices (Kleyer 1999; Kleijn & Verbeek 2000; Schippers 2000). As a result, many plant species grow in spatially fragmented populations. Local populations can function as a metapopulation when empty, suitable patches are colonized by seeds from other populations in the area (Levins 1970; Hanski 1985; Husband & Barrett 1996) or from the soil seed bank (Bakker *et al*. 1996; Husband & Barrett 1996). The concept of metapopulation dynamics was developed for animals, but some plant studies indicate that plants also function as metapopulations (see reviews by e.g. Eriksson 1996 and Husband & Barrett 1996). When applying the metapopulation concept to plant population dynamics, it is necessary to bear in mind the characteristics of plants in comparison with animals. The most obvious contrasts between plants and animals are that plants are rooted and often have long life spans and vegetative propagation. They also exist in the soil as a seed bank, and may have sporadic recruitment within established populations of perennial plants (Eriksson 1996; Husband & Barrett 1996). A particular consequence of seed banks and long life spans is that there is often a delayed response to changes from favourable to unfavourable environmental conditions. This 'capacity of population inertia' (Eriksson 1996) enables plants to bridge unfavourable conditions in time, resulting in a delay or even absence of local extinction events. It would therefore be expected that disturbances caused by agricultural activities would be a more important cause of local extinction, than demographic stochasticity. Most previous plant metapopulation studies have been done in ephemeral habitats, where environmental disturbance is the major cause of local

extinction. Demographic stochasticity as a source of local extinction has received less attention in plant studies, probably because it is not expected to be of much importance due to the capacity of population inertia.

The actual distribution pattern of species reflects the current habitat quality and the presence of other populations which function as sources of dispersing seeds. Many studies have approached this topic of safe site as compared with dispersal limitation. These studies led to the general conclusion that for many species the distribution of species is influenced by a combination of both factors (Primack & Miao 1992; Bakker & Berendse 1999; Van Groenendael *et al.* 2000). Furthermore, dispersal limitation was found by Tilman (1997) and Eriksson (1997) and safe site limitation by Wolf *et al.* (1999).

Seed availability consists of seeds produced in the surroundings of a focal site, but also of viable seeds in the soil (Pakeman *et al.* 1998; Wolf *et al.* 1999). The soil seed bank is the result of processes that have occurred in the past. Populations that were present in the past may have disappeared, but their seeds can still be present in the soil. When the above ground vegetation is removed by a large-scale disturbance event, only the soil seed bank community is left. The vegetation that then colonizes the site will largely consist of species that were present in the soil seed bank, in conjunction with species that have a well-developed dispersal capacity and were therefore able to colonize from populations elsewhere in the landscape. The age of a site can thus be considered the period since the last major disturbance event that removed the above ground vegetation.

Several studies on the relationship between the distribution of herbaceous plants in linear landscape elements and landscape structure have been carried out in landscape elements with trees, such as hedgerows (e.g. Marshall & Arnold 1995; Le Coeur *et al.* 1997; Grashof-Bokdam & Geertsema 1998). In studies of grassland vegetation few researchers have included the influence of seed sources in the surrounding landscape on the incidence of plants (e.g. for ditch banks: Van Dorp 1996 and for road verges: Nip-Van der Voort *et al.* 1979). Increasing occupation probabilities were found at decreasing distances from seed sources for all habitat types (Nip-Van der Voort *et al.* 1979; Marshall & Arnold 1995; Hutchings & Booth 1996a; Grashof-Bokdam & Geertsema 1998).

The aim of the present study was to investigate how the occupation probabilities of plant species in a network of ditches with variable habitat

quality were influenced by the spatial distribution of a species in the surrounding area and by the age of the habitat patches.

We have tried to answer the following questions:

(a) What is the influence of the spatial distribution of a species in the surrounding landscape and the age of the landscape elements on the occupation probability of the species?

(b) Do populations at short distances influence the occupation probabilities of species with poor dispersal ability more than the occupation probabilities of species with well-developed dispersal?

(c) Are species with a persistent seed bank more abundant in young habitat patches than species with a transient seed bank?

Methods

Study area

The study area was situated in the north-east of the province of Drenthe in the Netherlands (6°27' E and 52°47' N). The total area studied covered about 150 hectares, bordered in the north-west by forest and elsewhere by agricultural land. The soils were mainly peat on sand or sandy soils. This study area was selected as it consisted of arable fields containing various crops and containing ditch banks with contrasting species assemblages growing on both old and young ditches.

Land use consisted mainly of conventional arable farming systems. The crops in the area were mainly potatoes, but sugar beet and barley, some wheat, oats, blackcurrants and ornamental flowers were also present. The crops of potato and sugar beet received on average 165 kg N, 100 kg P and 150 kg K, cereals 70 kg N, 47 kg P and 140 kg K, blackcurrant 75 kg P and 75 kg K and ornamental flowers received 35 kg N, 100 kg P and 240 kg K (all ha^{-1} yr^{-1}).

The fields were separated by ditches, which sometimes contained non-productive strips, varying in width, between the banks and the crops. Some new ditches had been created in the area during a land improvement project in the period 1994 to 1996.

Selection of focal plant species

The plant species that were used for this study had to meet a number of criteria. Firstly they had to be negatively influenced by high amounts of fertilizers and

herbicides and by disturbance, as these are the factors that cause habitat fragmentation in the study area. Species that have been recorded to be indicative for management favouring nature conservation on ditch banks meet these criteria (Bruggink & Buitink 1995). Secondly the species needed to have contrasting dispersal and seed bank characteristics. Information on dispersal and seed bank characteristics was therefore collected in a literature study (CBS 1993; Hodgson *et al.* 1995; Thompson *et al.* 1997). The vegetation of species rich ditch banks consists mainly of perennial herbaceous species that favour moist to wet, nutrient rich conditions. Therefore we limited the selection to perennial species of those ecological groups. Using these criteria, we selected 13 plant species (table 3.1).

Table 3.1 Overview of focal species, their dispersal mode, seed bank characteristics and ecological group (CBS 1993; Hodgson *et al.* 1995; Thompson *et al.* 1997). Species are grouped by their dispersal and seed bank characteristics.

species name	dispersal	seed bank	ecological group
Achillea millefolium L.	wind	transient	moist, nutrient rich grasslands
Valeriana officinalis L.	wind	transient	wet, nutrient rich grasslands
Linaria vulgaris Mill.	wind	persistent	nutrient rich ruderal vegetation
Lychnis flos-cuculi L.	wind	persistent	wet, nutrient rich grasslands
Iris pseudacorus L.	water	transient	nutrient rich banks
Lysimachia vulgaris L.	water	transient	wet, nutrient rich grasslands
Galium palustre L.	water	persistent	nutrient rich banks
Ranunculus sceleratus L.	water	persistent	pioneer of nutrient rich soils
Stachys palustris L.	water	persistent	wet ruderal vegetation
Rorippa amphibia (L.) Besser	no adaptation	transient	nutrient rich banks
Symphytum officinale L.	no adaptation	transient	wet ruderal vegetation
Vicia cracca L.	no adaptation	transient	moist, nutrient rich grasslands
Plantago lanceolata L.	no adaptation	persistent	moist, nutrient rich grasslands

Incidence data: the dependent variable

The distribution patterns of the 13 species were studied in ditch banks. Data were collected in series of 10 m long patches (width of the patches equalled the width of the ditch banks). We recorded presence and absence of the 13 species in each patch. The surveys were carried out in 1998 in June, the end of July and the beginning of August. If a species was found at any of these times it was recorded as present. In this way the complete length of all the ditch banks was monitored.

For the analysis a spatial unit was required that indicated suitable habitat patches for local populations and the length of 10 m proved suitable for practical and biological reasons. Habitat suitability for plants depends on numerous parameters, which were impossible to measure in the total area for practical reasons. Instead a limited number of factors were recorded in all patches in order to indicate the habitat suitability for the focal plant species (see below).

The size of the patches should indicate the size of a local population but the limits of a local population of plants are also hard to determine in the field. These are determined by the interaction between the individual plants that constitute the local population. Seed and pollen dispersal are the major spatial processes that result in interaction between populations. It was decided that plants should be considered belonging to one local population if they grow closer to each other than the distance that is crossed by the majority of the dispersed seeds. Pollination is not a source of colonization and does not directly determine distribution patterns of plants so pollination distance was not used in the definition of local populations. Most herbaceous species deposit the majority of their seeds within a distance of 5 m from the parent plant (Willson 1993; Van Dorp *et al*. 1996). A number of species have dispersal distances that easily exceed 5 m, others disperse all their seeds within that distance. Taking the average of 5 m on both sides of the centre of a patch and projecting the local population in the centre of a patch, a patch length of 10 m was obtained.

Explanatory variables

The incidence data of the focal species was related to variables describing the spatial arrangement, age and habitat quality of the patches as shown in table 3.2.

Table 3.2 Overview of explanatory variables used in the multiple logistic regression analysis to explain occupation patterns of the 13 focal species.

HABITAT VARIABLES:

	scale		*scale*
vegetation type	patch	**management**	ditch bank
7 vegetation types,		mowing, hay removed	
description: see Results		mowing, hay not removed	
		'mulching'	
bank width	ditch bank		
0-3 m		**ditch width**	ditch bank
		0-8 m	
bank slope	ditch bank		
30-80°		**rotation**	field
		non-agricultural land use	
aspect	ditch bank	1 year cereals, 1 year root crop	
south east		1 year cereals, 2 year root crop	
south west		1 year cereals, 3 year root crop	
north east		mostly ornamental flowers	
north west		continuous blackcurrants	
width non-productive	ditch bank	**land use**	field
strip		non-agricultural land use	
0-4 m		potatoes	
		sugar beet	
		cereals	
		blackcurrants	
		ornamental flowers	

AGE and SPATIAL VARIABLES:

	scale
age of ditches	ditch
2-5 year	
> 10 year	
linear spatial variable	patch
D-OCC: distance to nearest occupied patch	
circular spatial variables	patch

N-OCC15: number of occupied patches within	15 m		
N-OCC25: " " "	15-25 m		
N-OCC50: " " "	25-50 m		
N-OCC100: " " "	50-100 m		
N-OCC200: " " "	100-200 m		

(a) *Habitat variables:* Based on the vegetation structure and dominant species we grouped all patches in ten preliminary vegetation types that contained comparable species assemblages. Fifty sites were selected that covered these vegetation types in the area with detailed information being collected on their quality. The width of the sites was the same as the width of the ditch banks in which they were located and the length was chosen in such a way that the total area would be 8 m^2 for all sites. In July 1998 the abundance of all plant species in the sites was determined using the Braun-Blanquet scale, the biomass of the peak standing crop was measured and soil samples were collected to determine NO_3, NH_4, PO_4, K, C/N, pH and organic matter content. The species abundance data were analyzed with the TWINSPAN algorithm to produce a table grouping sites with comparable species composition together. The results of the classification defined the vegetation types that were later used in the analysis of the incidence data of the 13 focal species. The vegetation types produced by the TWINSPAN analysis were compared with the Dutch vegetation classification described in Schaminée *et al.* (1996, 1998) and Stortelder *et al.* (1999).

Data on land use, rotation, herbicide use, fertilization and management of the ditches and ditch banks were obtained from a questionnaire that was distributed among the farmers in the area. Fertilization and herbicide use were not included separately in the analysis because they were strongly correlated with the crop grown. The management of the ditches was relatively consistent throughout the study area and involved cleaning out the ditches in October or November each year. We therefore excluded this factor from the analysis. The slope angle of the ditch banks was measured with a compass and the width of the non-productive strips, the ditch banks and the ditches were also measured.

(b) *Spatial variables:* The spatial variables were calculated with the use of the GIS software ArcView (ESRI 2000). We used a linear spatial variable: distance from each patch to the nearest conspecific occupied patch, termed D-OCC, and circular spatial variables: the number of conspecific occupied patches in circles of increasing radius around each patch, termed N-OCC15, N-OCC25, up to N-OCC200, for radii of 0-15, 15-25, up to 100-200 m.

(c) *Age:* The age of the ditches was based on information provided by farmers and maps of the study area. At the time of the study, about 20% of the length of the ditches were 2 to 5 years old and 80% were older than 10 years. There were no ditches of intermediate age. The two age classes were used in the analysis.

Statistical analysis

The Genstat 5.4.1 procedure IRREML (Iteratively Reweighted Residual Maximum Likelihood) (Keen & Engel 1998) was used to analyze which variables gave the best explanation of the incidence data of each species. IRREML is a procedure for multiple logistic regression analysis that corrects for correlation of the data by including the source of correlation as a random factor in the analysis. In this chapter the spatial scale 'ditch' was included in the regression model as a random factor in order to correct for the correlation between the observations within one ditch.

The regression model was constructed by first adding significant habitat parameters to the model to correct for their effects. Using a backward elimination procedure the significant habitat variables ($p < 0.05$) were identified. Vegetation type was always included in the regression model, as it was expected to represent the combined effect of a large number of abiotic, biotic and antropogenic factors, including factors that were not represented by one of the other habitat parameters. Table 3.3 shows correlation coefficients between the habitat and age variables. Because most correlation coefficients were low, only values > 0.250 (positive or negative) are shown.

The remaining variation was further analyzed to investigate the effect of age and spatial variables. The variables age, distance to the nearest occupied patch and the number of occupied patches around a patch were analyzed separately. The effect of the number of occupied patches around a patch was analyzed by sequentially adding N-OCC15, N-OCC25, N-OCC50, N-OCC100 and N-OCC200 to the model. In this way the radius of the sphere of influence could be determined for each of the species (Vos & Stumpel 1996).

We quantified the relationship between the occupation probability of species and one measure of isolation i.e. the distance to nearest occupied patch. This analysis was limited to the species that showed a significant relationship between the distance to the nearest occupied patch and occupation probability. The same statistical models were used for those species as in the former analysis, i.e. with significant habitat variables and vegetation type as covariables and the spatial level 'ditch' as random factor to correct for the correlation between the observations of a species within one ditch. These statistical models were used to predict the occupation probabilities of the species for a range of values of distance to the nearest occupied patch, while the probability was corrected for the effect of the habitat quality.

Table 3.3 Correlation matrix for the habitat variables. Only correlations > |0.250| are shown. Correlations between classes of one variable are also excluded (e.g. correlation between management by mowing & removal and by mulching)

	type 2	type 3	type 7	bank width	bank slope	width non-prod. strip[1]	management: mulching	ditch width[1]	rotation[2]:R1	R2	R3
bank slope			−.524	−.480							
width non-prod. strip[1]	−.346		.683		−.341						
aspect: NW					.266						
					−.255		.269				
man: mowing			−.488		.332	−.578		−.505			
mowing & removal	−.297	−.258	.760	−.341	−.408	.817					
ditch age								.876			
rotation[2]: R1						−.269	−.502				
R2				.250	−.299		−.328				
R4							.266				
land use: potatoes						−.297			.524	−.356	
beets										.450	−.281
cereals									−.320		
ornam. flowers											.342

[1] values of the width of the non-productive strip and the width of the ditch were ln-transformed. [2] R1 = 1 year cereals, 1 year root crop; R2 = 1 year cereals, 2 year root crop; R3:1 year cereals, 3 year root crop R4: mostly ornamental flowers.

Results

A total of 11.18 km of ditches was surveyed, equalling 22.36 km ditch banks or 2236 patches. The most abundant species, *Symphytum officinale,* was found in 25.7% of all patches (574 patches). *Lychnis flos-cuculi* was the least abundant with 2.8% of all patches occupied (62 patches). To get an impression of the distribution patterns in the landscape, examples of distribution patterns of *L. flos-cuculi* and *Linaria vulgaris* are shown in figure 3.1. *L. flos-cuculi* has a concentrated distribution pattern, while *Lin. vulgaris* has a dispersed distribution pattern.

Lychnis flos-cuculi

Linaria vulgaris

occupation of species in patches in ditch banks

———— species not present in one of the opposite patches

— one of opposite patches occupied

● both opposite patches occupied

0   250   500   Meters

Figure 3.1 Two examples of distribution patterns of studied species: *Lychnis flos-cuculi* and *Linaria vulgaris.* The figures show whether a species is present in one or two of the 10 m long patches that are located opposite each other in the ditch banks along a ditch. Inserted: the location of the study area in the Netherlands.

Table 3.4 Level of significance of variables on the occupation probability of the focal species, determined by multiple logistic regression analysis. Effect of age and spatial variables are corrected for the significant habitat variables (always including vegetation type). Species are sorted by their dispersal mode and seed bank characteristics.

	Achillea millefolium	*Valeriana officinale*	*Linaria vulgaris*	*Lychnis flos-cuculi*	*Iris pseudacorus*	*Lysimachia vulgaris*	*Galium palustre*	*Ranunculus sceleratus*	*Stachys palustris*	*Rorippa amphibia*	*Symphytum officinale*	*Vicia cracca*	*Plantago lanceolata*
dispersal mode:	wi	wi	wi	wi	wa	wa	wa	wa	wa	-	-	-	-
seed bank:	T	T	P	P	T	T	P	P	P	T	T	T	P
habitat variables:													
vegetation type	*		***	***	*			~			***	***	~
bank width											***		
bank slope		***	***	*			~	**		**	**		
aspect	***	***	**	***	*					*		~	~
width non-prod. strip[1]	**	~				***	*						***
management								**	~				
ditch width[1]	**	***					*	**					
rotation			***		*	*		***			**	~	
land use	**	**	**								**	***	
significant habitat variables + age:													
age of the ditches	*	*											~
significant habitat variables + spatial variables:													
D-OCC[1]	***	***	***	~	***	***	***	***	***		***	***	***
N-OCC15[1]	***	***	***	~	*	***	*	***	***		***	***	***
N-OCC25[1]		***	***				**	**	*		**		~
N-OCC50[1]					**			*		**			
N-OCC100[1]										**			
N-OCC200[1]						.	*	*					

Dispersal mode: wi = dispersal by wind, wa = dispersal by water, - = no adaptations for long distance dispersal. Seed bank: P = persistent seed bank, T = transient seed bank. D-OCC: distance to nearest occupied patch; N-OCC15, N-OCC25, ...N-OCC200 = number of occupied patches within a radius of 15 m, 15-25 m, ... 100-200 m around a patch.The effect of N-OCC25, ..., N-OCC200 is corrected for the effect of the number of conspecific occupied patches in the preceding circles. Level of significance based on F-values ~: $p < 0.1$; * $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$; where level of significance is missing, the relationship was not significant. [1] = ln-transformed.

In Appendix 3-I an overview is given of the relationship between the separate habitat variables, age and the occupation of the plant species. Appendix 3-I shows which part of patches, per class or category of the variables, was occupied by the focal species. Table 3.4 shows the results of the IRREML analysis.

Effects of the habitat variables

The significant habitat variables that were selected using the backward elimination procedure are shown in table 3.4. Note that the significance level of a variable was defined as the level of significance given the effect of the other significant variables in the regression model. *Stachys palustris* was the only species that showed no significant relation with any of the habitat variables.

(a) *Vegetation type:* the ten preliminary vegetation types were regrouped by TWINSPAN into seven vegetation types because the species composition of a number of the preliminary types was relatively similar. When preliminary vegetation types were grouped together, also the patches that belonged to the preliminary vegetation types were grouped together. The seven vegetation types consisted often of a mixture of the vegetation types as described by Schaminée *et al.* (1996, 1998) and Stortelder *et al.* (1999) and could be clustered in two groups (see Appendix 3-II). The first cluster (types 1, 2, 3 and 5) was on average less species rich than the second cluster (types 4, 6 and 7). Cluster I was characterized by nutrient rich, ruderal vegetations and had affinities with the *Galio-Urticetea*. Vegetation type 1 had also some characteristics of the *Convolvulo-Filipenduletea* class, vegetation type 2 of the *Bidention tripartitae* and *Nanocyperion flavescentis*, vegetation type 3 of the *Dauco-Melilotion* and type 5 of the *Melampyrion pratensis*. Cluster II had less affinity with the *Galio-Urticetea* than cluster I, but a closer relationship with the *Nanocyperion flavenscentis*. Type 4 also had some characteristics of the *Dauco-Melilotion*, whereas type 6 had the largest contribution of the *Digitario-Illecebretum* association. Type 7 had some characteristics of the *Molinio-Arrhenatheretea* class.

Organic matter, pH, PO_4 and C/N were most discriminating variables between the vegetation types (table 3.5). Vegetation type 7 showed the highest number of significant differences with other groups ($p < 0.05$), while types 1 and 2 and types 3 and 4 were relatively similar. Vegetation type 7 had the lowest pH and highest organic matter content, C/N ratio and NH_4 ($p < 0.05$).

In the statistical analysis vegetation type had a significant relation ($p < 0.05$) with the distribution pattern of approximately half of the focal species. The majority of the focal species was most abundant in vegetation type 7. *L. flos-cuculi, Iris pseudacorus* and *Rorippa amphibia* belong to this majority and showed a significant relation with vegetation type. Other significant effects of vegetation type were found for *Achillea millefolium* which showed a preference for type 6 and *Lin. vulgaris* which was found more often in vegetation types 2-5 and less in types 1, 6 and 7. *Vicia cracca* was the only species with highest abundance in type 5.

Table 3.5 Biomass of peak standing crop and soil characteristics of vegetation types in the study area, based on data of 50 samples. Different superscript letters indicate significant differences between the biomass or soil characteristics of vegetation types as determined by analysis of variance ($p < 0.05$)

veg. type	biomass (ton/ha)	pH	organic matter	C/N (%)	NO$_3$ (mg kg^{-1} soil)	NH$_4$ (mg kg^{-1} soil)	PO$_4$ (mg kg^{-1} soil)	K (mg kg^{-1} soil)
1	6.00[a]	5.43[ab]	0.08[ab]	22.08[a]	2.48	5.43[a]	0.66[abc]	78.59
2	3.99[ab]	5.07[acd]	0.20[ab]	25.21[a]	4.51	8.32[a]	3.75[ac]	43.57
3	3.47[b]	5.66[b]	0.08[a]	23.58[a]	1.64	4.17[a]	0.84[bc]	55.26
4	2.79[bcd]	5.31[abc]	0.09[a]	23.96[a]	0.67	6.32[a]	0.23[b]	46.76
5	2.93[bd]	4.79[cd]	0.36[b]	34.55[bc]	1.20	7.24[a]	5.90[acd]	43.40
6	1.82[c]	4.49[d]	0.22[ab]	26.19[ab]	1.14	3.54[a]	2.02[c]	37.12
7	2.31[d]	4.10[e]	0.78[c]	40.94[c]	0.87	19.11[b]	7.79[d]	86.19

(b) *Bank width, slope angle and aspect*: the average width of the ditch banks was 2 m (minimum 0.5; maximum 3.1). Most species tended to be more abundant in wider ditch banks. The effect was only significant for *S. officinale*. The angles of the slopes varied between 30° and 80° (average 51°). Most species had a generally higher abundance on gentler slopes than on steeper ones. For *Lin. vulgaris, L. flos-cuculi, Ranunculus sceleratus* and *R. amphibia* this relationship was significant. *Valeriana officinalis* and *S. officinale* seemed to have significant higher abundances on steeper slopes. Most species had slightly higher abundances on south-eastern exposed banks than on other banks, especially *A. millefolium, Lin. vulgaris, L. flos-cuculi* and *R. amphibia*. *V. officinalis* also had a significant relationship with aspect but had lowest abundances on south-eastern exposed banks.

(c) *Width of non productive strip*: non-productive strips between ditch banks and fields were rare (maximum width 4 m, average width 0.8 m). The

abundance of most species was positively correlated to the width of the non-productive strip between the ditch bank and the adjacent field. For *A. millefolium, Lysimachia vulgaris, Galium palustre* and *Plantago lanceolata* this relationship was significant.

(d) *Management of the ditch banks*: the majority of the species had their highest abundance on ditch banks that were mown and where the hay was removed. This relationship was only significant in the statistical analysis for *G. palustre*.

(e) *Width of the ditch*: the average width of the ditches was 1.6 m and varied from 0 m (dry, very narrow ditches) to 8 m. Most species had higher percentages of occupied patches along wider ditches than along narrower ones. This was significant for *A. millefolium, V. officinalis, G. palustre* and *R. sceleratus*.

(f) *Land use and rotation*: in 1998 none of the species was limited to any type of adjacent land use or rotation. However, some were more abundant in ditch banks adjacent to certain types of land use and a number of species did not occur adjacent to crops of blackcurrants or ornamental flowers. *Lin. vulgaris, S. officinalis* and *V. cracca* all showed a significant effect of both adjacent land use in 1998, and the rotation on the adjacent fields in the former years. *A. millefolium* and *V. officinalis* only had a significant effect of adjacent land use in 1998, the year when the observations were made.

Effect of age

Most species had a higher occupation probability on banks of ditches that were older than 10 years. *Lin. vulgaris, R. sceleratus, S. palustris* and *S. officinale* had comparable occupation percentages on old and young ditch banks. Except for *S. officinale* these species have persistent seeds. In the IRREML model we corrected for habitat quality by first adding the significant habitat variables and vegetation type to the model. When subsequently age was added, the positive relationship between age and occupation probability was only significant for *A. millefolium* and *V. officinalis* ($p < 0.05$), whereas it was almost significant for *P. lanceolata* ($p < 0.1$).

Effects of the spatial variables

(a) *Distance to nearest occupied patch:* after correction for the significant habitat variables and vegetation type, the occupation probabilities of 11 of the 13 species showed a highly significant relation to the distance to the nearest

occupied patch (p < 0.001) (table 3.4). Only for *L. flos-cuculi* and *R. amphibia* was no significant relation found. Figure 3.2 shows that, after correction for the significant habitat variables, the predicted occupation probability of those 11 species declined with the distance to the nearest occupied patch. With the exception of *V. officinalis,* the occupation probability of suitable sites dropped below 0.05 when the nearest occupied patch was further away than 55 m, and at a distance larger than about 400 m, below 0.025. There was no clear relationship between the dispersal characteristics of the species and the effect
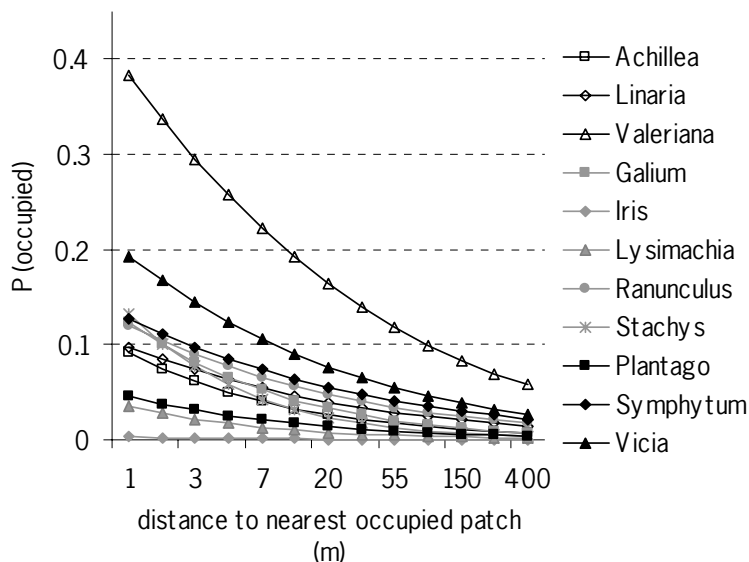

Figure 3.2 Predicted occupation probabilities after correction for habitat at different distances from nearest occupied patches for species that showed a significant effect in the regression analysis for distance to nearest conspecific local populations. Open symbols & black line: wind dispersed, grey symbols & grey line: water dispersed, closed black symbols & black line: no adaptation for (long distance) dispersal.

of distance to the nearest occupied patch on the occupation probabilities.

(b) *Number of occupied patches around a patch:* the number of occupied patches in the adjacent area influenced all species after correction for habitat quality, except *L. flos-cuculi* (table 3.4). *R. amphibia* was only influenced by the number of occupied patches within 50 m. The strongest effect was found for the number of occupied patches within 15 m around a patch. For half of the

species also the number of occupied patches at a distance up to 25 m significantly affected the occupation probability and for a few species also the number of patches at distances up to 200 m significantly influenced the occupation probability. There was no clear relationship between dispersal characteristics and the effect of the number of occupied patches at different distances from the patches on the occupation probabilities (table 3.4).

Discussion

Spatial variables

The results of the study show that the occupation probability decreased with increasing distance to the nearest occupied patch as well as with a decreasing number of occupied patches in the near vicinity of the focal patch. The relationship between occupation probability and isolation is an indication that the studied species function as metapopulations in the study area (Opdam 1990). Both the linear and circular spatial variables indicated that the impact of the ambient area was strongest within 25 m. This can be attributed to the combined effect of colonization and extinction the preceding years. Although it is not known which populations were seed sources for other populations, we conclude from our data that most colonization occurred within 25 m of a seed source. The low occupation probabilities at larger distances indicate that the distribution of many species is at least partly limited by dispersal. At short distances regeneration by seeds, but also by vegetative regrowth is likely to be the way all species expand, except *R. sceleratus* (Hodgson *et al.* 1995). The impact of the presence of occupied patches at a larger distance was weak. Colonization over these distances could have occurred at low frequencies. Still, the low colonization probabilities at large distances might be very important for the long term survival of plant species in discontinuous habitats at the landscape level (Cain *et al.* 2000; Nathan & Muller-Landau 2000).

The differences between the species with different adaptations for dispersal were not consistent. We expected that the occupation probability of species with adaptations for dispersal by wind or water would be more influenced by the presence of other populations at larger distances than species lacking those adaptations. Nip-Van der Voort *et al.* (1979) showed that colonization rates of herbaceous plants on road verges in a new polder were influenced by the dispersal characteristics of the plant species. The order of

immigration rates into new habitat related to the dispersal characteristics was: water ≥ wind >> humans ≥ animals ≥ none. However, in the present study this gradient was not reflected by the analysis of the impact of the spatial variables. The functioning of other dispersal mechanisms such as mowing machinery (Strykstra *et al*. 1996) could cause the lack of differences between the dispersal characteristics of species in ditch banks. However, Coulson *et al.* (2001) found differences in the efficacy of mowing machinery as a dispersal vector for two grassland species. They emphasize that mowing should take place at the moment of seed set but not before. Finally, animals could also have operated as dispersal vectors.

Age

Most species had a lower abundance in young ditch banks compared to the older ditch banks. The species that had comparable occupation percentages in old and young ditch banks were species that have the ability to build up a persistent soil seed bank i.e. *Lin. vulgaris, R. sceleratus* and *S. palustris. G. palustre, L. flos-cuculi* and *P. lanceolata* also have persistent seeds, but had not colonized the new ditch banks to an occupation percentage to the degree reached on the older ditch banks. This could be due to the absence of viable seeds in the soil. Another possible explanation is that the patches are not yet suitable for these species because the latter three species belong to grassland vegetation, whilst the former three belong to ruderal vegetation. *S. officinale* is classified as a species with a transient seed bank. However, the occupation probability of young ditch banks is comparable to that of the older ditch banks and *S. officinale* is a species of ruderal habitats, which may explain its presence in young ditch banks.

The lack of effect of age in the regression model after correction for habitat quality was probably caused by its correlation with other habitat variables. The majority of the patches in vegetation types 5, 6 and 7 was older than 10 years and many of the species were found in higher abundances in these types compared to vegetation types 1-4. However, the correlation coefficients did not reflect the correlation between age and vegetation types as shown in table 3.3. This is probably because age was more evenly distributed over vegetation types 1-4, so old ditches were not limited to vegetation types 5-7.

Habitat quality

The different variables that make up habitat quality were important explanatory variables of the occupation probability of the focal species. Therefore, not only dispersal restrictions, but also safe site limitation, determine the distribution patterns of the studied species (except *S. palustris*). Vegetation type, slope angle and aspect of the ditch bank, adjacent land use and rotation had most frequently significant effects on the incidence of the species. Although all focal species are associated with moist to wet nutrient rich vegetations, some belong to grasslands and others to more ruderal vegetation (CBS 1993). The distribution of the species in the vegetation types corresponds to the ecology of the focal species. *Lin. vulgaris, R. sceleratus, S. palustris* and *S. officinale* which belong to ruderal or pioneer vegetation were relatively abundant in the more ruderal vegetation types 1-3 and 5. The other species that were more abundant in vegetation types 4, 6 and 7 belong mainly to grasslands or bank vegetations (CBS 1993).

Most species in the present study had a tendency to be more abundant on gentler slopes. Van Strien *et al.* (1989) found higher floristic diversity on ditch banks with steep, south facing slopes than gentle slopes. However, the steepest slopes in that study did not exceed 35°, which is comparable to the gentlest slopes in the present study.

South facing slopes generally had higher occupation probabilities than other slopes, which is in accordance with Van Strien *et al.* (1989). South facing slopes receive more insulation, which promotes germination and the establishment of seedlings and may therefore promote higher occupation probabilities of the species.

Land use and rotation were closely related to the use of fertilizers and herbicides in the study area. The conclusion agrees with Kleijn & Verbeek (2000). This relationship can explain the effect of land use and rotation on the distribution of the focal species.

Mowing, with removal of hay, lowers the biomass of the vegetation in the long term, and is essential for high diversity in grasslands (Olff & Bakker 1991). The apparent lack of management effect in the multiple regression models might be caused by the correlation between management and other habitat variables (table 3.3), where the effect of other habitat variables already accounts for the effect of management.

Implications for conservation

Measures taken by farmers to increase the diversity of herbaceous vegetations of linear landscape elements are focussed primarily on management practices. The effect of these measures is expected to increase when the influence of the surrounding landscape and the dynamics of the area are taken into account (Smeding & Joenje 1999).

The results demonstrate that it is important that populations of the focal species are present within 25 m of landscape elements with good habitat quality. A landscape with a coarse network of wide landscape elements, or a dense network of narrow elements, provides spatial structures that enable this situation for plants that inhabit the linear landscape elements. Wide landscape elements and large fields are more suitable for agricultural practices and not only provide more habitat at short distances, but also lower the negative impact of agricultural practices in adjacent fields.

After large-scale disturbances, such as the excavation of ditches, it may take many years before the habitat is colonized by species, especially those with a transient seed bank. It is important therefore to prevent these large-scale disturbances.

Appendix 3-I. Overview of the influence of the separate habitat variables and age of the ditches on the occupation frequencies of focal species. The dispersal mechanism (Wi = wind, Wa = water, no ad. = no adaptations for long distance dispersal), and seed bank characteristics (T = transient, P = persistent) of each species are given. The table shows which part of the patches, per class or category of the variables, was occupied by the focal species; for example one patch of the 108 patches of vegetation type 1 was occupied by *Achillea millefolium* = .009 (1/108). (n)¹: number of patches in each class or category of the variable.

	Ach.mil.	*Val.off.*	*Lin.vul.*	*Lyc.f-c.*	*Iri.pse.*	*Lys.vul.*	*Gal.pal.*	*Ran.sce.*	*Sta.pal.*	*Ror.amp*	*Sym.off.*	*Vic.cra.*	*Pla.lan.*
dispersed by:	Wi	Wi	Wi	Wi	Wa	Wa	Wa	Wa	Wa	no ad.	no ad.	no ad.	no ad.
seed bank:	T	T	P	P	T	T	P	P	P	P	T	T	P
vegetation type													
type 1 (108)¹	.009	.102	.074	.009	.000	.000	.000	.074	.065	.000	.453	.065	.037
type 2 (680)	.040	.099	.153	.000	.025	.069	.028	.190	.057	.022	.362	.113	.007
type 3 (708)	.048	.148	.189	.003	.023	.099	.016	.229	.045	.018	.254	.103	.021
type 4 (207)	.077	.121	.135	.005	.034	.072	.058	.217	.039	.000	.242	.111	.016
type 5 (196)	.041	.260	.148	.000	.020	.056	.066	.031	.010	.000	.199	.474	.028
type 6 (125)	.632	.000	.080	.000	.000	.000	.192	.000	.000	.016	.016	.024	.712
type 7 (212)	.160	.448	.057	.274	.137	.750	1.00	.524	.066	.269	.038	.038	.198
bank width (m)													
0-0.5 (8)	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
0.5-1 (45)	.000	.022	.022	.000	.000	.044	.000	.000	.000	.000	.222	.044	.000
1-1.5 (246)	.037	.183	.037	.000	.037	.053	.008	.093	.033	.004	.138	.126	.110
1.5-2 (1044)	.068	.203	.146	.009	.034	.151	.104	.314	.053	.045	.331	.147	.047
2-2.5 (653)	.054	.138	.219	.081	.041	.191	.239	.152	.047	.060	.217	.123	.096
2.5-3 (240)	.350	.025	.083	.000	.008	.017	.100	.046	.033	.000	.175	.075	.396
bank slope (°)													
30 (95)	.074	.474	.147	.116	.063	.526	.674	.379	.042	.232	.032	.053	.242
40 (582)	.251	.167	.177	.084	.046	.244	.302	.273	.072	.103	.165	.072	.204
50 (613)	.057	.091	.144	.002	.036	.042	.020	.237	.065	.003	.313	.179	.073
60 (776)	.014	.124	.148	.001	.019	.095	.014	.140	.021	.004	.274	.126	.030
70 (108)	.000	.426	.019	.009	.028	.074	.259	.102	.000	.000	.583	.204	.093
80 (62)	.000	.226	.048	.000	.000	.032	.000	.016	.000	.000	.113	.113	.226
aspect													
south east (445)	.225	.072	.196	.037	.045	.116	.247	.213	.029	.061	.171	.207	.267
south west (673)	.080	.158	.119	.029	.033	.196	.071	.244	.040	.048	.330	.070	.049
north east (673)	.013	.165	.083	.011	.025	.196	.073	.205	.033	.009	.250	.029	.068
north west (445)	.081	.236	.153	.028	.031	.074	.189	.144	.090	.049	.243	.150	.080

Appendix 3-I, continued

	Ach.mil.	Val.off.	Lin.vul.	Lyc.f-c.	Iri.pse.	Lys.vul.	Gal.pal.	Ran.sce.	Sta.pal.	Ror.amp.	Sym.off.	Vic.cra.	Pla.lan.
width non-prod. strip(m)													
0 (1290)	.062	.114	.178	.002	.021	.081	.009	.258	.057	.021	.333	.079	.009
0-1 (153)	.000	.196	.078	.000	.033	.039	.007	.065	.065	.000	.327	.118	.007
1-2 (15)	.000	.000	.067	.067	.000	.133	.000	.000	.000	.000	.000	.067	.000
2-3 (93)	.011	.194	.344	.000	.022	.161	.097	.043	.000	.011	.151	.301	.097
3-4 (321)	.109	.361	.062	.181	.100	.498	.202	.352	.044	.184	.131	.156	.202
management													
mown, hay removed (527)	.222	.224	.066	.112	.066	.324	.452	.222	.027	.112	.093	.186	.364
mown, hay not rem. (1285)	.049	.114	.129	.002	.022	.089	.039	.233	.042	.020	.320	.104	.024
'mulching' (424)	.045	.210	.292	.000	.024	.040	.007	.104	.080	.005	.269	.125	.026
ditch width (m)													
0 (970)	.020	.102	.109	.001	.025	.074	.013	.133	.044	.022	.337	.174	.063
0-1 (482)	.048	.087	.170	.004	.004	.071	.029	.193	.021	.015	.205	.108	.050
1-2 (384)	.130	.188	.234	.003	.047	.065	.070	.320	.018	.005	.258	.099	.057
(2-3, not present)	-	-	-	-	-	-	-	-	-	-	-	-	-
3-4 (188)	.388	.245	.186	.000	.000	.064	.133	.027	.149	.000	.218	.090	.452
(4-5, not present)	-	-	-	-	-	-	-	-	-	-	-	-	-
(5-6, not present)	-	-	-	-	-	-	-	-	-	-	-	-	-
6-7 (64)	.109	.703	.000	.172	.078	.734	1.00	.469	.031	.344	.000	.047	.359
7-8 (148)	.182	.338	.081	.312	.162	.757	1.00	.547	.081	.236	.054	.034	.128
rotation													
non-agri. land use (549)	.186	.124	.091	.005	.035	.060	.075	.122	.071	.051	.302	.220	.282
1 yr cer. 1 yr root crop (353)	.051	.156	.232	.000	.045	.144	.059	.150	.023	.011	.252	.088	.023
1 yr cer. 2 yr root crop (661)	.073	.171	.136	.015	.030	.145	.159	.253	.067	.042	.295	.101	.048
1 yr cer. 3 yr root crop (565)	.054	.186	.181	.092	.023	.191	.195	.288	.019	.048	.165	.101	.067
mostly ornam. flowers (41)	.000	.000	.024	.000	.000	.024	.000	.098	.000	.000	.024	.073	.024
continuous blackcurrant (67)	.000	.194	.000	.000	.075	.194	.209	.104	.000	.000	.448	.075	.000
land use													
non-agricultural land use (549)	.214	.116	.082	.003	.018	.036	.059	.003	.010	.003	.134	.250	.379
potatoes (900)	.059	.150	.150	.032	.044	.168	.127	.257	.037	.049	.213	.077	.028
sugar beets (247)	.158	.344	.134	.012	.036	.259	.340	.372	.036	.093	.239	.134	.113
cereals (540)	.043	.104	.165	.054	.017	.106	.104	.241	.104	.033	.424	.078	.028
blackcurrant (67)	.000	.194	.000	.000	.075	.194	.209	.104	.000	.000	.448	.075	.000
ornamental flowers (94)	.010	.213	.383	.000	.032	.032	.000	.000	.000	.011	.128	.404	.202
age													
2-5 year (646)	.065	.014	.159	.002	.019	.060	.023	.217	.071	.008	.260	.007	.009
>10 year (1590)	.099	.217	.140	.038	.038	.165	.174	.202	.035	.052	.255	.152	.143

Appendix 3-II Synoptic table of the 50 relevés (sites of 8 m^2) illustrating the species composition in the two clusters and seven vegetation types. Presence of the species in the relevés per type is indicated by Roman figures: I = 0-20%, II = 21-40%, III = 41-60%, IV = 61-80%, V = 81-100%. Bold figures indicate that a species is discriminating between two or more types.

cluster	cluster 1			cluster 2			
type	1	2	3	5	4	6	7
# relevés	5	7	13	7	8	5	5
number of species (avg.)	9	11	13	14	16	16	26
Phragmitis australis	**V**	-	**III**	I	-	-	-
Holcus mollis	III	V	II	III	V	II	IV
Elytrigia repens	IV	V	IV	V	III	II	I
Urtica dioica	**III**	**III**	**III**	**II**	**II**	-	-
Galium aparine	**III**	**III**	**III**	**III**	-	I	-
Glechoma hederacaea	**II**	**III**	**II**	**II**	-	-	-
Myosotis arvensis	-	II	-	-	I	-	-
Polygonum maculosa	-	**II**	**IV**	**III**	**II**	-	-
Fallopia convolvulus	-	-	**II**	-	-	-	-
Mentha arvensis	-	-	II	I	-	-	-
Typha latifolia	-	-	**II**	**II**	-	-	-
Taraxacum spec.	-	-	**II**	**III**	**II**	-	-
Mentha aquatica	-	-	-	**II**	-	-	-
Dactylis glomerata	II	II	II	II	**V**	I	-
Vicia hirsuta	-	-	-	-	**IV**	-	-
Rumex acetosa	-	-	-	-	**II**	-	-
Trifolium dubium	-	-	-	-	**II**	-	-
Veronica chamaedris	-	-	-	-	**II**	-	-
Vicia sativa-nigra	I	-	-	-	**III**	I	-
Anthoxantum odoratum	-	-	-	-	II	I	-
Valeriana officinalis	-	**II**	-	-	**II**	-	**II**
Festuca rubra	-	I	-	I	**IV**	**IV**	**III**
Achillea millefolium	-	-	I	II	II	III	-
Molinea caerulea	-	-	-	-	-	**III**	-
Hieracium pilosella	-	I	-	-	-	II	-
Juncus effusus	-	I	II	**V**	I	**V**	**V**
Rumex acetosella	-	I	-	**III**	-	**IV**	**V**
Galium palustre	-	-	-	-	I	**III**	**V**
Hypochaeris radicata	-	I	-	I	-	**III**	**IV**
Cerastium fontanum-vulgaris	-	I	I	II	II	**IV**	**IV**
Trifolium repens	-	-	I	I	-	I	**III**
Lysimachia vulgaris	-	I	-	-	I	II	**IV**
Lotus pedunculatus	I	II	I	III	III	II	**V**
Polytricha sp.	-	-	-	-	-	-	**V**
Dryopteris carthusiana	-	-	-	-	I	-	**V**
Myosotis scorpioides	-	-	-	-	-	-	**V**
Vaccinium corymbosum	-	-	-	I	-	-	**IV**
Cardamine pratense	-	-	-	-	-	-	**III**
Hydrocotyle vulgaris	-	-	-	-	-	I	**III**
Lolium perenne	I	-	I	I	-	-	**III**
Lycopus europaeus	-	-	-	I	-	-	**III**
Luzula campestris	-	-	-	-	-	-	**II**
Lychnis flos-cuculi	-	-	-	-	-	-	**II**
Juncus acutiflorus	-	-	I	-	-	-	II

chapter 4

Spatial dynamics of plant species in an agricultural landscape

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submitted in revised version to Ecography

Abstract

1. The changes in distribution patterns of thirteen perennial herbaceous species were monitored from 1998 to 2000 in ditch banks along arable fields in the Netherlands. The species had contrasting dispersal and seed bank characteristics. Colonization, extinction and persistence of local populations were monitored in 10 m segments (patches) of the ditch banks and related to isolation of the patches.

2. All species frequently colonized empty patches and occupied patches frequently went extinct. The average colonization rates (proportion new local populations) were 0.32 in 1999 and 0.35 in 2000. The average extinction rates (proportion extinct patches) were 0.33 in 1999 and 0.22 in 2000.

3. The colonization probabilities of all species were negatively correlated to the level of isolation of the patches. The extinction probabilities of all but one of the species were positively correlated to the level of isolation of the patches. Most colonization events were found within 50 m of conspecific source patches in the preceding year, but colonization events at distances over 200 m were also observed. There was no relation between colonization distances and dispersal characteristics of the species.

4. Colonization can be the result of germination of seeds from the seed rain or the seed bank. Species with persistent seeds had more colonizations at longer distances from the source patches. The ratio between lowest 90% and the upper 10% of the average colonization distances indicated the steepness of decrease of the number of colonizations with distance from source patches. This ratio was higher for species with persistent seed banks than for species with transient seed banks.

5. The differences between the colonization patterns of species with persistent and transient seeds may have been caused by the cumulative result of the seed rain of several years of species with persistent seeds.

6. This study indicated that all species had characteristics of metapopulation dynamics because both colonization and extinction were related to the level of isolation.

Key words: colonization, dispersal, extinction, metapopulation, seed bank

Introduction

Many plant species have patchy distribution patterns on various scales. The patchy distribution at the landscape scale is the result of the heterogeneity of habitat quality in space and time on the one hand and colonization and extinction of local populations on the other hand (Primack & Miao 1992; Tilman 1993). Local populations can go extinct due to local disturbances while colonization of empty habitat patches can result in new local populations. Plant species can only persist in dynamic fragmented landscapes if local extinctions are compensated by colonizations in empty habitat patches (chapter 2). Examples of fragmented and dynamic habitats are the semi-natural landscape elements, such as ditch banks, hedgerows and other linear landscape elements in North Western European agricultural landscapes. These landscape elements are of major importance for the survival of plants in the agricultural landscapes of North Western Europe (Boatman *et al*. 1999). However, in recent decades many plant species disappeared from these landscapes (CBS 1993; Joenje & Kleijn 1994; Hodgson *et al.* 1995). This decline of species can be related to the decrease of habitat quality (McLaughlin & Mineau 1995) and the increased fragmentation and disturbance of the landscape elements by agriculture related activities. Fragmentation and disturbance resulted in an increased isolation of habitat patches in space and time. Studies of the distribution patterns of species at the landscape scale (several km^2) showed that spatial isolation of habitat decreased the occupation probability of species (Ouborg 1993; Marshall & Arnold 1995; Quintana-Ascencio & Menges 1995; Grashof & Geertsema 1998; chapter 3). The sensitivity for isolation of habitat could be related to the dispersal capacity of the species in some studies (Ouborg 1993; Grashof-Bokdam 1997).

A network of fluctuating local populations that are linked by dispersing seeds can be described by metapopulation dynamics (Opdam 1990). This theory can be a useful background for the study of distribution patterns of species in fragmented landscapes. The metapopulation approach was developed and tested mostly for animals. The application to plants is complicated by typical plant characteristics such as the potential longevity and the ability to build up persistent soil seed banks and spread vegetatively (Eriksson 1996; Husband & Barrett 1996). Long-lived species and species with persistent seed banks possess life cycle characteristics buffering unfavourable environmental conditions. The result is a long time to extinction in declining populations

(Elberse *et al.* 1983; Eriksson 1996). Despite the existence of a time lag in the response to environmental conditions several studies indicated that populations of perennials had characteristics of metapopulations (Ouborg 1993; Antonovics *et al.* 1994; Quintana-Ascencio & Menges 1995; Grashof-Bokdam 1997; Valverde & Silvertown 1997; Harrison *et al.* 2000).

Extinction of local populations may be caused by demographic stochastic processes in small populations, by a negative growth rate due to low habitat quality and by disturbances (Opdam 1990). Small isolated populations may have higher extinction probabilities than non-isolated populations because they receive less seeds from other populations. The reproductive success and persistence of isolated populations is also hampered by a decrease of gene flow by reduced pollen dispersal (Richards 2000; Wolf & Harrison 2001). However, it is expected that environmental stochasticity is the more important source of local extinction for perennial plant species (e.g. Valverde & Silvertown 1997).

Sources of colonization are the seed rain and the soil seed bank (Bakker *et al.* 1996). The colonization capacity varies among species because of differences between dispersal ability and seed bank persistence. Species with a well developed dispersal ability may 'jump' over unsuitable areas in order to colonize spatially isolated patches. Species with a persistent seed bank may 'wait' in the soil and '(re)colonize' a temporally isolated patch that reappears on the same spot after a period of unsuitable growing conditions (chapter 2).

The knowledge of dispersal distances on the landscape scale is limited because on that scale dispersing seeds are very hard to observe. An alternative way to increase our understanding of dispersal is to study the outcome of the dispersal and establishment processes by monitoring colonization patterns (Antonovics *et al.* 1994; Grashof-Bokdam & Geertsema 1998; Harrison *et al.* 2000). The spatial pattern of colonization events can give an indication of dispersal distances. However, whether the seed rain or the regeneration from the soil seed bank was the source of colonization cannot be determined by the study of colonization patterns in the field. Comparative studies of species with transient or persistent seeds and species with or without adaptation for long distance dispersal may increase our understanding of the role of the soil seed bank and dispersal in the dynamics of fragmented populations.

Local populations may be less sensitive to spatial as well as temporal isolation when they receive more seeds from other local populations or where a soil seed bank adds to the local population. It is therefore expected that the survival probabilities of species are related to the colonization capacity of the

species as well as to the degree of fragmentation and dynamics of the landscape (chapter 2).

The aim of this chapter is to measure the rates and the spatial patterns of colonization and extinction of perennial herbaceous plant species in a network of ditch banks in an agricultural landscape in the Netherlands. I analyzed the dynamics of the distribution of thirteen species during three years. The species had contrasting dispersal and seed bank characteristics. Colonization and extinction were expected to depend on isolation of habitat (distance to seed sources in the preceding year) and on the dispersal capacity and seed bank characteristics of the species.

The aim was to answer the following questions:

(1) What are the colonization and extinction rates of the plant species?

(2) Does isolation of patches decrease colonization probabilities and increase extinction probabilities of the species?

(3) Are differences between species (colonization and extinction rates and their relations with isolation) related to their dispersal and seed bank characteristics?
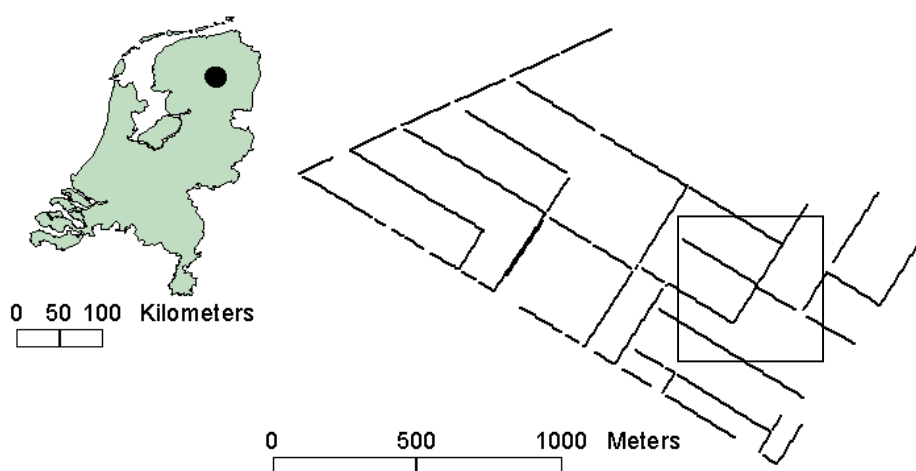

Figure 4.1 Location of the study area in the north of the Netherlands and an overview of the pattern of ditches in the study area. The study area consists of arable fields, it is bordered at the north western side by forest, in the other directions the agricultural area continued. The square in the study area indicates a representative section that is illustrated in figure 4.2.

Methods

Study area

The study area (150 ha) consisted of an agricultural area with mainly arable fields. It is located in the north of the Netherlands (6°27' E and 52°47' N, figure 4.1). The area was bordered at one side by a forest and in the other directions the agricultural area continued. A total of 11.18 km of ditches was monitored, equalling 22.36 km ditch banks. Common crops in the area were potatoes, sugar beet and barley, all grown by conventional farmers. Ditches separated the fields and the habitat of the studied plant species was limited to the ditch banks and road verges. The soils were mainly peat on sand or sandy soils. The vegetation of the ditch banks varied from very species poor vegetations with a few dominant grass species to species-rich grassland vegetations. Management of the ditch banks consisted of mowing once a year (in September-October). In some ditch banks the hay was removed each year but in the majority it was left on the slope. For a detailed description of the study area see chapter 3.

Table 4.1 Overview of the studied species, their dispersal mode and seed bank (CBS 1993; Hodgson *et al.* 1995; Thompson *et al.* 1997). Transient seeds persist 1-5 years in the soil, persistent seeds persist > 5 years in the soil. Species are grouped by their dispersal and seed bank characteristics.

species name	dispersal	seed bank
Rorippa amphibia (L.) Besser	no adaptation	transient
Symphytum officinale L.	no adaptation	transient
Vicia cracca L.	no adaptation	transient
Iris pseudacorus L.	water	transient
Lysimachia vulgaris L.	water	transient
Achillea millefolium L.	wind	transient
Valeriana officinalis L.	wind	transient
Plantago lanceolata L.	no adaptation	persistent
Galium palustre L.	water	persistent
Ranunculus sceleratus L.	water	persistent
Stachys palustris L.	water	persistent
Linaria vulgaris Mill.	wind	persistent
Lychnis flos-cuculi L.	wind	persistent

Studied species

In this chapter the spatial population dynamics of thirteen herbaceous plant species were studied (table 4.1). The species were selected because they represented a variety of dispersal and seed bank characteristics, which was a precondition for the study. Information about dispersal and seed bank characteristics (table 4.1) were derived from literature (CBS 1993; Hodgson *et al.* 1995; Thompson *et al.* 1997). The species were suitable for the study, because they were limited to the ditch banks in the study area and they were negatively influenced by high amounts of fertilizers and herbicides and by disturbance (Bruggink & Buitink 1995). These factors caused a heterogeneous pattern of habitat quality in the study area resulting in a patchy distribution of the studied species. The distribution patterns of the thirteen focal species were related to a suite of parameters describing habitat quality of the ditch banks and to the spatial isolation of the patches (chapter 3).

Measuring colonization and extinction rates

The distribution patterns of the thirteen focal species were monitored during three growing seasons from 1998 to 2000. The two ditch banks along the ditches were considered as separate units and monitored separately. The spatial units for the measurements, the patches, were defined as 10 m long segments of the ditch banks; the width of the patches equalled the width of the ditch banks (minimum 0.5; maximum 3.1, average 2 m). Each year, in late May-June and in late July-August, the presence and absence of the species was monitored in all patches by recording the visible, above ground parts of the plants. If a species was found in any of these periods, it was recorded as present. A total of 2236 patches were used in the analysis, covering the total length of the ditch banks. Colonization and extinction rates were calculated as the number of newly occupied or extinct patches per conspecific occupied patch (according to Antonovics *et al.* 1994):

Colonization rates:
(# patches not occupied in year T-1 and occupied in year T)/(# patches occupied in year T)

Extinction rates:
(# patches occupied in year T-1 and not occupied in year T)/(# patches occupied in year T-1)

Colonization and extinction rates are expected to be related to habitat quality. Each patch was classified into one of the seven vegetation types that were distinguished in the ditch banks in the study area (chapter 3). The colonization and extinction rates were also calculated in each vegetation type.

Measuring isolation distance

The relationships between extinction and colonization rates and the spatial isolation of the patches were explored. The pattern of the ditches was digitized and the isolation measures of the patches were determined with the Geographical Information System ArcView (ESRI 2000). Isolation was determined for each patch and was defined as the distance to the nearest occupied patch in the year before. The distance was measured in a straight line (according to chapter 3), from the centre of each patch to the centre of other patches, indicating the distance that has to be travelled by seeds dispersed by wind. For seeds that are dispersed along the network (water dispersed seeds) it underestimates the actual isolation distance only at longer distances. Patches located on opposite sides of a ditch were projected in the centre of the ditch for the determination of the isolation distances.

Statistical analysis

The relationships between isolation and colonization and extinction probabilities were analyzed separately for the thirteen species. Genstat 5.4.1 was used for the analyses. It was expected that isolation would decrease the colonization probability and increase the extinction probability of a patch. These predictions were tested with one-way Anova tests. The isolation distances of colonized patches were compared with the isolation distances of patches that were not colonized. The isolation distances of occupied patches that became extinct were compared with the isolation distances of patches in which the species persisted from one year to the next.

Because the variances of the isolation were unequal for colonized compared to not colonized patches and for extinct compared to persisting occupied patches, the distances were ln-transformed. The ln-transformation resulted in similar variances.

The colonization events were divided for each species in the lower 90% with the shortest distances and the upper 10% with largest distances. The average colonization distances of the lower 90% were compared with the

average colonization distances of the upper 10% of the colonization events. In this way the shape of the dispersal curve could be analyzed: if the difference between the two averages was small, the species had few colonizations at relatively large distances. The ratio between the lower 90% and upper 10% was also calculated: (avg. distance lower 90%) / (avg. distance upper 10%). A higher value for this ratio implies a less steep decrease of the curve.

Both seed dispersal and the soil seed bank could have been sources of colonization. Therefore we compared the colonization distances (relative distances) of the thirteen species to see if these differences in the shape of the dispersal curve could be explained by the dispersal and seed bank characteristics of the species. The Mann-Whitney U test was used to test the differences between species with persistent and transient seed banks.

Results

Colonization and extinction rates

The distribution patterns of four species during the years of study are illustrated in figure 4.2 for a representative section of the study area. Colonization and extinction rates varied between the years and the species but occurred frequently (figure 4.3). A number of species had low colonization and extinction rates in both years, like *Symphytum officinale* L.*, Lysimachia vulgaris* L.*, Valeriana officinalis* L. and *Galium palustre* L.. Others showed a more dynamic pattern, like *Ranunculus sceleratus* L..

The colonization rates slightly exceeded the extinction rates when both years were taken together. The average colonization rate was 0.32 in 1999 and 0.35 in 2000, the highest rates were found for *Rorippa amphibia* (L.) Besser (0.84 in 1999) and *Ranunculus* (0.77 in 2000) and the lowest for *Galium* (0.10 and 0.14 in 1999 and 2000 respectively). The average extinction rates were 0.33 and 0.22 in 1999 and 2000 respectively, the maximum rate was found for *Ranunculus* (0.61 in 1999) and for *Stachys palustris* L. (0.58 in 2000) and the minimum for *Plantago lanceolata* L. (0.15 in 1999) and for *Lysimachia* and *Valeriana* (0.05 in 2000).

No relationship was observed between the dispersal or seed bank characteristics of the species and their colonization and extinction rates (figure 4.3). The colonization and extinction rates varied strongly among species, irrespective of the type of seed bank or dispersal strategies.
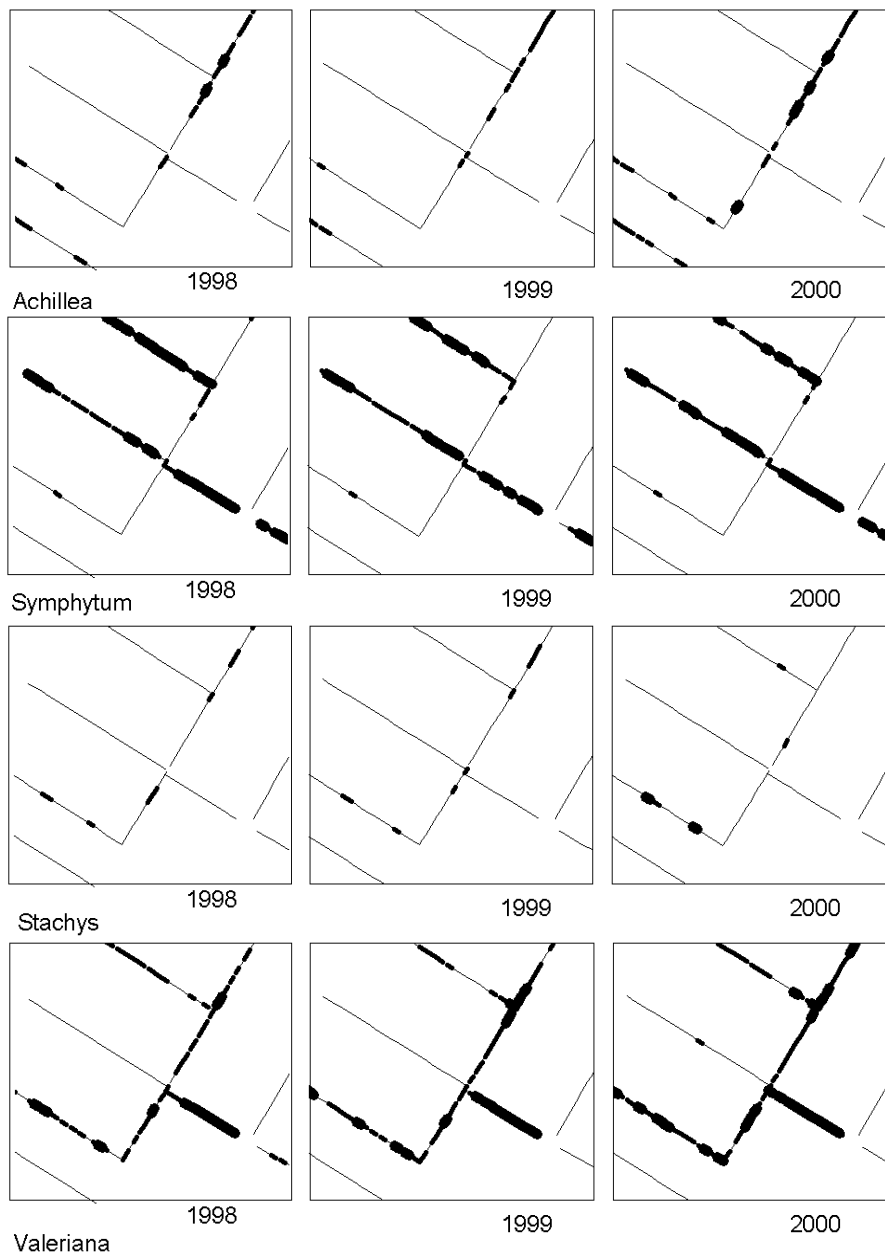
Figure 4.2 Dynamics of spatial distribution patterns of four of the studied species in a representative section (500 x 500 m) of the study area. Thin lines indicate parts of the ditches that are not occupied by the species, fat black lines indicate that one of the two patches (10 m long) that are located opposite each other in opposite ditch banks is occupied, very fat lines indicate that both opposite patches are occupied. The location of the section in the study area is indicated in figure 4.1.
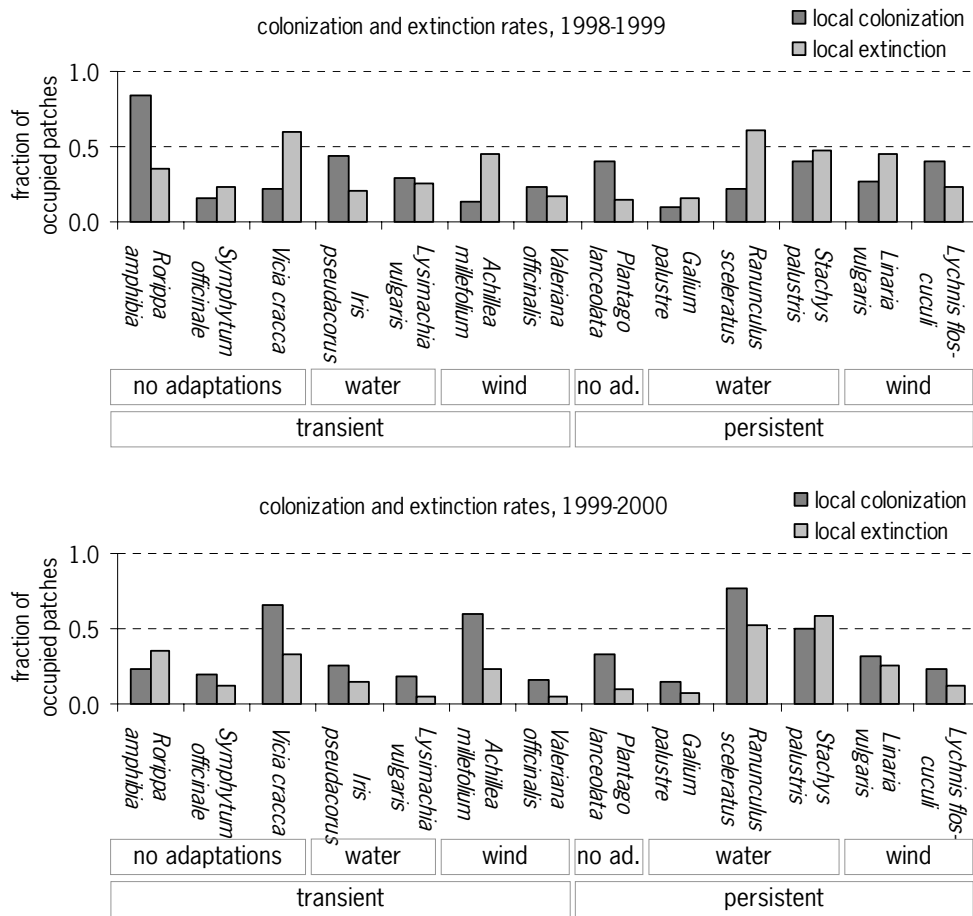
Figure 4.3 Colonization and extinction rates for the focal species in 1998-1999 and 1999-2000. Colonization rate is calculated as the fraction of occupied patches in one year that was not occupied in the year before. Extinction rate is calculated as the fraction of occupied patches in one year that went extinct in the next year.

Table 4.2 Colonization and extinction rates per species per vegetation type. The results of 1999 and 2000 are taken together. Colonization rate is calculated as the fraction of occupied patches in one year that was not occupied in the year before. Extinction rate is calculated as the fraction of occupied patches in one year that went extinct in the next year. The total number of occupied patches in 1999 and 2000 are given between brackets for colonization rates and in 1998 and 1999 for extinction rates. '-' indicates that species did not occur in that vegetation type.

Colonization rates

veg. type: 1	2	3	4	5	6	7
Achillea - (0)	0.42 (33)	0.40 (68)	0.13 (8)	0.20 (5)	0.21 (111)	0.53 (51)
Galium 1.0(1)	0.43 (7)	0.70 (33)	0.38 (8)	0.30 (43)	0.43 (54)	0.00 (409)
Iris 0.2(5)	0.41 (17)	0.36 (44)	0.30 (23)	0.33 (9)	- (0)	0.27 (86)
Linaria 0.48(23)	0.26 (188)	0.36 (200)	0.53 (38)	0.34 (35)	0.22 (33)	0.33 (23)
Lychnis - (0)	0.50 (2)	0.67 (6)	0.40 (5)	0.57 (5)	0.75 (7)	0.20 (126)
Lysimachia 0.0 (3)	0.33 (70)	0.31 (91)	0.25 (28)	0.10 (29)	0.59 (108)	0.24 (341)
Plantago 0.75 (12)	0.48 (46)	0.61 (49)	0.34 (94)	0.31 (78)	0.11 (196)	0.35 (117)
Ranunculus 0.80 (10)	0.50 (175)	0.44 (207)	0.75 (4)	0.80 (5)	1.00 (12)	0.52 (216)
Rorippa 1.00 (1)	0.55 (29)	0.53 (75)	0.50 (4)	0.80 (5)	1.00 (1)	0.34 (119)
Stachys 0.43 (7)	0.49 (41)	0.49 (74)	0.57 (23)	0.75 (4)	1.00 (1)	0.48 (23)
Symphytum 0.19 (91)	0.17 (317)	0.20 (444)	0.12 (49)	0.22 (147)	0.53 (17)	0.18 (11)
Valeriana 0.24 (17)	0.22 (175)	0.23 (179)	0.15 (67)	0.17 (81)	0.23 (9)	0.21 (247)
Vicia 0.50 (22)	0.45 (83)	0.54 (103)	0.43 (67)	0.43 (89)	0.71 (38)	0.11 (9)

Extinction rates

veg. type: 1	2	3	4	5	6	7
Achillea 1.0 (1)	0.53 (54)	0.43 (51)	0.25 (23)	0.19 (12)	0.45 (106)	0.37 (51)
Galium 1.0 (1)	0.83 (23)	0.75 (16)	0.71 (14)	0.11 (35)	0.26 (42)	0.02 (421)
Iris 0.0 (2)	0.42 (24)	0.21 (33)	0.13 (15)	0.20 (10)	- (0)	0.10 (71)
Linaria 0.44 (18)	0.36 (214)	0.42 (200)	0.44 (55)	0.40 (50)	0.18 (22)	0.18 (22)
Lychnis 1.0 (1)	0.0 (1)	1.0 (4)	0.0 (4)	0.0 (4)	0.0 (2)	0.15 (119)
Lysimachia - (0)	0.38 (79)	0.37 (92)	0.23 (30)	0.16 (32)	0.10 (51)	0.05 (318)
Plantago 0.13 (8)	0.20 (25)	0.30 (43)	0.16 (49)	0.09 (100)	0.03 (149)	0.19 (99)
Ranunculus 1.00 (10)	0.62 (268)	0.57 (238)	0.98 (45)	1.00 (7)	0.33 (3)	0.60 (163)
Rorippa 1.00 (1)	0.55 (20)	0.36 (56)	0.00 (2)	0.00 (2)	1.00 (2)	0.35 (124)
Stachys 0.45 (11)	0.61 (61)	0.60 (60)	0.26 (23)	0.00 (3)	- (0)	0.57 (28)
Symphytum 0.21 (99)	0.19 (371)	0.17 (428)	0.19 (96)	0.28 (60)	0.80 (5)	0.19 (13)
Valeriana 0.22 (18)	0.14 (123)	0.13 (187)	0.13 (61)	0.21 (96)	0.00 (2)	0.05 (205)
Vicia 0.41 (17)	0.27 (110)	0.60 (137)	0.54 (37)	0.44 (127)	0.56 (9)	0.33 (12)

vegetation types (after chapter 3):

Types 1, 2, 3, and 5: nutrient rich, ruderal vegetation and affinities with the *Galio-Urticetea*.

Type 1: characteristics of *Convolvulo-Filipenduletea*

Type 2: characteristics of *Bidention tripartitae* and *Nanocyperion flavescentis*

Type 3: characteristics of *Dauco-Melilotion*

Type 5 characteristics of *Melampyrion pratensis*.

Types 4, 6, and 7 less nutrient rich, grassland vegetations, less affinity with *Galio-Urticetea*, more with *Nanocyperion flavenscentis*.

Type 4: characteristics of *Dauco-Melilotion*

Type 6: characteristics of *Digitario-Illecebretum*.

Type 7: characteristics of *Molinio-Arrhenatheretea*.

Colonization and extinction rates of the thirteen species varied between the vegetation types (table 4.2). In general the rates of colonization and extinction were highest in two of the ruderal vegetation types (type 2 and 3). The extinction and colonization rates were relatively low in two of the grassland vegetation types (types 6 and 7). The differences were more distinct for the extinction rates than for the colonization rates. *Achillea millefolium* L. was the only species with relatively high colonization rates in vegetation type 7 whereas *Lysimachia, Symphytum* and *Vicia cracca* L. showed high colonization rates in vegetation type 6. The colonization rates of *Iris pseudacorus* L.*, Linaria vulgaris* Mill.*, Ranunculus, Stachys* and *Valeriana* showed little variation between the vegetation types.

Colonization and isolation

The relationship between isolation distance and the number of colonized patches is shown in figure 4.4. Most of the colonization events occurred within 50 m of the patches that were occupied in the preceding year. However, colonization distances exceeding 200 m were no exception (figure 4.4, table 4.3). Patches that were colonized were significantly less isolated than the patches that were not colonized (One-Way Anova, $p < 0.001$). This pattern was found for all species in both years.

There was no clear relationship between the dispersal characteristics of the species and the colonization distances (figure 4.4, table 4.3). *Symphytum* had short colonization distances and no adaptations for long distance dispersal, but other species without adaptations for dispersal reached colonization distances up to 300 m (*Rorippa* and *Plantago*). The longest colonization distance was found for *Lychnis flos-cuculi* L. (max: 1090 m, average upper 10%: 446 m), a wind dispersed species with persistent seeds. *Galium* has adaptations for dispersal by water and had persistent seeds as well, but showed relatively short colonization distances (max: 116 m, average upper 10%: 59 m).

Species with persistent seeds had less steep colonization curves than species with transient seed banks (figure 4.4, table 4.3). The Mann-Whitney U test showed that species with persistent seeds had the longest maximum colonization distances ($p < 0.05$), the highest values for the lower 90% ($p < 0.05$) and the highest values for the ratio between the lower 90% and the upper 10% of colonization distances ($p < 0.01$). The values of the upper 10% of species with persistent seed banks were higher than those of species with transient seeds, but this difference was not significant.
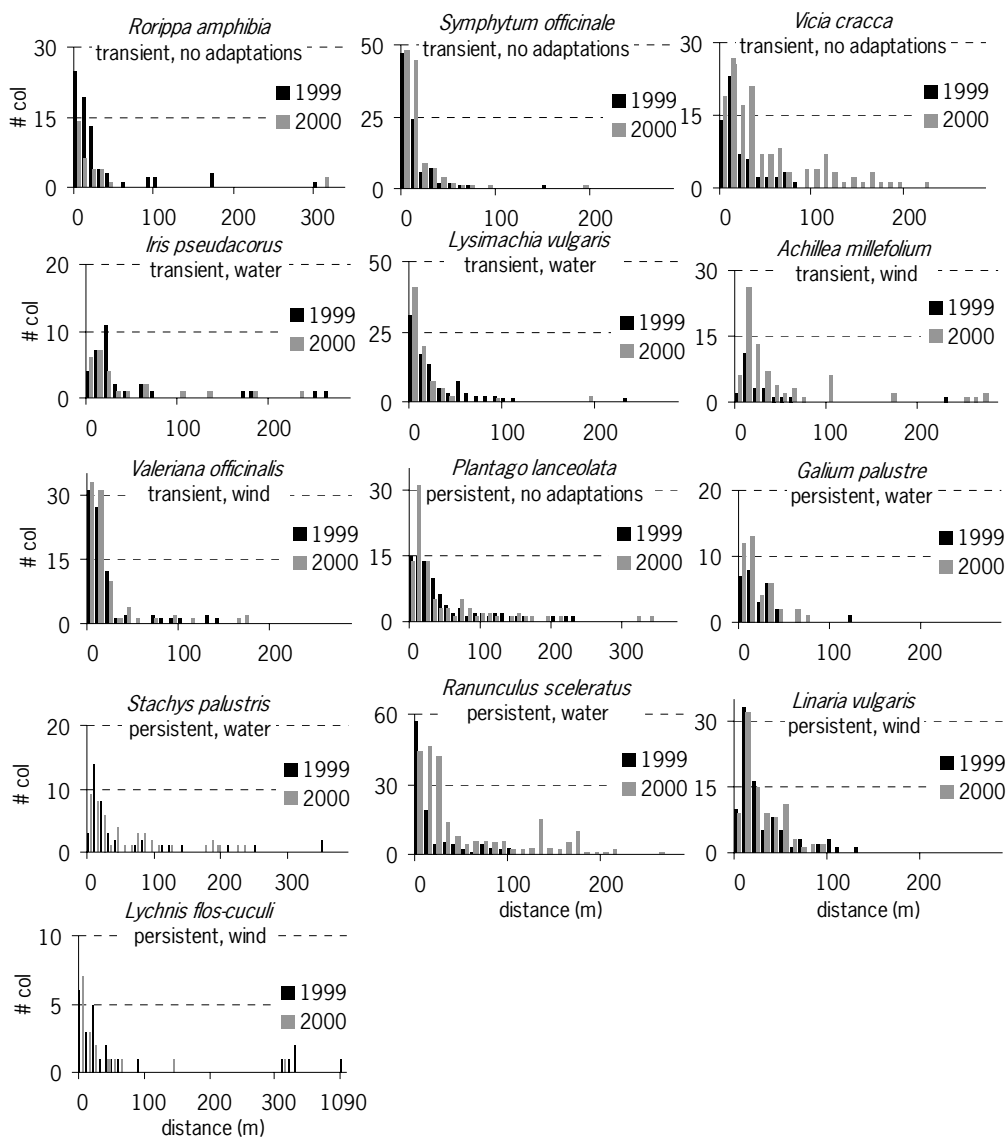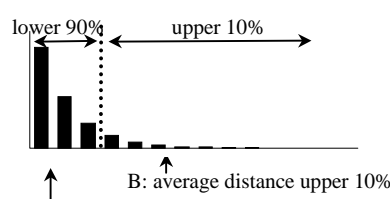
Figure 4.4 Relation between the number of colonized patches in 1999 and 2000 and the distance to the nearest occcupied conspecific patch in 1998 and 1999 respectively. Species are sorted by their seed bank and disperal characteristics.

Table 4.3 Colonization distances for the focal species, their adaptations for dispersal and seed bank characteristics (T = transient, seeds persist 1-5 years; P = persistent, seeds persist > 5 years). Colonization distances given in meters: maximum distance, average distance 90% of the colonizations closest to conspecific occupied patches in the former year (A), average distances for 10% of the colonizations furthest from occupied patches in the former year (B) and the ratio A/B, indicating the steepness of the curve. Colonization distances of 1999 and 2000 are taken together. The table is sorted on the seed bank and dispersal characteristics of the species.

lower 90%   upper 10%

B: average distance upper 10%

A: average distance lower 90%

			max. distance	A lower 90% (m)	B upper 10% (m)	A/B
Rorippa	no adaptation	T	304	9.51	165.65	0.06
Symphytum	no adaptation	T	180	6.11	54.63	0.11
Vicia	no adaptation	T	219	23.74	136.33	0.17
Iris	water	T	252	19.87	204.15	0.10
Lysimachia	water	T	224	8.98	93.65	0.10
Achillea	wind	T	269	19.27	187.70	0.10
Valeriana	wind	T	163	7.14	99.82	0.07
Plantago	no adaptation	P	331	28.06	178.02	0.16
Galium	water	P	116	11.27	59.49	0.19
Ranunculus	water	P	250	22.39	156.37	0.14
Stachys	water	P	344	31.78	235.87	0.13
Linaria	wind	P	126	17.74	79.93	0.22
Lychnis	wind	P	1090	26.87	446.05	0.06

Extinction and isolation

Extinction occurred frequently in all species and was found for isolated patches as well as for patches that were adjacent to conspecific occupied patches (figure 4.5). Patches that became extinct were relatively more isolated than patches that remained occupied from one year to the next (table 4.4). For most species this difference was significant (p < 0.05) for at least one of the two years. The only exception was *Iris*, where this difference was not significant in any year. The average isolation of patches with *Iris* or *Lychnis* that persisted from 1999 to 2000 was higher than of the extinct patches, but these differences were not significant.

Table 4.4 Results of comparison of average isolation distances of local populations that persisted with local populations that became extinct in 1999 and 2000 for the thirteen studied species. Species are sorted by seed bank characteristics (T = transient, P = persistent seed bank) and dispersal characteristics (no ad.: no adaptations for long distance dispersal, wa = dispersed by water, wi = dispersed by wind). Distances of persisting and extinct populations were ln-transformed and compared with a One-Way Anova test, significance of differences are given: ***: $p < 0.001$, **: $p < 0.01$, * : $p < 0.05$, n.s. : not significant.

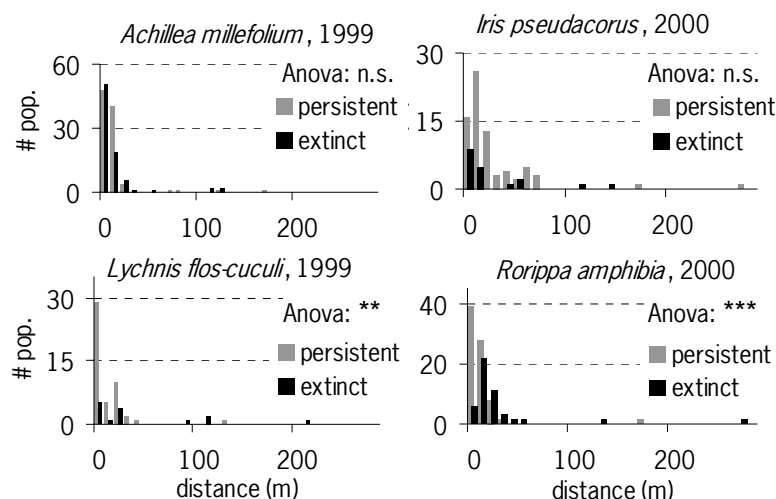|				avg isolation distance (m)		
				persistent	extinct	significant?
Rorippa	T	no ad.	1999	12.0	52.0	n.s.
			2000	7.1	19.3	***
Symphytum	T	no ad.	1999	5.7	8.0	**
			2000	5.9	11.6	n.s.
Vicia	T	no ad.	1999	9.9	13.7	**
			2000	17.1	17.2	n.s.
Iris	T	wa	1999	29.6	46.3	n.s.
			2000	22.3	17.0	n.s.
Lysimachia	T	wa	1999	5.2	13.7	***
			2000	5.8	23.9	***
Achillea	T	wi	1999	8.9	9.2	n.s.
			2000	11.8	32.0	*
Valeriana	T	wi	1999	7.7	13.3	**
			2000	7.1	15.2	**
Plantago	P	no ad.	1999	9.2	29.4	n.s.
			2000	9.0	26.8	*
Galium	P	wa	1999	1.9	24.5	***
			2000	3.5	21.5	***
Ranunculus	P	wa	1999	4.3	7.2	n.s.
			2000	7.0	10.1	*
Stachys	P	wa	1999	19.0	21.0	n.s.
			2000	12.7	33.8	*
Linaria	P	wi	1999	11.3	14.3	n.s.
			2000	11.8	21.6	*
Lychnis	P	wi	1999	7.7	40.6	**
			2000	30.5	12.7	n.s.

Figure 4.5 Four examples of the relation between isolation (distance to nearest conspecific patch) and the number of occupied patches that became extinct or persisted from one year to the next. The isolation of extinct and persisting patches was compared in a One-Way Anova test, significance of the differences are given in the figures: ***: $p < 0.001$, **: $p < 0.01$, * : $p < 0.05$, n.s. : not significant.

Discussion

Colonization and extinction rates

The results show that colonization and extinction frequently occurred in all species. The rates differed between the two years, but when the rates of both years were averaged, the colonization and extinction rates were rather similar for individual species. Colonization and extinction of individual plant species have been studied on a variety of spatial and temporal scales. Among the spatial scales were 10×10 m quadrates within a 14.5 ha forest (Fröborg & Eriksson 1997), 50×50 m grids in a 220 ha agricultural landscape (Van Dorp 1996), 0.1-35 ha grasslands separated by several kilometres (Ouborg 1993; Fischer & Stöcklin 1997) but also 40 m roadside segments in an area of 25×25 km (Antonovics *et al.* 1994). Some studies monitored changes from year to year (Van der Meijden *et al.* 1992; Antonovics *et al.* 1994; Van Dorp 1996; Husband & Barrett 1998). In other studies the period between the years of observation was much longer, with no information about what happened on the annual basis, from e.g. 16 year (Harrison *et al.* 2000) to more than 20 years (Ouborg 1993; Fröborg & Eriksson 1997; Fischer & Stöcklin 1997). Despite differences in spatial and temporal scale colonization and extinction were

observed in most studies. The colonization and extinction rates in the present study are similar to those found for a number of grassland species (colonization average 0.40 and extinction 0.36, Van Dorp 1996) and for e.g. *Silene alba* (colonization 0.19-0.42 and extinction 0.09-0.30, Antonovics *et al.* 1994). Husband & Barrett (1998) found hardly any colonization but an extinction rate of 0.36 for populations of the annual *Eichhornia paniculata* in ephemeral habitats. They state that this value may be a feature of plants in ephemeral habitats subject to environmental stochasticity. In the present study and the studies of Van Dorp (1996) and Antonovics *et al.* (1994) population dynamics were observed in linear habitats for perennial species. Therefore it may be concluded that for perennial species in linear habitats an extinction rate of ca 0.35 also seems to apply.

Colonization rates are sometimes calculated as the number of newly occupied patches per empty patch (e.g. Fröborg & Eriksson 1997), which is better applicable in systems with clearly defined patches or quadrates. In the present study colonization rate was calculated as the number of new occupied patches per occupied patch. Antonovics *et al.* (1994) also used this measure and worked in a continuous network of potential habitat patches (40 m segments) in road verges, which is similar to the system of ditch banks. In these systems it is difficult to discriminate between suitable and unsuitable patches so the number of new occupied patches per occupied patch is a more suitable way to calculate the colonization rate.

It has been suggested that populations of perennial species may persist for many generations even in unfavourable conditions and hardly show local colonization and extinction (see in Eriksson 1996). The high colonization and extinction values that were found in the present study do not support this idea. The high values that I found may be due to the system that I studied. The plants are limited to narrow strips between arable fields. Because of their linearity parallel to the adjacent fields, the suitability of the habitat in these landscape elements is influenced by the adjacent land use (De Snoo & Van der Poll 1999; Kleijn & Verbeek 2000). The adjacent land use is typically dynamic in arable systems and therefore the habitat quality in the landscape elements is also dynamic. The roadsides studied by Antonovics *et al.* (1994) were frequently mowed and disturbed as well. The disturbance causes local extinction but by destroying parts of the vegetation it can also create gaps that may be colonized, which may explain the high colonization rates. The observed correlation between colonization and extinction rates and the vegetation types supports this

hypothesis. In general both colonization and extinction seemed to occur more frequently in ruderal compared to the more stable grassland vegetation types. Ruderal vegetation types are an indication that disturbance occurred more frequently in the ditch banks concerned.

Colonization and extinction rates were not related to the seed bank or dispersal characteristics of the species. A well developed dispersal ability might decrease demographic stochasticity by adding seeds to small isolated populations and thus decrease the extinction probability, known as the rescue effect (Brown & Kodric-Brown 1977). The soil seed bank might also buffer the effect of demographic and environmental stochasticity. Both the seed rain and the soil seed bank are sources of colonization. Therefore higher colonization rates could be expected for species with these characteristics. The lack of differences between the colonization and extinction rates of the species with different dispersal and seed bank characteristics may be due to the relatively short time scale at which the processes have been observed. At longer time scales the annual variation is levelled out and the relation with dispersal and seed bank characteristics may emerge.

The colonization rates seem to compensate the extinction rates during the years of this study, but the colonization and extinction rates that were calculated for 1999 and 2000 vary a lot. Results of a simulation model also indicated high year to year variations of colonization and extinction rates, therefore three years of observation may not represent the long term trends very well (chapter 6). So the period of observation in the present study seems to be too short to draw conclusions for the long term persistence of the species in the area.

The disturbance rate may be high, but disturbances occured on relatively small spatial scales in 1998-2000 (personal observation). When larger areas would have been disturbed, it may have been harder to compensate the extinctions, especially for species without adaptations for long distance dispersal or without a persistent seed bank. Indeed I found that species with persistent seeds had higher occupation probabilities in young ditches (2-5 years old) than species with transient seeds (chapter 3). This also indicates that there may not be a long term equilibrium between colonization and extinction rates for most of the species.

Colonization, extinction and isolation

The distributions of colonization distances that were observed show the typical negative exponential curve that has been observed in many other studies (e.g. Antonovics *et al.* 1994; Grashof-Bokdam & Geertsema 1998; Coulson *et al.* 2001). Also the distances crossed are in the same order of magnitude as those studies, with most of the colonization events within 50 m from source patches, but also a considerable amount of colonizations at distances over 200 m. In this study I did not directly measure dispersal. The colonization events that were observed can be the result of the establishment of seeds from the seed rain but also from the seed bank for the species with persistent seeds. The colonization distances of species adapted to wind dispersal or without adaptations for dispersal often exceeded the dispersal distances that have been measured in the field or under experimental conditions (Willson 1993; Van Dorp *et al.* 1996; Bullock & Clarck 2000). Vegetative expansion can be an important source of local expansion but does not seem to be an important source of colonization on the spatial scale of this study.

Both extinction and colonization are correlated to the distance to the nearest possible source in this study. The colonization rates decreased with distance for all species in both years. The extinction rate increased with distance for most of the species for at least one year. Similar relations between colonization and extinction probabilities and isolation were found by Harrison *et al.* (2000), Antonovics *et al.* (1994) and Ouborg (1993) but not by Husband & Barrett (1998). The populations in the latter study were isolated from each other by distances exceeding 1 km. This distance may have been large compared to the dispersal capacity of the species, so that colonization events were rare or absent. Indeed, colonization events were virtually absent. The effect of isolation in my study can be understood by considering the limited dispersal distances. Most seeds are apparently dispersed close to the source populations. Seeds arriving in other populations can increase the persistence of extant populations (rescue effect) or result in colonization of empty suitable patches. Isolated extant populations receive fewer seeds from neighbouring populations and have therefore higher extinction probabilities (Ouborg 1993; Antonovics *et al.* 1994). Seeds in the soil seed bank may have the same rescuing effect as the seed rain. However, this was not reflected in the results: the relation between extinction and isolation did not differ between populations of species with persistent seeds and populations of species with transient seeds.

Perhaps this pattern would have occurred when the dynamics of the populations were observed over a longer period.

It was expected that species with adaptations for long distance dispersal would have more colonization events at larger distances from source patches than species without these adaptations. This was not reflected by the results. The reason for this may be that other dispersal vectors play a role in the landscape. Machinery for cleaning the ditches and mowing machinery may also be effective dispersal vectors for some of the species (Strykstra *et al.* 1996; Coulson *et al.* 2001). The cleaning and mowing in the study area is done in September or October, after the crops on the fields had been harvested. In this period the studied species have set seed, which make them liable to dispersal by machinery. It is also possible that the classification of the species in dispersal categories does not adequately reflect the role of wind and water as dispersal vectors or that the seeds are dispersed by a combination of the vectors.

Seed banks in metapopulations

The results suggest that all species had characteristics of metapopulation dynamics because both colonization and extinction were related with isolation (Opdam 1990). The seed bank complicates the interpretation of the functioning of metapopulations. The colonization patterns of species with persistent seeds differed slightly from those of species with transient seeds. Species with a persistent seed bank had more colonization events at longer distances from the presumed source populations than species with transient seeds. For species with persistent seeds colonization reflects the germination and establishment of seeds that survived several years in the soil together with new seeds from the seed rain. The distribution of the seeds in the soil is the cumulative result of the seed rain of many years so the seeds of these species may be more spread over the landscape, also at large distances from the presumed seed sources. This is a possible explanation of the relative higher number of colonization events of species with persistent seeds at longer distances from seed sources.

The role of the soil seed bank in the population dynamics of perennial plants that may show metapopulation dynamics has not often been studied. Within the context of metapopulation studies there is some debate whether patches with only a seed bank present should be considered occupied. In metapopulations occupied patches are sources of the seed rain and therefore decrease the spatial isolation of empty habitat patches. In that sense, patches

with only a seed bank present should not be considered occupied, because they do not contribute to the seed rain. The soil seed bank can be a source of colonization though. The higher the persistence of the seeds, the longer they keep the potential to contribute to the colonization rate. Therefore, a persistent soil seed bank can be considered a way to decrease the temporal isolation of patches. In the context of metapopulation dynamics a separate status should be given to patches that only contain a soil seed bank and no above ground conspecific plants.

In this study both species with persistent and with transient seeds were analyzed, which produced some new insights in this field of research. Both colonization and extinction of species with contrasting dispersal and seed bank characteristics were influenced by isolation. The underlying demographic processes like germination, establishment and mortality of individual plants were not studied as such. Combining the methods in this study with experimental and modelling approaches may result in better knowledge of the underlying processes that can be translated to guidelines for management and landscape planning of agricultural landscapes.
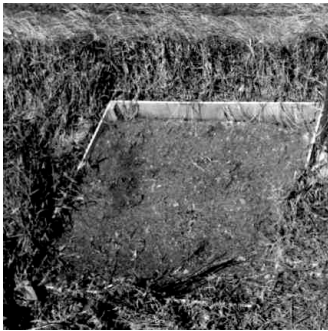
chapter 5

Colonization in an agricultural landscape: dispersal and seed bank experiments

W. Geertsema and M.J. Kropff

Abstract

In this chapter we studied the role of seed dispersal and the seed bank in the colonization of plants using an experimental approach. The study was conducted in the non-productive vegetations in field margins and ditch banks in an agricultural landscape. We tested the following hypothesis: colonization of species in experimental dispersal plots reflects dispersal strategies, whereas the distribution of species in the seed bank of sites of different age reflects the seed bank strategies. Existing classifications of species with respect to dispersal strategies are often based on anecdotal information. Therefore we first measured floating and drop time of seeds of ten species to evaluate the classification of water and wind dispersed species. Next, dispersal plots were created in ditch banks to monitor colonization by dispersal. The soil seed bank was studied by monitoring germination from soil samples.

      The number of species that colonized the dispersal plots was lower than the number of species present in the surrounding vegetation. Species without adaptations for long distance dispersal were more often also found in the surrounding vegetation than species with adaptations for long distance dispersal. The number of species that were found in the soil seed bank was higher than the number of species in the surrounding vegetation. The seed bank of young ditch banks had more seeds but fewer species compared to older ditch banks. Species with a transient seed bank were more often found in seed banks of old ditches than of young ditches. The consequences of the results for landscape management are discussed.

      Key words: terminal velocity, floating time, agricultural landscape, fragmentation, disturbance

Introduction

The habitat of many plants in agricultural landscapes in North Western Europe, but also parts of North America and Australia, is highly fragmented and often dynamic due to agricultural activities (Merriam 1988; Hobbs & Saunders 1991; Fry 1994; Le Coeur *et al.* 1997). Fragmentation and dynamics of habitat disrupt the continuity of populations and are a threat to the survival of many species (Opdam 1990). Fertilizer and pesticide use further decreases the quality of the

growing conditions for plant species (Van Strien *et al.* 1989; De Snoo & Van der Poll 1999; Kleijn & Verbeek 2000). Species that once were abundant are rare nowadays or have even disappeared from the agricultural scene, leading to a decrease of the botanical diversity of agricultural landscapes (Joenje & Kleijn 1994; Power & Cooper 1995).

The botanical diversity of agricultural landscapes is concentrated in landscape elements that are not directly used for agricultural production (Melman *et al.* 1988; Merriam 1988; Marshall & Arnold 1995; Kiss *et al.* 1997; Corbit *et al.* 1999; Opdam *et al.* 2000). The elements constitute a more or less continuous network of potential habitat and dispersal corridors (Melman *et al.* 1988; Marshall & Arnold 1995; Corbit *et al.* 1999). The habitat quality for plant species is heterogeneous in space and time in the habitat network (Merriam 1988; Fry 1994). This habitat heterogeneity divides populations into local populations in the landscape. The local populations may show colonization and extinction dynamics (Robinson & Quinn 1988; Van Dorp 1996; Fröborg & Eriksson 1997; chapter 4). Species can survive at the landscape scale when local extinctions are compensated by local colonizations. It is therefore important that measures to increase the botanical diversity of agricultural landscapes should not only be based on increasing the quality of local growing conditions (by means of adjusting management) as discussed by Kleijn *et al.* (2001), but also on the arrangement and dynamics of suitable habitat and the colonization ability of the target species (Hodgson & Grime 1990; Le Coeur *et al.* 1997; Opdam *et al.* 2000).

Sources of local colonization can either be the seed rain or the soil seed bank (Putwain & Gillham 1990; Bakker *et al.* 1996; Fröborg & Eriksson 1997; Pakeman *et al.* 1998). The potential role of the seed rain and the soil seed bank for (re)colonization differs between species and vegetation types (Grime & Hillier 1992; chapter 2). Both the colonization characteristics of species and the arrangement and dynamics of habitat influence distribution patterns of species. Distribution patterns and survival probabilities in fragmented and dynamic landscapes were explained by the colonization strategies of species (Hodgson & Grime 1990; Eriksson 1997; chapter 2). Species with poor colonization ability will have lower survival probabilities in fragmented and dynamic landscapes than species with well developed colonization ability. A persistent seed bank will be advantageous in dynamic habitats whereas adaptations for long distance dispersal are advantageous in landscapes with spatially

fragmented habitats. In dynamic habitats, long distance dispersal is also advantageous when enough seed producing plants are present.

The potential of the seed bank and the seed rain for restoration of natural vegetations is often limited due to the limited seed persistence and dispersal ability of plant species (Hutchings & Booth 1996a; Bakker & Berendse 1999; Bekker *et al.* 2000). The colonization ability of species is not only crucial in restoration projects but also in the long-term survival in fragmented and dynamic landscapes because local extinctions have to be compensated by local colonizations. In a three-year study of distribution patterns of plant species in a network of ditch banks along arable fields frequent colonization and extinction were observed (chapter 4). The species differed in dispersal and seed bank strategies. However, the relation of the dynamics of populations with the dispersal strategies of the species was not always clear in that study. The classification into dispersal categories was based on two databases (CBS 1993; Hodgson *et al.* 1995). In these databases, the classification of species into dispersal groups is often based on anecdotal information; sometimes the dispersal capacity of species is derived from the seed morphology and the habitat in which the plants are growing and the seeds are shed (e.g. aquatic plants are supposed to have water dispersed seeds) (Hodgson *et al.* 1995).

In observational studies of local colonizations one cannot be sure whether a colonization event originated from seed dispersal or from the soil seed bank. An experimental approach is needed to distinguish between both sources of colonization (e.g. Hutchings & Booth 1996; Pakeman *et al.* 1998). Most studies of dispersal and seed bank focused on weed communities or the seed bank of natural vegetations (heathland, forests, grasslands). Few studied the soil seed bank of vegetations in linear landscape elements in intensively used agricultural landscapes (Marshall 1989).

In this chapter we study the role of seed dispersal and the seed bank in the colonization of suitable patches in an agro-ecosystem using an experimental approach. The dispersal and seed bank characteristics of the species are taken into account. An agricultural area in the north of the Netherlands was used as study area because detailed knowledge of distribution patterns of thirteen species was available. The study aims at obtaining further insight in the processes of colonization, which is needed for the improvement of landscape management measures for increasing botanical diversity.

In the first part of the chapter, the ability for dispersal by wind and water is studied by measuring drop time and floating time of seeds of focal species.

The aims were to evaluate the dispersal categories to which the species were classified in literature and to quantify dispersal ability of the species.

In the second part, the focus is on realized dispersal and subsequent germination in dispersal plots. The aim was to test the hypothesis that colonization patterns in dispersal plots reflect the dispersal strategies of the species: species adapted to long distance dispersal will more often colonize plots, while they are not present in the surrounding vegetation, than species with adaptations for short distance dispersal.

In the third part the composition of the soil seed bank was studied in a germination experiment. The aim was to test the hypothesis that the distribution of species in the soil seed bank of sites of different age reflect the seed bank strategies of the species: species with a persistent seed bank will more often be present in seed banks of young, disturbed vegetations than species with a transient seed bank.

Methods

Study area

The study area (ca 150 ha) is located in the north of the Netherlands (6°27' E and 52°47' N). It consists of arable fields that are separated from each other by a network of ditches (11.3 km total). The most common crops in the area are potato, sugarbeet and barley. The vegetation of the ditch banks varies from very species poor vegetations that are dominated by a few species such as *Elytrigia repens repens, Urtica dioica* and *Holcus lanatus*, to species rich vegetations with characteristics of *Molinio-Arrhenatheretea* grasslands (Schaminee *et al.* 1996). About one third of the ditches were created in the period 1994-1996, the remainder of the ditches were created before 1980. For a detailed description see chapter 3.

Dispersal: floating and drop time

For ten species, drop times and floating times were measured as indicators for the dispersal capacity by wind and water respectively. The species were selected for their contrasting dispersal and seed bank characteristics (table 5.1) and because their distribution patterns have been studied in the study area (chapter 3; chapter 4). Drop time can be translated into the terminal velocity (V_t) which is a widely used indicator of dispersability by wind (Jongejans &

Telenius 2001) and an important parameter in dispersal models (Greene & Johnson 1989; Jongejans & Schippers 1999). V_t quantifies the constant velocity of falling seeds, when gravity and friction are equal. Seeds with low V_t have low vertical velocity which give falling seeds more time for horizontal movement, resulting in larger dispersal distances. Floating time quantifies the time that a seed can float on a water surface. It is an important indicator of the dispersability of seeds by water (Bulle *et al.* 1994; Danvind & Nilsson 1997). In September and October 1999 seeds of the species were collected in the study area, so that the seeds were not older than two months during the measurements.

Table 5.1 Thirteen focal species which were used in the dispersal and seed bank experiment, species with an asterix were used in the floating time and drop time experiments. For all species the distribution patterns in the study area were known.

species name	dispersal	seed bank	ecological group
Achillea millefolium L.*	wind	transient	moist, nutrient rich grasslands
Linaria vulgaris Mill.*	wind	persistent	nutrient rich ruderal vegetation
Lychnis flos-cuculi L.*	wind	persistent	wet, nutrient rich grasslands
Valeriana officinalis L.	wind	transient	wet, nutrient rich grasslands
Galium palustre L.	water	persistent	nutrient rich banks
Iris pseudacorus L.*	water	transient	nutrient rich banks
Lysimachia vulgaris L.*	water	transient	wet, nutrient rich grasslands
Ranunculus sceleratus L.*	water	persistent	pioneer of nutrient rich soils
Stachys palustris L.*	water	persistent	wet ruderal vegetation
Plantago lanceolata L.*	no adaptation	persistent	moist, nutrient rich grasslands
Rorippa amphibia (L.) Besser	no adaptation	transient	nutrient rich banks
Symphytum officinale L.*	no adaptation	transient	wet ruderal vegetation
Vicia cracca L.*	no adaptation	transient	moist, nutrient rich grasslands

a) Drop time experiment: For each species, 20 seeds were randomly selected for the drop time experiment. Drop time was electronically measured as the time needed for an individual seed to fall through a 15.83 m high fall-tower (Jongejans & Schippers 1999). The drop time was related to the species' characteristics seed weight and seed load, which is the ratio between seed surface and seed weight. The average weight was calculated using the total weight of the 20 seeds per species. The seed surface was calculated by translating the seed shape to 'standard shapes', such as disks, ellipses, spheres, for which simple formulas exist to calculate the surface.

b) Floating experiment: For each species, 100 seeds were randomly selected for the floating experiment. The seeds were scattered in small plastic boxes filled with ditch water. The boxes were slightly shaken for 15 minutes at

noon and for 15 minutes at midnight by an orbital shaker each day to simulate natural movement of water in ditches. After the first week the boxes were manually shaken to wet the seeds all over. Sunken seeds were counted on a daily basis during this 37-days experiment. Seeds of *Achillea millefolium* germinated while floating. Green germules were expected to be viable and were counted like floating seeds. Brown germules were not expected to be viable anymore (Grime *et al.* 1988) and were removed from the experiment.

Dispersal: colonization of dispersal plots

Fifty 'dispersal plots' were constructed in ditch banks in June 1999. The sites for the creation of the plots were selected because they were located at different distances from local populations of the thirteen focal species (table 5.2). Plots were 1×1m. The upper layer of 15 cm of the soil was removed, and filled up with sterile potting soil. This minimized potential colonization from the soil seed bank since most of the seeds are concentrated in the upper layer of the soil (Hutchings & Booth 1996; Pakeman *et al.* 1998; Bekker *et al.* 2000). The plots were laterally shielded from the surrounding soil by wooden frames of 15 cm high to prevent vegetative ingrowth of the surrounding vegetation.

Table 5.2 Number of plots located at different distances from local populations of a number of focal species. Total number of plots is 50. One plot can for example be located at < 10 m from *Achillea millefolium* and at > 40 m from *Lychnis flos-cuculi*.

	< 10 m	10-40 m	> 40 m
Achillea millefolium	10	15	25
Lychnis flos-cuculi	6	8	36
Lysimachia vulgaris	23	18	9
Plantago lanceolata	10	10	30
Stachys palustris	10	14	26
Valeriana officinalis	10	15	25
Vicia cracca	23	16	11

Since the vegetation in the direct vicinity of the plots will be the major source of colonization, the presence of all species at each side of the plot was recorded in June-July 1999. Five meters at each side and the opposite ditch banks were surveyed this way (figure 5.1). Five plots were located adjacent to ditches that were more than 5 m wide. For these plots the vegetation of the opposite ditch banks was not surveyed. In the following the vegetation within 5 m from the plots will be referred to as 'surrounding vegetation'.
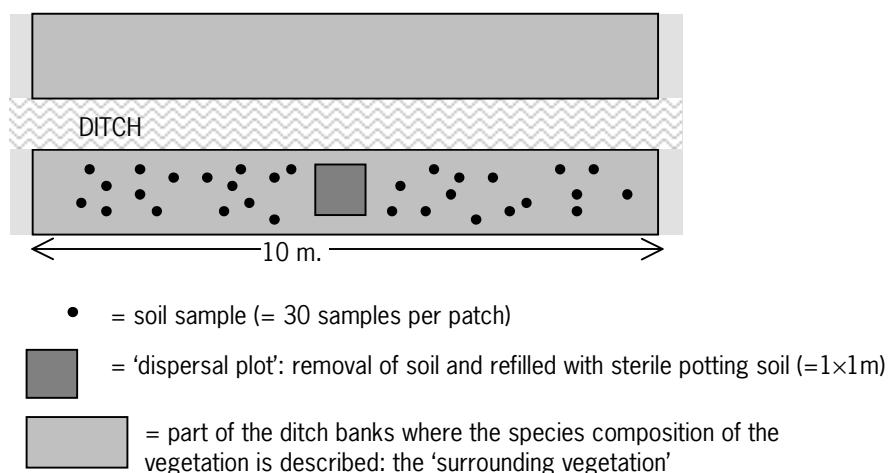
= soil sample (= 30 samples per patch)

= 'dispersal plot': removal of soil and refilled with sterile potting soil (=1×1m)

= part of the ditch banks where the species composition of the vegetation is described: the 'surrounding vegetation'

Figure 5.1 Lay out of experiment in the field: location of dispersal plot, soil samples for seed bank study and part of the ditch of which the vegetation composition is described.

Species that colonized the plots were recorded. Colonization was recorded in autumn 1999, summer and autumn 2000 and summer 2001. Dominance of species in the plots was prevented by cutting part of the above ground biomass.

Seed bank

Soil samples were collected in April 2000 at the sites where the dispersal plots had been created. The samples were collected within the first five meters at both sides of the plots (figure 5.1). At each side of the plot 15 subsamples were collected at random locations. The subsamples had a diameter of 3.5 cm and a depth of 7 cm (total area sampled per plot: 0.03 m^2). The above ground vegetation was not included in the samples but the litter layer was included.

The 15 subsamples collected at one side of each plot were combined. The 100 combined samples were sieved and washed conform Ter Heerdt *et al.* (1996). This procedure removed coarse material of > 4 mm (roots, small stones) as well as the smallest soil particles of < 0.2 mm. The washed samples were spread in a thin layer (max 3 mm) on top of a 4 cm layer of sterile soil in 100 trays of 40×60 cm. The trays were kept well watered in an unheated green house. Germination was monitored once a week during the first two months and from then on once every two weeks. Seedlings that were identified at the species level were counted and removed. Seedlings that could not be identified

were individually transplanted for later identification. After seven months germination in most trays ceased, partly due to colonization of the trays by mosses and liverworts. By that time the upper layer of the soil (ca 1 cm) was disturbed in order to expose seeds to the light that may have been covered by soil too much, which might have hampered germination. The experiment lasted until all seedlings were identified, which was 10 months after the experiment started. Very few seedlings had died before they could be identified.

Analysis

The composition of species that colonized the dispersal plots was compared with the composition of the surrounding vegetation. *SI(plot)*, the similarity index of a plot, quantified which fraction of the species that colonized a dispersal plot was also found in the surrounding vegetation:

SI(plot) = s.p. / t.p.   (5.1)

s.p.   = number of species in a dispersal plot, similar to the species in the surrounding vegetation

t.p.   = total number of species in a dispersal plot

Species that were found in the plots or in the surrounding vegetations were categorized in long and short distance dispersed species based on the dispersal vectors described by Hodgson *et al.* (1995). The following species were categorized as long distance dispersers: species dispersed by animals (adhesive or ingested), water or wind and species whose seeds have no morphological features facilitating dispersal, but which are dispersed by agricultural activities. The following species were categorized as short distance dispersers: species dispersed by ants, species whose seeds have no morphological features facilitating dispersal and species dispersed by water or ants (only one species: *Symphytum officinale*).

For each species two indices were calculated: *C.c.,* the fraction of the plots that were colonized by a species where the species was also found in surrounding vegetation and *C.f.,* the fraction of the plots that were colonized by a species where the species was not found in the surrounding vegetation.

C.c.   = p.s. / p.t.   (5.2)
C.f.   = p.n. / p.t.   (5.3)
C.c.   = the colonization index for colonized species also found close
            to the plots
C.f   = the colonization index for colonized species growing further
            away from the plots
p.s.   = number of plots colonized by a species where it was also
            found in the surrounding vegetation
p.n.   = number of plots colonized by a species where it was not
            found in the surrounding vegetation
p.t.   = total number of plots colonized by a species.

Only species that were found at least four times in the plots or the surrounding vegetation were used. Six species for which no dispersal vector was given in Hodgson *et al.* (1995) were also omitted. *C.c.* and *C.f.* for species with long and short distance dispersal were compared using a one-way Anova in Genstat 5.4.2. (Lawes Agricultural Trust 2001).

Colonization of the thirteen target species in a dispersal plot while not present in the surrounding vegetation of the plot was related to the shortest distance to the conspecific populations (potential seed sources) in the landscape in 1999.

The relation between the composition of the seed bank and the surrounding vegetation was expressed by *SI(sb-site)*, a similarity index for the seed bank of each site, i.e. the fraction of species found in the seed bank which were also found in the surrounding vegetation.

SI(sb-site) = s.sb. / t.sb.   (5.4)
s.sb.   = number of species in the seed bank of a site, similar to the
            species in the surrounding vegetation
t.sb.   = total number of species in the seed bank of a site

In a similar way, a similarity index was calculated for each species in the seed bank:

SI(sb-spec) = sb.s. / sb.t. (5.5)
sb.s.   = number of sites where the species was found in both the seed
            bank and the surrounding vegetation

sb.t.   = total number of sites where the species was found in the seed bank

The composition of the seed bank of old ditches was compared with that of young ditches. Data about seed bank persistence were collected from literature (CBS 1993; Thompson *et al.* 1997). When more than one seed bank class was given, which was the case for most of the species, the class that was mentioned most often was used as the seed bank class. For fourteen species no information on seed bank class was given, these were omitted from the analysis.

Similar to the dispersal plots, the presence of the thirteen target species in the soil seed bank was related to the presence of conspecific populations in the above ground vegetation. When seedlings of the thirteen target species were observed in the samples while not present in the surrounding vegetation, the shortest distance from the sample site to conspecific populations (potential seed sources) in the landscape in 1998 and 1999 were determined. Conspecific populations in 1998 were considered potential seed sources for the seed bank but not anymore for the dispersal plots that were constructed more than half a year after the plants in 1998 had shed their seeds.

Results

Dispersal: drop and floating time

The V_t values of the species are given in table 5.3. *Vicia cracca* had the highest terminal velocity (7.22 m s^{-1}) and *Linaria vulgaris* the lowest (1.20 m s^{-1}). The high V_t of *Vicia* seeds coincides with a high seed load. Seeds of *Vicia* are ball-shaped resulting in a small seed surface per weight unit (= high seed load). Seeds of *Iris pseudacorus* were heaviest of all species, but due to their disk-like shape they do not have the highest V_t. The lowest terminal velocity is expected to correlate with the longest dispersal distances when seeds are to be dispersed by wind. The results correspond reasonably well with the dispersal classes given in Hodgson *et al.* (1995): low values of V_t were found for species classified as wind dispersed. *Ranunculus sceleratus* and *Lysimachia vulgaris* were classified as water dispersed, but had lower V_t values than *Lychnis flos-cuculi*, a wind dispersed species according to Hodgson *et al.* (1995). However, the differences between those species were small. The correlation between

terminal velocity and seed load was statistically highly significant (log-linear relationship, $R^2 = 0.92$, $p < 0.001$) (figure 5.2).

The results of the floating time experiment are shown in figure 5.3. 50% of the seeds of *Plantago lanceolata* and *Vicia cracca* floated for less than one day, 50% of the seeds of *Achillea millefolium, Lychnis flos-cuculi* and *Symphytum officinale* floated for less than 5-11 days and 50% of the seeds of *Linaria vulgaris* floated for less than 30 days.

Table 5.3 Results of the drop time experiment. Results based on measurements of 20 seeds per species: mean, standard error of mean terminal velocities, mean weight of 20 seeds (total weight 20 seeds/20) and seed load = the ratio between the weight and surface of a seed. Table is sorted by V_t. Dispersal vectors are according to Hodgson *et al.* (1996).

|	dispersal vector	terminal velocity V_t (m s^{-1})		weight (mg)	seed load (mg mm^{-2})
		mean	s.e.		
Linaria vulgaris	wind	1.20	0.05	0.16	0.04
Achillea millefolium	wind	1.77	0.06	0.13	0.05
Ranunculus sceleratus.	water	2.25	0.05	0.15	0.15
Lysimachia vulgaris	water	2.60	0.05	0.35	0.05
Lychnis flos-cuculi	wind	2.98	0.03	0.20	0.12
Stachys palustris	water	3.90	0.13	1.35	0.26
Plantago lanceolata	ants	4.15	0.09	1.77	0.25
Iris pseudacorus	water	5.08	0.10	50.77	0.60
Symphytum officinale	water/ant	5.29	0.11	11.87	0.27
Vicia cracca L.	no adaptation	7.22	0.13	23.66	4.21
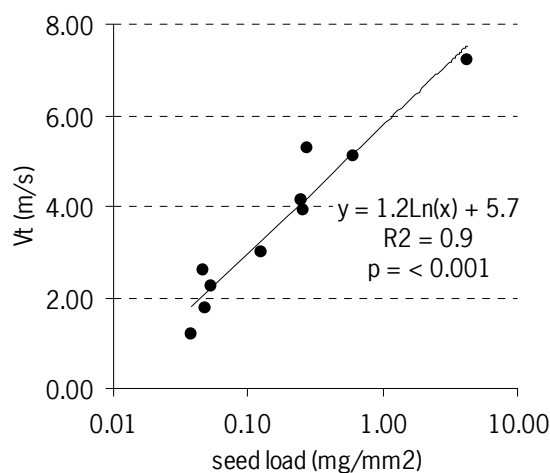
Figure 5.2 Results of the drop time experiment for 10 species: mean terminal velocity (20 seeds per species) related to the seed load.

At the end of the experiment more than 85% of the seeds of *Lysimachia vulgaris*, *Ranunculus sceleratus* and *Stachys palustris* were still floating. All seeds of *Iris pseudacorus* were still floating at the end of the experiment. The results correspond reasonably well with the dispersal classes given by Hodgson *et al.* (1995): the four species with the best floating ability were classified as water dispersed. *Symphytum officinale* was also classified as being water dispersed (besides being dispersed by ants), but in our experiment the seeds floated for less than ten days. *Linaria vulgaris* was classified as wind dispersed, but had a relative good floating ability as well.
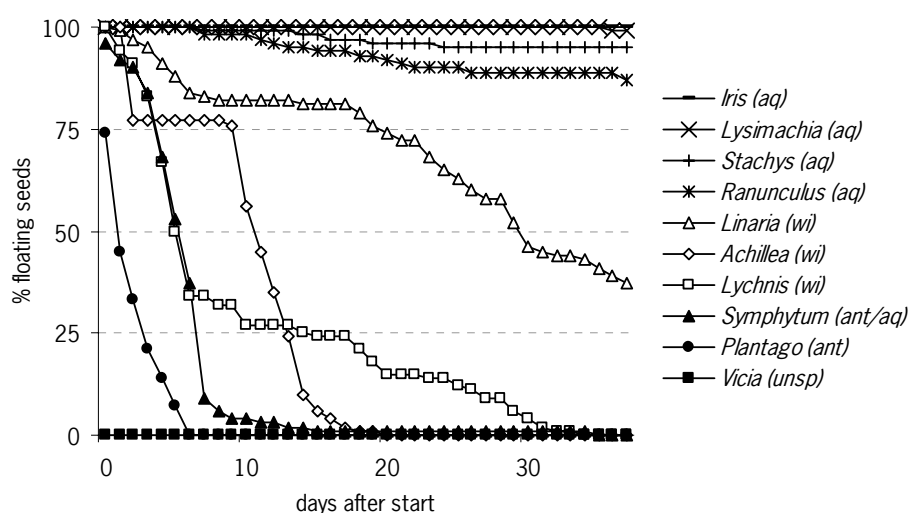
Figure 5.3 Floating ability of the seeds of all selected species. Adaptations for dispersal vectors according Hodgson *et al.* (1996) are given (aq: water, wi: wind, ant: ants, unsp: seeds not adapted to specialized dispersal).

Dispersal: colonization of dispersal plots

All dispersal plots were colonized by plants. A few plots were colonized by vegetative growth from underground plant parts, because the sterile soil layer slightly slid down the slope of the ditch bank or because of activity of animals (probably mice) but the underlying, original, soil was never exposed. A few other plots were partly covered by soil from the adjacent field as a result of plowing. Because of these sources of disturbance a few more species were able to colonize the plots by these other mechanisms. However, they all came from

outside the plot and not from the soil seed bank. Therefore all species observed in the plots were included in the results.

A total of 75 species were found in the plots. *Epilobium tetragonum* and *Elytrigia repens repens* were found most frequently in the plots (in 47 and 37 plots respectively). Small seedlings were found for *Epilobium tetragonum*, indicating colonization from the seed rain, whereas *Elytrigia repens repens* plants seemed to originate from vegetative underground parts. In the dispersal plots less species (mean 11.2, s.e. 0.60) were found in the plots than in the surrounding vegetation (17.3, s.e. 0.61) (figure 5.4). The correlation between the number of species in the surrounding vegetation and the number of species in the plots was statistically significant ($R^2 = 0.38$, $p < 0.001$). The correlation between the number of species found in the dispersal plots that were also found in the surrounding vegetation and the total number of species in the surrounding vegetation was also statistically significant (figure 5.4, $R^2 = 0.28$, $p < 0.001$). The mean *SI(plot)* was 0.61 (s.e. 0.024). A mean fraction of 0.62 of the species that were found in the surrounding vegetation was not found in the plots.
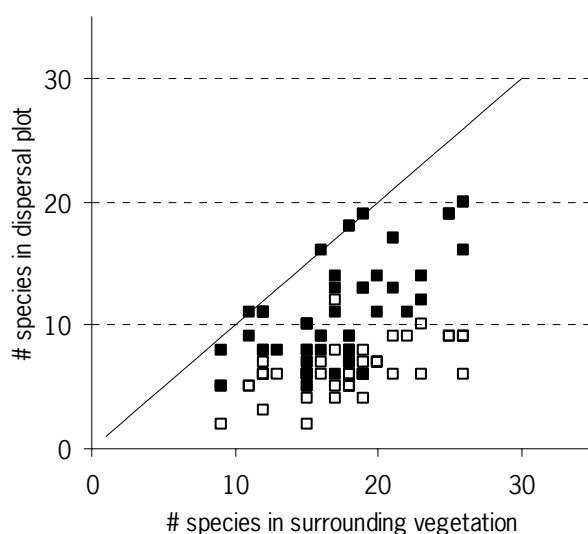

Figure 5.4 Relation between number of species found in the disperal plots and the number of species in the surrounding vegetation (< 5 m of plots). Diagonal indicates # species in plots = # species in vegetation surrounding the plots. Filled squares: all species found in the dispersal plots, open squares: species found in dispersal plots and also found in the surrounding vegetation.

Table 5.4 Results of colonization in dispersal plots. Colonization indices *C.c.* and *C.f.* quantify the average fraction of the number of dispersal plots that were colonized by a species where it was also present in the surrounding vegetation (*C.c.*) or where it was not present (*C.f.*), see also text for explanation. Colonization indices of species with different dispersal stategies are compared with one-way Anova.

		C.c.	*C.f.*	p		F
dispersal class	short distance	0.661	0.340	*	(0.02)	5.812
	long distance	0.497	0.503	n.s.	(0.94)	0.005

Table 5.5 Total number of plots colonized as well as the number of plots colonized where the species was not found in the surrounding vegetation within the first 5 m. For the latter plots the shortest distances to conspecific populations in the landscape in 1999 are given.

	# plots colonized		(mean) distance to nearest conspecific population (m)
	total	not present < 5m	'99
Achillea millefolium	4	2	15
Linaria vulgaris.	2	1	10
Plantago lanceolata	1	1	10
Symphytum officinale	3	0	
Vicia cracca	3	2	10

The majority of the species that were found in the dispersal plots were adapted to long distance dispersal (mean no. species with long dispersal per plot: 6.2, s.e. 0.44). A minority was classified as short distance dispersers (mean no. species with short distance dispersal per plot: 4.3, s.e. 0.24). Species adapted to long distance dispersal that were found in the dispersal plots were for 50% of these plots also found in the surrounding vegetation. Species adapted to short distance dispersal were for 66% of these plots found in the surrounding vegetation. This was quantified by the indices that indicate the distance to potential source plants for each species, *C.c.* and *C.f.* (table 5.4). For species with long distance dispersal the *C.c.* and *C.f.* indices were not statistically significantly different (one-way Anova, $p = 0.9$, $F = 0.005$), but for species with short distance dispersal *C.c.* was statistically significantly higher than *C.f.* (one-way Anova, $p = 0.02$, $F = 5.81$).

Only five of the thirteen focal species were found in a few dispersal plots (table 5.5). Potential source populations were either present in the surrounding vegetation (< 5 m) or further away, but still at short distances.
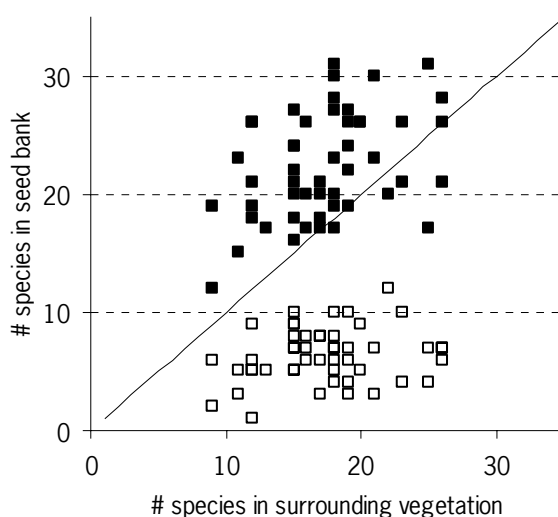
Figure 5.5 Relation between number of species found in the soil seed bank and the number of species in the surrounding vegetation (< 5 m of plots). Diagonal indicates # species in seedbank = # species in vegetation. Filled squares: all species found in the seed bank, open squares: species found in the seed bank and also found in the surrounding vegetation.

Seed bank

A total of 48997 seedlings were found in the trays and 97 species were identified. Seedlings of *Agrostis, Carex, Juncus* and *Poa* could not always be identified at the species level, therefore these were aggregated. It was clear that most of the *Juncus spp.* were either *Juncus effusus* or *Juncus bulbosus*. A fast majority of the seedlings belonged to the *Juncus spp.*: 32000 seedlings. The other species that were very frequently found were *Chenopodium album* (1211), *Polygonum maculosa* (1295), *Gnaphalium uliginosum* (1342), *Matricaria recutita* (1404), *Urtica dioica* (2799) and *Epilobium tetragonum* (2988). *Epilobium tetragonum* and *Juncus spp.* were found in all 50 plots. Other species that were present in samples of almost every plot were *Oxalis cornicultata* (48 plots), *Polygonum maculosa* (45 plots), *Urtica dioica* (43 plots) and *Gnaphalium uliginosum* (43 plots). The mean seedling density projected to the field situation was 32665 seedlings m^{-2} (s.e. 2812.6), excluding the *Juncus spp.* seedlings: 11331 m^{-2} (s.e. 853.3).

In most sites, more species were found in the soil seed bank than were present in the surrounding vegetation (figure 5.5). The correlation between the

number of species found in the seed bank and the number of species found in the surrounding vegetation was statistically significant ($R^2 = 0.14$, p < 0.01). The species composition of the seedlings that were found in the trays differed considerably from the species composition of the surrounding vegetation. No statistically significant correlation was found between the number of species in the surrounding vegetation and those found in the seed bank as well as in the surrounding vegetation (figure 5.5, $R^2 = 0.03$, n.s.). *SI(sb-site)* reflected the low similarity between the seed bank of a site and the surrounding vegetation. The mean *SI(sb-site)* was 0.29 (s.e. 0.015) for all samples. *SI(sb-site)* was also calculated for samples from the old and young ditches separately, but the difference was not statistically significant (p = 0.6).

The mean number of seedlings was only slightly higher in the samples of young plots than of the old plots (*Juncus spp* not included, one-way Anova n.s.) (figure 5.6). Most of the seedlings that germinated from the soil samples belong to species with a short term persistent seed bank (Thompson *et al.* 1997); a few species were classified as species with a long term persistent or transient seed bank. The number of seedlings of species with a transient seed bank was higher in old ditches than in young ditches, whereas the number of seeds of species with a short- and long term persistent seed bank was higher in young ditches, but these difference were not statistically significant.
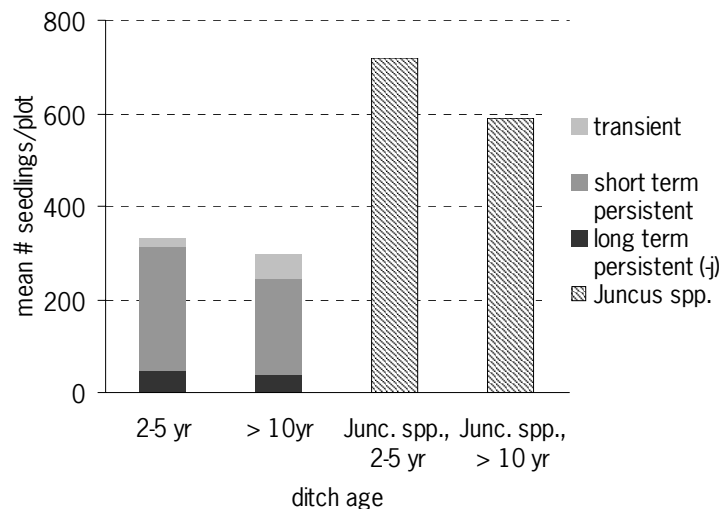

Figure 5.6 Mean number of seedlings found in the soil samples per plot. Differences of the total numbers of seedlings plot[-1] and number of seedlings plot[-1] for separate seed bank classes were not significant between the age classes of the ditches. Data of *Juncus spp.* are given separately because of their high numbers. Means over 50 plots.
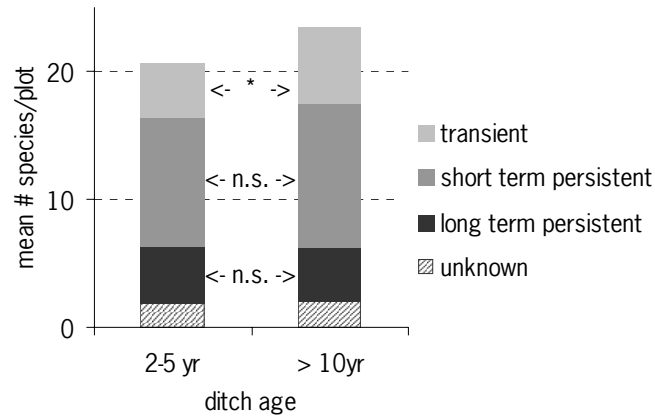
Figure 5.7 Mean number of species found in the soil samples of plots from young and old ditches. Means are given over 50 plots, level of significance between the age classes of ditches (one-way Anova) is given per seed bank class. $* = p < 0.05$, n.s. = not significant.
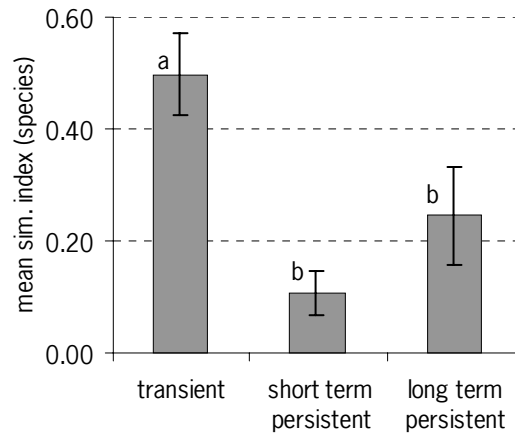

Figure 5.8 Mean similarity indices (SI(sb-spec)) for species with different seed bank persistence between source vegetation and seedlings in the soil seed samples, error bars: se. Similarity index is calculated as: (number of plots in which the species was found in the seed bank as well as in the surrounding vegetation) / (number of plots in which the species was found in the seed bank). Characters 'a' and 'b' indicate significant differences between the seed bank persistence groups (one-way Anova, $p < 0.05$).

The mean number of species was statistically significantly higher in the samples of old plots (one-way Anova, $p < 0.05$, $F = 4.51$) (figure 5.7). The difference between the number of species of old and young ditches

could be ascribed to the higher number of species with a transient seed bank in old ditches compared to young ditches (one-way Anova $p < 0.05$).

$SI(sb\text{-}spec)$ was calculated separately for species in the three seed bank classes in each sample (figure 5.8). Species with a transient seed bank that were found in the seed bank were, on average, in 50% of the cases also present in the surrounding vegetation. The mean $SI(sb\text{-}spec)$ of species with a transient seed bank (0.50 s.e. 0.074) differed statistically significantly from species with a short term persistent seed bank (mean similarity = 0.11, s.e. 0.038, one-way Anova $p < 0.001$) and species with a long term persistent seed bank (mean similarity = 0.24, s.e. 0.089, one-way Anova $p < 0.05$). The similarities of species with a short term and long term persistent seed bank did not differ statistically significantly (one-way Anova $p = 0.10$).

The timing of germination differed between species. Examples of the germination over time are shown in figure 5.9. Species of ruderal or weedy vegetations (e.g. *Chenopodium album, Gnaphalium uliginosum* and *Urtica dioica*) germinated more quickly than species of later succession stages (e.g. *Juncus spp.* and *Lotus pedunculatus*).
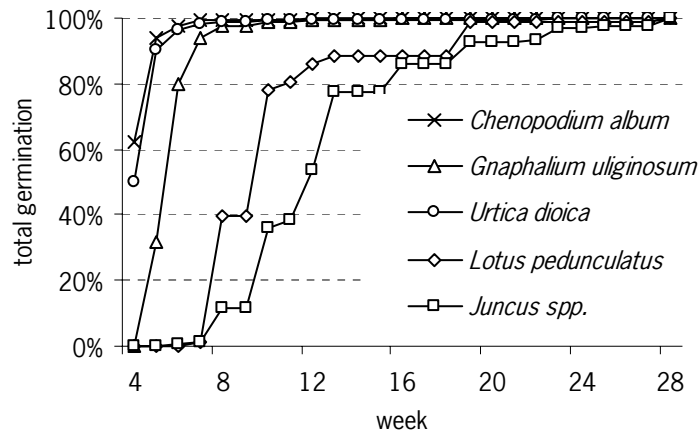

Figure 5.9 Germination of 5 species over time. *Chenopodium album, Gnaphalum uliginosum* and *Urtica dioica* represent species of ruderal or weedy vegetations, *Lotus pedunculatus* and *Juncus spp.* represent species of later successional stages.

Seven of the thirteen target species were found in the samples. In some cases the species were not present in the surrounding vegetation (table 5.6). The mean distance to the nearest conspecific (potential) source populations varied between the species and also between 1998 and 1999. Some of the species that where found in the seed bank had (mean) distances > 40 m to conspecific above ground populations in both years (*Achillea millefolium, Lysimachia vulgaris, Ranunculus sceleratus*).

Table 5.6 Total number of seed bank samples where a target species was found and those where the species was not found in the surrounding vegetation within the first 5 m. For the latter seed bank samples the distances (mean and range where appropriate) to the nearest conspecific above ground populations in the landscape in 1998 and 1999 are given.

	# seed bank samples		mean (range) distance to nearest conspecific population (m)	
	total	not present < 5 m	'98	'99
Achillea millefolium	3	1	70	210
Galium palustre	1	1	10	160
Linaria vulgaris.	9	7	6 (5.5-10)	33 (5.5-70)
Lysimachia vulgaris	4	2	45 (5.5-85)	45 (5.5-85)
Plantago lanceolata	1	1	30	140
Ranunculus scelaratus	37	26	93 (5.5-180)	100 (5.5-190)
Symphytum officinale	1	0		

Discussion

Floating and falling time

Both the results of the terminal velocity and the floating time of the ten species reflected the classification of Hodgson *et al.* (1995) reasonably well. *Ranunculus sceleratus* and *Lysimachia vulgaris* were classified as water dispersed species, and are also among the species with the lower V_t values. However, their V_t values were higher than those found in other studies for plumed seeds (Hensen & Müller 1997; Jongejans & Schippers 1999). Seeds with similar V_t as found in this study had dispersed over few meters only (Jongejans & Telenius 2001).

V_t is a key parameter in dispersal models (e.g. Greene & Johnson 1989; Jongejans & Schippers), but values cannot directly be translated into dispersal distances by wind. Other characteristics are of great importance as well: plant height compared to surrounding vegetation, structure of surrounding vegetation and wind speed (Van Dorp *et al.* 1996; Hensen & Müller 1997; Jongejans &

Schippers 1999; Jongejans & Telenius 2001). At higher wind speeds, dispersal distances by wind will increase. V_t has a minor influence on the dispersal distances at wind speeds above 2 m s^{-1} (Hensen & Müller 1997).

The number of days that the seeds floated is in accordance with other studies (Bulle *et al.* 1994; Danvind & Nilsson 1997). Depending on environmental conditions, even seeds that float for only a few days can potentially be transported over considerable distances, (> 1 km, unpublished data and Bulle *et al.* 1994). The realized dispersal distance by water in ditches, however, will be much lower, due to all kind of obstacles in the ditches. Seeds that float on water need to arrive at a site with suitable habitat for germination and establishment. For species such as *Achillea* and *Plantago,* which are species of moist grasslands, the zone of the ditch bank where they land may be too wet for successful colonization. Fluctuating water levels may enlarge the potential for landing at a site suitable for colonization.

Dispersal: colonization of experimental plots

Colonization by dispersal was limited. Fewer species were found in the colonization plots than in the surrounding vegetation. Besides limited dispersal capacity the reasons for this can be manifold. Some species may have succeeded to disperse into the dispersal plots but failed to germinate because the bare soil is not optimal for germination or due to seed dormancy. We did not test the suitability of the plots for germination. However, species with different environmental requirements were found in different plots, indicating that the quality of the plots did not systematically hamper germination. Limited establishment in experiments in which the soil seed bank was eliminated was also observed by others (Marks & Mohler 1985; Hutchings & Booth 1996a). Pakeman *et al.* (1998) on the other hand found on average more species in the seed rain than in the standing vegetation per sampling site, but their sampling sites of the standing vegetation were rather small (30×30cm).

The majority of the species found in the dispersal plots were also present in the surrounding vegetation. The differences between the dispersal strategies were reflected in the realized colonization of the plots. Colonizing species with short distance dispersal were often also present in the vegetation within 5 m of the plots. This implies a minimum dispersal distance smaller than 5 m. However, we do not know for sure which plants were the actual seed sources. Populations further away than 5 m may also have functioned as seed sources. Decreasing dispersal and colonization success with increasing distance to seed

sources was observed by many others (Marks & Mohler 1985; Primack & Miao 1992; Hutchings & Booth 1996; Bullock & Clarke 2000).

Species with short distance dispersal were not always growing within 5 m of the colonized dispersal plot. Dispersal of these species may have been promoted by management activities, such as mowing of the ditch banks (Strykstra *et al.* 1996; Coulson *et al.* 2001). The ditch banks in the study area are mown in October when most of the species will have set seed, so ripe seeds may indeed have been dispersed by machinery. Strong autumn winds may also have dispersed some seeds over longer distances.

Species with adaptations for long distance dispersal that colonized the plots were just as often present as not present in the surrounding vegetation. When using e.g. 50 in stead of 5 m as a measure of the direct surroundings, different similarities between the colonized species and the species present within 50 m or further away than 50 m might emerge.

A small number of the target species colonized a small number of plots. For all colonization events conspecific populations were present within 15 m from the plots. The numbers were too small to perform any statistical test or to relate the colonization success with distance to potential source populations. However, this anecdotal information emphasizes once again limited dispersal events over larger distances or the difficulty to observe them. In a study of local colonization of the same target species in the study area (chapter 4), colonization events were observed at distances over 100 m from conspecific source patches, also for species without adaptations for long distance dispersal and with transient seed banks. This implies minimum dispersal distances of over 100 m. We conclude that although dispersal over larger distances is limited (as indicated by the colonization of experimental plots), long distance dispersal does occur (as observed by the spatial distribution of local colonization events). The results of the experiments confirm the hypothesis that fragmentation of the landscape is a larger threat to species with short distance dispersal than for species with long distance dispersal. However, the distance that can be crossed by dispersing seeds of species with different dispersal strategies remains unclear and needs further study. The effectivity of the different dispersal vectors related to seed characteristics should be included in future studies.

Seed bank

The high number of *Juncus spp.* seedlings was striking. Yet it was not a dominant species in the vegetation. In the seed bank of analysis of grasslands Bekker *et al.* (2000) observed a similar pattern of very high numbers of seedlings of *Juncus* species in the seed bank while it was not very abundant in the standing vegetation. High numbers of *Juncus spp.* seedlings in the seed bank compared to the presence in the surrounding vegetation can be that germination opportunities are high under experimental conditions but opportunities for successful establishment in the field are low. The reason for the high number in the seed bank may be the combination of high persistence of the seeds and a high abundance in the past. Before the study area was converted to intensive arable land, it consisted of a matrix of heathland, peat, grassland and arable land (Wieberdink 1990).

The seedling density in the study varies widely over the area and depends on whether or not *Juncus spp.* are included, but the density is in the same order as the densities found for grassland communities and arable land (Silvertown 1982).

The number of species in the seed bank was higher than the number of species in the standing vegetation. Higher numbers of species in the soil seed bank compared to the standing vegetation have been observed by others as well (Hutchings & Booth 1996a; Pakeman *et al.* 1998). In our study the arable fields are directly adjacent to the sampled ditch bank vegetation. Many annual, weedy species that are present in the seed bank of the ditch banks are found in the adjacent arable fields. These species were not found in the surrounding vegetation in the ditch bank, but may have shed their seeds in the ditch banks from the adjacent fields. However, they have not been able to establish a population in the ditch bank vegetation (Marshall 1989).

More seedlings but fewer species were found in the younger ditch banks compared to old ditches. Young ditches had more seedlings of a few species with persistent seeds and less seedlings of a larger number of species with transient seeds. These differences can be explained by the history of the succession of the ditches. The vegetation of the younger ditch banks was removed about five years ago. This disturbance set back the vegetation successional stage of the young ditches. Early successional species, which often have a persistent seed bank, will have colonized the ditch banks first. This is illustrated by the faster germination of species like *Chenopodium album* (early successional) compared to species like *Lotus pedunculatus* (late

successional). Seeds of later successional stages could germinate in the experimental conditions because competing seedlings of species of the early species were removed. In a field situation germination of the later successional species, often with transient seeds, may be hampered by the abundance of the early species (Kleijn 1997). The germinability of these species in the soil seed bank will diminish after a few years, explaining the lower number of species with a transient seed bank in the seed bank samples of young ditches. As succession proceeds, species with a transient seed bank may colonize the ditch banks by dispersal and can thus be found in the seed bank again. Bekker *et al.* (2000) and Pakeman *et al.* (1998) also observed trends of a decreasing number of species with a persistent seed bank and increase of species with a transient seed bank with succession.

Species with transient seeds were more often found in both the surrounding vegetation and the soil seed bank of a site than species with a persistent seed bank. This confirms the reasoning above: species with a persistent seed bank in the seed bank partly represent former vegetations and will direct vegetation succession after large scale disturbance, whereas species with a transient seed bank in the seed bank follow rather than direct vegetation succession (Bekker *et al.* 2000).

The target species that were found in the seed bank but not in the vegetation, were all classified as species with persistent seeds (Hodgson *et al.* 1995). *Linaria vulgaris* and especially *Ranunculus sceleratus* were found in rather high numbers of samples without being present in the above ground vegetation. Sometimes the closest conspecific population was more than 100 m away. Both species are adapted to long distance dispersal (Hodgson *et al.* 1995), which may explain their frequent presence in the seed bank without being present in the surrounding vegetation.

Conclusions

We conclude that the colonization success depends on the dispersal and seed bank characteristics of plant species. Colonization of species that are not present in the soil seed bank depends on their dispersal capacity and the distance to potential seed sources. The colonization ability of species without adaptation for long distance dispersal (and without a persistent seed bank) is limited. Measures that aim at the recolonization of these species should

therefore be taken at short distances from existing populations. For the long term survival of these species a spatially continuous network of landscape elements is crucial. It still remains unclear how to translate the adaptations for dispersal to the actual distances that can be crossed by dispersing seeds. The other factor, which may be of major importance, is the presence of dispersal vectors. Strong winds that often occur in autumn, when most species have ripe seeds, may result in dispersal distances that do not depend anymore on the adaptation to wind dispersal of the seeds. Dispersal by agricultural machinery can also result in dispersal distances that do not depend on the dispersal adaptation of seeds (Schippers *et al.* 1993). The knowledge of these dispersal vectors is still limited and needs more study.

From the high number of species in the soil seed bank it may be concluded that it is a very rich source of (re)colonization. However, our results indicate that large scale disturbance of ditch bank vegetations will favour a vegetation of ruderals and weedy species with persistent seeds in the first years. After a few years the species with transient seeds will have lost their viability and will not attribute to the new vegetation as much as might be expected from the original soil seed bank. Although species with transient seed banks may be present in the soil seed bank, it is important to have populations in the landscape, which can function as a source for dispersing seeds. For the survival of species with transient seeds it is crucial that the habitat network is temporally continuous in order to protect populations that function as seed sources for colonization of empty habitat.
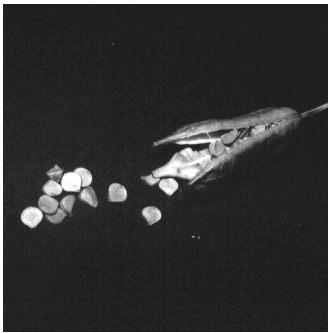
chapter 6

Plant survival in a dynamic habitat network: a modelling experiment with dispersal and seed bank strategies

W. Geertsema and J.M. Baveco

Abstract

A spatially explicit, individual-based single-species model was developed to study the relationship between plant species survival and the dynamics and fragmentation of habitat. The modelled landscape consists of a network of linear landscape elements with varying habitat quality and fields unsuitable for survival of plants. The population dynamics of the local plant populations that are connected by seed dispersal are simulated. We studied the survival of four model species with contrasting dispersal (short or long distance) and seed bank characteristics (transient or persistent) in landscapes of varying spatial and temporal continuity. The survival of the four model species decreased statistically significantly when spatial or temporal continuity of habitat decreased. Species with transient seed banks were most sensitive for a decrease of temporal continuity. Long distance dispersal was an effective strategy for survival in fragmented landscapes. A persistent seed bank was not only an effective strategy for survival in dynamic landscapes but also for survival in fragmented landscapes.

Differences between the survival of species with contrasting colonization strategies was very clear when taking long-term processes into account, however when data of only a few years are taken into account, these differences did not emerge. The rates and spatial distribution of colonization and extinction events according to the model were compared with field data of distribution patterns of plant species (observations in 1998-2000). The spatial patterns of local colonizations and extinctions were similar for species with long distance dispersal or a persistent seed bank or both. Apparently a persistent seed bank enables a species to colonize and persist in isolated habitat (> 200 m from conspecific local populations), even when its seeds are dispersed over short distances.

Introduction

Linear landscape elements contain a large part of the botanical diversity in agricultural landscapes (Fry 1994). The fields that are used for agricultural production are virtually unsuitable for many plant species due to high soil disturbance rates and the use of fertilizers and pesticides. The semi-natural linear landscape elements (e.g. hedgerows, ditch banks, streams) that are not

used for agricultural production potentially form a network of habitat. However, this network is not continuous, neither in space nor in time (Merriam 1988; Fry 1994). Dynamics and fragmentation of habitat originate from natural causes (e.g. death of plants, succession, frost, and disturbance by small mammals), management of the landscape elements themselves and from disturbance by agricultural activities on the adjacent fields. Because of their linear shape, the landscape elements are very susceptible to the activities on the adjacent fields. Habitat dynamics and fragmentation often have a detrimental effect on the survival of species on the landscape scale (Fahrig 1992; Ouborg 1993).

In recent decades the botanical diversity of agricultural landscapes decreased (e.g. Joenje & Kleijn 1994). If we want to increase the diversity again, we need to understand under which conditions plant populations can still persist in a landscape. These conditions not only relate to the local habitat quality, but also to the spatial arrangement and the dynamics of habitat (chapter 2, chapter 3).

In spatially and temporally fragmented landscapes, plant species will be divided into local populations. Local plant populations can go extinct due to chance processes in small populations (demographic stochasticity), but in linear landscape elements in agricultural landscapes most extinctions may be caused by environmental changes, e.g. drift from herbicides, imprecise tillage or inaccurate management of the landscape elements. Persistence on the landscape scale is only possible if (re)colonizations compensate the local extinctions. The seed rain and the soil seed bank are the most important sources of colonization (Bakker *et al.* 1996). Species with well-developed colonization abilities are expected to have higher survival probabilities in highly fragmented or dynamic landscapes than species with poor colonization abilities (chapter 2).

Several studies have shown a relation between the distribution and survival of plant species and fragmentation and dynamics of habitat (e.g. Quintana-Ascencio & Menges 1995; Grashof-Bokdam & Geertsema 1998; Prins *et al.* 1998). In a study of the distribution of plant species in a network of ditch banks along arable fields it was found that species with persistent seeds had a higher colonization rate in young ditch banks of five years old than species with transient seeds (chapter 3). However, in a three-year field study colonization strategies had limited effects on the colonization patterns of plant species in ditch banks (chapter 4), probably because a three year period is rather short for the study of the dynamics of perennial plant species. The last

example illustrates the apparent disadvantage of empirical studies of the relation between survival of plant species and habitat fragmentation and dynamics. In empirical studies it is impossible to do large scale, long term experiments. At the same time many aspects of plant population dynamics typically function on larger temporal and spatial scales.

Therefore, we turn to simulation models to explore population behaviour on larger temporal and spatial scales. Models have been developed to explore the survival of plants in fragmented landscapes. The models often use the spatially implicit metapopulation model of Levins (1969) as a starting point, assuming an infinite number of identical patches, with equal colonization chances. Later models have become more realistic by adding spatial heterogeneity and more detailed population dynamic algorithms (e.g. Van Dorp *et al.* 1997; Kalisz & McPeek 1993). The role of seed banks has been studied in metapopulation models, but mainly (as far as we know) for annual species (e.g. Kalisz & McPeek 1993; Perry & Gonzalez-Andujar 1997). Most metapopulation models for plants have been developed for annual plant species, because it is a relatively simple system to model and to test in the field (e.g. no survival of adults from year to year). However, the behaviour of perennial species should also be studied in more detail, because many of these species suffer from habitat fragmentation (Ouborg 1993). Some studies have relaxed the assumption of a static landscape (e.g. Fahrig 1992; Wu & Levin 1994; Keymer *et al.* 2000). Keymer *et al.* (2000) analyzed a metapopulation model with a dynamic landscape in which suitable sites change to unsuitable and vice-versa. They showed that in a landscape with a high amount of suitable patches but also a high habitat turnover rate, species with a low propagule production rate (their equivalent of colonization ability) were not able to persist. Comparing a spatially explicit (interacting particle system) with a spatially implicit (mean field) model, they showed that spatial explicity increases the sensitivity of metapopulations for landscape dynamics and the amount of habitat available.

We follow this line of thought and will add more spatial realism to the approach used by Keymer *et al.* (2000). We want to test the hypothesis that habitat fragmentation (decrease of spatial continuity) and habitat dynamics (decrease of temporal continuity) decrease the survival probability of plant metapopulations. We expect that species with different dispersal and seed bank strategies respond differently to different levels of spatial and temporal continuity. Long distance dispersal will increase the survival probability in

fragmented landscapes, as it enables a species to colonize empty isolated patches and it enables seeds to disperse into local isolated populations, thus increasing the survival probability of local populations (rescue effect, Brown & Kodric-Brown 1977). A persistent seed bank increases the survival probability in dynamic landscapes, as it enables species to (re)colonize empty patches and it buffers the extinction risk of small isolated populations (rescue effect of seed bank, Kalisz & McPeek 1993).

Using a spatially explicit simulation model we will study the impact of habitat continuity in this dynamic network of habitat and the role of colonization strategies (dispersal capacity and seed bank persistence) on population survival. Perennial species will be considered, as they make up the majority of the semi-natural vegetations in linear landscape elements. The system we aim at has been described in a conceptual model (chapter 2).

The model consists of a dynamic landscape part in which land use dynamics are simulated as a stochastic two-compartment model. The land use dynamics determine the habitat suitability for the local populations. Local populations are linked in space by dispersing seeds. Local populations are stage-structured and the seed bank is age-structured.

Description of the model

We have modelled the population and landscape dynamics in a way that is similar to methods used in the field studies of plants in a network of ditch banks in the north of the Netherlands (chapter 3; chapter 4). In the field studies we observed spatial turnover of local populations of thirteen grassland species. Because of the difficulty to determine the limits of local populations in a field situation, we decided to use segments of the ditch banks of a fixed length (10 m) as patches that could be occupied by a local population (similar method used by Antonovics *et al.* 1994). The set of patches with different habitat quality covered the total network of ditches. Despite the more or less trivial limits that were imposed to the size of local populations and patches, this method proved to be convenient.

The model was developed in the object-oriented programming environment Smalltalk, using the EcoTalk modelling framework (Baveco & Smeulders 1994). The model is individual based and discrete in time. Each

time-step represents one year, within the time-step the whole life cycle of the species and landscape dynamics are represented by a series of events.

The landscape

The landscape in the model consists of polygons (fields) and arcs (linear landscape elements). The fields represent agricultural fields and the lines ditches, including the ditch banks. Habitat is limited to the ditches, the fields were considered unsuitable for survival of the plants. The ditches function as dispersal corridors, because water and machines driving along the field edges are expected to be important dispersal vectors (chapter 2). The model can use real landscapes represented by a digital map of the area as input. However, in this chapter a computer-generated landscape (Voronoi tessellation, Haydon & Pianka 1999) is used (figure 6.1). The spatial structure of the landscape is comparable with agricultural landscapes in which the arrangement of the fields follows the abiotic and geological features of the area (for example the sea reclamation areas in the northern part of the Netherlands). The average length of the ditches is 250 m.
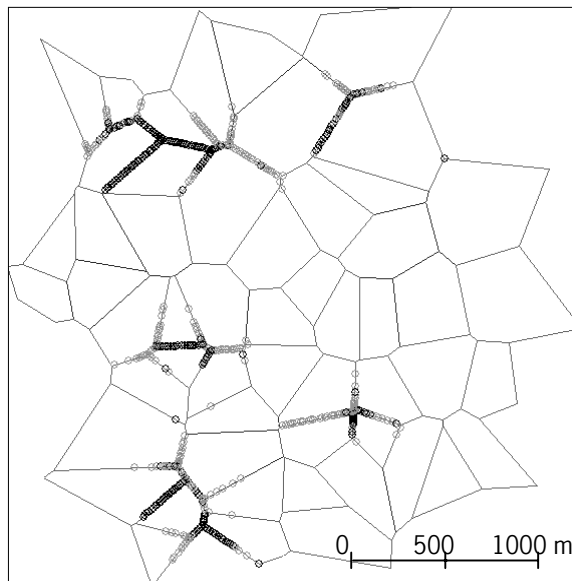

Figure 6.1 The voronoi-landscape that was used in the simulation experiments. Lines represent ditches that intersect the fields, circles represent populations present at a random time in a simulation: black circles = populations with plants, gray circles: populations with soil seed bank, but without plants.

habitat quality: Habitat for the simulated plant species is limited to the linear network of ditches. The two adjacent fields determine habitat quality of the ditches. Fields have either favourable or unfavourable use. Favourable implies no negative effects on the adjacent ditch e.g. by drift of fertilisers or herbicides. This might be the situation in ecological farming systems, or when there is a non-productive strip between the ditch and the field. Unfavourable land use negatively affects the habitat quality of the ditches by drift of fertilisers and herbicides. The two states of land use of both adjacent fields result in three possible values of habitat quality of the ditches (table 6.1).

spatial composition and dynamics of habitat: Land use dynamics are simulated as a stochastic two-compartment model, with two parameters: the probability that a favourable field becomes unfavourable (P_{fu}) and vice versa (P_{uf}). From these parameters, the expected composition of the fields and the ditches can be calculated (table 6.2). Whereas the ratio between P_{uf} and P_{fu} determines the spatial continuity, the absolute values of P_{uf} and P_{fu} determine the temporal continuity of the habitat.

The population dynamics

We apply a stage-structured model for the plant stages (adults and seedlings) and an age-structured model for the seed bank stage (figure 6.2). The plants occur in local populations inhabiting a location ("patch") in the habitat network and are connected through dispersing seeds. The local population dynamics and the composition and dynamics of the habitat determine local extinction and colonization rates which in their turn determine the survival of the species in the landscape. The collection of the local populations will be referred to as the metapopulation.

local populations: A local population is represented by an occupied patch in the habitat network. A local population can consist of seeds in the soil seed bank, seedlings and reproducing adult plants. The number of adult plants is limited by the carrying capacity of a patch. The 'seed incorporation distance' determines the size of a patch that can be inhabited by a local population. When seeds are dispersed to a position in the habitat network within this incorporation distance from an existing local population, seeds are added to that existing population, otherwise a new local population is established (first only consisting of a seed bank).

Table 6.1 Relation between land use quality of the adjacent fields and habitat quality of the ditches.

adjacent land use (two sides)	habitat quality of ditch
unfavourable + unfavourable	unsuitable
unfavourable + favourable	marginal
favourable + favourable	suitable

Table 6.2 Relation between P_{uf} and P_{fu}, the expected fractions of unfavourable (U) and favourable (F) fields and the expected fractions of suitable, marginal and unsuitable habitat quality in the ditches. The nine combinations of P_{uf} and P_{fu} are used in simulations.

		fraction of fields		fraction of ditches		
P_{uf}	P_{fu}	U $[(P_{uf}/P_{fu}) + 1]^{-1}$	F $(P_{uf}/P_{fu}) \times [(P_{uf}/P_{fu}) + 1]^{-1}$	unsuitable $= U^2$	marginal $= 2FU$	suitable $= F^2$
0.06	0.04	0.4	0.6	0.16	0.48	0.36
0.18	0.12			"	"	"
0.3	0.2			"	"	"
0.05	0.05	0.5	0.5	0.25	0.50	0.25
0.15	0.15			"	"	"
0.25	0.25			"	"	"
0.04	0.06	0.6	0.4	0.36	0.48	0.16
0.12	0.18			"	"	"
0.2	0.3			"	"	"

seed bank dynamics: New seeds are added to an existing local population or establish a new one after dispersal. Each year, a certain proportion of seeds in the soil seed bank dies, the surviving seeds increase one year in age. The persistence of the seed bank is determined by the maximum seed bank age.

germination and establishment: Each year, seeds in the soil seed bank can germinate with a probability that depends on the habitat quality of the ditch but not on the age class of the seeds. Seeds of the youngest age class cannot germinate, they first have to progress into the next age class. Seeds in the maximum available age class die if they fail to germinate. After germination seeds become seedlings. Plants remain in the seedling stage until the next growing season. Seedlings either die or progress into the adult stage. Seedling mortality depends on the habitat quality. The establishment of adult plants is
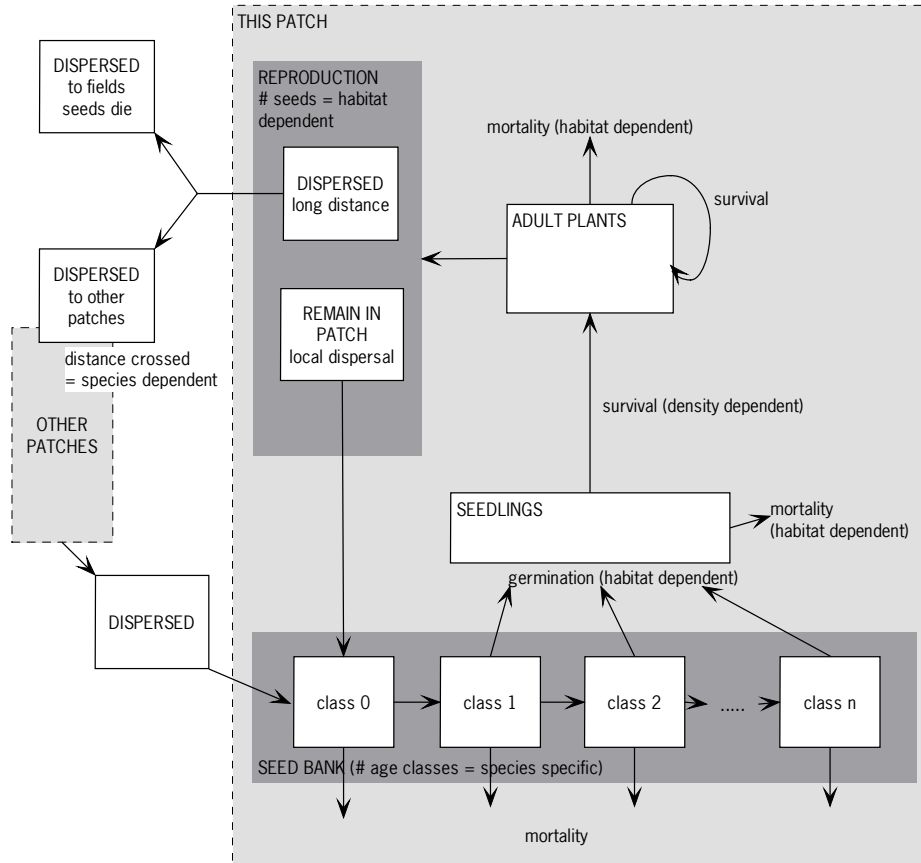
Figure 6.2 Scheme of population dynamics simulated in the model.

density dependent: establishment can occur when the carrying capacity is not exceeded, otherwise the seedlings die.

reproduction and mortality: Individuals do not reproduce in their first year, which is simulated by the seedling stage. Adult plants produce a number of seeds each year. The number of seeds depends on habitat quality and is represented by a Poisson distribution, determined by its mean. Adult plants die with a probability that depends on habitat quality.

dispersal: Part of the seeds produced remains in the patch of origin. The other seeds are dispersed, but part of the dispersing seeds arrives in the adjacent

fields and is removed from the model system. The remainder of the seeds is dispersed through the ditch network. The dispersal distance is assumed to be negatively exponentially distributed. Each individual seed travels a distance drawn from this distribution through the network of the ditches. At junctions of ditches a random direction is chosen, but excluding the turn-back option (seeds thus perform a self-avoiding random walk).

Parameterisation

landscape parameters: The distribution of marginal, suitable and unsuitable ditches is based on a field study of ditch banks (chapter 3). Ditch bank vegetations that were dominated by a few dominant graminae species were considered unsuitable, vegetations with both ruderal and a few grassland species marginal, and the most species rich grassland vegetations were considered suitable. 25% unsuitable, 50% marginal and 25% suitable habitat is a realistic estimation for such a system. This habitat distribution is achieved when landscape parameters P_{fu} and P_{uf} are equal. The dynamics of the habitat quality are more difficult to estimate. In the field study the quality of the majority of the ditch banks remained constant. The habitat dynamics of the ditches is determined by the dynamics of the adjacent fields, we therefore decided to keep the majority (95%, 85% and 75%) of the quality of the fields stable each year, therefore $P_{fu} = P_{uf} = 0.05$, 0.15 and 0.25 were used. P_{fu} and P_{uf} were varied to test other combinations of spatial and temporal continuity as well (tables 6.2, 6.3).

Table 6.3 Values of landscape parameters P_{fu}, P_{uf} used in the simulations. Values of P_{fu}, P_{uf} determine the land use quality of the fields and the habitat quality of the adjacent ditches. They also determine the spatial and temporal continuity of habitat in ditches: high ("+"), intermediate ("±") and low ("−") spatial and temporal continuity.

| | | | temporal continuity | | |
			+	±	−
		P_{fu}, P_{uf}	$P_{fu} + P_{uf} = 0.1$	$P_{fu} + P_{uf} = 0.3$	$P_{fu} + P_{uf} = 0.5$
spatial continuity	+	$P_{fu}/ P_{uf} = 1.5$	0.06, 0.04	0.18, 0.12	0.3, 0.2
	±	$P_{fu}/ P_{uf} = 1$	0.05, 0.05	0.15, 0.15	0.25, 0.25
	−	$P_{fu}/ P_{uf} = 0.67$	0.04, 0.06	0.12, 0.18	0.2, 0.3

plant parameters: The population dynamics of perennial grassland herbs were simulated. The aim of the chapter was to compare the viability of plant species that only differed in dispersal distance and seed bank persistence, therefore the value of the other demographic parameters remained constant for the four model species (table 6.4). In reality no species have the same demographic parameters and we do not claim that the values represent the average of perennial grassland herbs, if such a thing exists. However, errors in the estimation of the 'constant' parameters are the same in any simulation experiment, therefore the impact of the colonization characteristics of the species and the landscape characteristics can still be compared.

Table 6.4 Overview of the plant parameter values in the simulations, derivation of the values is described in the text.

(a) parameters determining species strategy, taking on different values — *source*

dispersal distance (mean exponential distribution)	50 m "short distance"	250 m "long distance"	literature, estimate
maximum seed bank age	1 year "transient"	5 years "persistent"	literature

(b) species parameters remaining constant among simulations

- habitat dependent species parameters

	unsuitable	marginal	suitable	
mortality probability seedling	1.0	0.8	0.6	literature
number of seeds produced (Poisson mean)	0	25	75	literature
germination probability	0.00	0.01	0.05	literature
mortality probability adult plants	1.0	0.7	0.3	literature
carrying capacity of patches	0	2	6	personal observation

- habitat independent species parameters

fraction local dispersal	0.45	model VELDDIS
fraction seeds in arable fields	0.45	model VELDDIS
seed bank mortality	0.5	literature
incorporation distance = patch size	10 m	literature, personal observation

i. parameters remaining constant for all model species

incorporation distance: The incorporation distance, which determines the local patch size, was set to 10 m. In a field study 10 m segments of ditch banks proved to be a suitable measure to study the distribution of the herbaceous species in ditch banks in an agricultural landscape (chapter 3; chapter 4).

carrying capacity: Based on personal observations (unpublished data) the average carrying capacity of a patch was set at six plants for suitable and two for marginal habitat. We assume a vegetation of rather high biomass, due to high fertilizer pressure and sub-optimal management. The conditions limit the number of individuals of some herbaceous species that have their optimum in vegetations with lower biomass. This results in a lower carrying capacity than often mentioned in literature (Van Dorp *et al.* 1997).

seed bank mortality: The death of seeds in the soil seed bank is influenced by numerous biotic and abiotic factors (Silvertown 1982; Bekker 1998), The mortality probability of seeds in the soil found in field studies varies widely, ranging from 0.1-0.98. We fixed the mortality probability of seeds of any age class to 0.50, approximately the median value of the available data.

germination probability: The probability that a seed germinates and establishes as a seedling, depends on many environmental and species factors (Fenner 1985). Values of germination and establishment probabilities vary widely in literature. Some values used in model studies ranged from 0.0006-0.018 for perennials (Van Dorp *et al.* 1997) to 0.5 (Perry & Gonzalez-Andujar 1994) or 0.98 (Moloney & Levin 1996) for annuals; in empirical studies also large variation was found among species and sites: from 0.008 (Meyer & Schmid 1999) to 0.04-0.4 (Hutchings & Booth 1996b). In our model the germination probability depended on the habitat quality. Using the available data we set the germination probability to 0.01 for marginal and 0.05 for suitable habitat.

seedling mortality: Falinska (1991) found seedling mortality rates in recently and less recently abandoned meadows to be on average 0.82 and 0.66 respectively. Rademaker & De Jong (1999) measured seedling mortality rates of 0.8-0.89 for *Cynoglossum officinale*. We set the mortality in marginal habitat at 0.8 and in suitable habitat at 0.7. Van Dorp *et al.* (1997) used a mortality of

0.2 for vegetative plants of all ages. However, we assume one-year old seedlings to have higher mortality rates than adult vegetative plants.

plant mortality: Van Dorp *et al.* (1997) used a mortality probability of 0.2 for flowering and vegetative plants in their model. We used a mortality probability of adult plants of 0.3 in suitable habitat and 0.7 in marginal habitat. We accounted for the negative influence of the adjacent agricultural use on survival of plants and used higher mortality probabilities, especially for marginal habitat.

reproductive output: The values reported for the reproductive output of plants in field studies and simulation models were highly variable and depended on the species and sites studied. Fecundity parameters used in models were e.g. 21 (Perry & Gonzalez-Andujar 1994) or 50-1500 (Van Dorp *et al.* 1997); values found for empirical studies were e.g. 11-27 (Wu & Levin 1994), 4-70 or 500-4000 (Falinska 1991). Pre-dispersal mortality can be considerable (> 90%, Fenner 1985). We used an estimate of 10% pre-dispersal survival, resulting in 25 (marginal) and 75 surviving seeds $plant^{-1}year^{-1}$ (suitable habitat).

local dispersal and dispersal into the unsuitable fields: We used the model VELDDIS (Van Dorp *et al.* 1997) to determine which fraction of the seeds would remain in the patch of origin, which fraction would be dispersed outside the patch and which fraction of the dispersed seeds would be lost in the adjacent fields. In VELDDIS we used a corridor existing of two parallel ditch banks of 2×10 m along a ditch with a width of 2 m. Realized dispersal distances in VELDDIS are drawn from a negative exponential distribution with slope α. We used α = 1, as the approximate mean of values mentioned for a large range of herbaceous species (Willson 1993). The results of model runs with VELDDIS indicated that a fraction of 0.55 of the seeds was dispersed outside the patch and that a fraction of 0.45 of the dispersed seeds was lost in the adjacent fields.

ii. parameters determining the colonization strategy of model species
maximum age seed banks - persistent or transient: Thompson *et al.* (1997) classified seeds that only survive one season as transient (so maximum age is one year), seeds that survived up to five years as short term persistent and

longer than five years as long term persistent. Five years can be considered an average period of viability for persistent seed banks. The seed bank characteristics of the model species was determined by the maximum age of the soil seed bank: species with a transient seed bank have a maximum age of one year, species with a persistent seed bank have a maximum age of five years.

dispersal distance - long or short: The dispersal distance was the other parameter that determined the species strategies. In Cain *et al*. (2000) and chapter 2 dispersal over more than 100 m was classified as long distance dispersal. Therefore we set 50 m as the average of the short distance dispersal strategy and 250 m as the average of the long distance dispersal strategy.

Population growth rate

The demographic parameters determine the growth rate of a local population. A Leslie model was used to calculate the population growth rates without taking spatial or density dependent aspects into account. The resulting growth rates were 0.55 and 0.66 (declining populations) in marginal habitat and 1.17 and 1.28 (increasing populations) in suitable habitat for species with transient and persistent seed banks respectively. Due to immigrants from the suitable habitat patches populations in marginal habitat may persist (Eriksson 1996). The growth rates fall within the range of those found by Kalisz & McPeek (1993) who classified years with $\lambda=0.4$ as 'bad' years and $\lambda=1.8$ as 'good' years. Our choice of the values of the individual parameters was based on both literature and biologically sensible educated guesses; the values of λ indicate that the combination of the parameters is sufficiently realistic.

Simulations

The population dynamics of four model species with contrasting dispersal and seed bank characteristics were simulated. Landscape parameters were varied to study the survival of the four species in different combinations of spatial and temporal fragmentation. Nine combinations of three values for spatial composition and three values for temporal continuity were simulated (table 6.2, 6.3).

At the start of each simulation run 10,000 seeds were distributed over 14 ditches. Simulations were run for 250 years. Each landscape – model species

combination was run 10 times. The effect of the landscape characteristics was quantified by the following population statistics:

(1)   *survival* = percentage of the runs in which the metapopulation survived for at least 250 years,

(2)   *time to extinction, T(ext)* = median time to metapopulation extinction per simulation when the metapopulation became extinct within 250 years. Species with persistent seed banks sometimes showed pseudo-extinction: the above ground vegetation was extinct, but within a few years re-colonization occurred from the soil seed bank. Only when no local populations reappeared from the soil seed bank the species was considered extinct.

(3)   *number of local populations, Npop* = mean number of local populations in the final 50 years (year 201-250) of the simulations. The final 50 years were used, because it takes time to build up the metapopulation.

(4)   *colonization and extinction rates, C and E =*
Colonization rates, *C*: $N_t(C)/N_t(T)$;
Extinction rates, *E*: $N_t(E)/N_{t-1}(T)$.
$N_t(C)$ = number of new local populations in year *t*,
$N_t(T)$ = total number of local populations in year *t*,
$N_t(E)$ = number of extinct local populations in year *t*
Mean *C* and *E* were calculated for the final 50 years of the existence of a metapopulation. For metapopulations that became extinct before year 50, all years were used.

(5)   *colonization and extinction distances, Cdist and Edist* = the minimum distance (in a straight line) from colonized or extinct local populations in year *t* to other local populations in year *t-1* in an additional simulation run for each model species. Distances were determined for the local populations in year 11-15 in the simulations in a landscape with intermediate spatial continuity and high temporal continuity.

The colonization and extinction rates and distances were compared with similar data from the three-year field study of distribution patterns for thirteen plant species in a network of ditch banks (chapter 4).

Results

Survival and extinction of metapopulations and number of local populations

The number of local populations fluctuated strongly within and between the runs. Examples of the number of local populations in landscapes with intermediate dynamics and highest spatial continuity are given in figure 6.3. Despite strong fluctuations, the number of populations increased with increasing dispersal capacity and seed bank persistence.

Decrease of spatial continuity and decrease of temporal continuity both decreased the survival of the four model species (figure 6.4). The model species with transient seeds and short distance dispersal had the lowest survival percentages. It only survived in 20% of the runs in the most stable and least fragmented landscape (figure 6.4A). Changing the dispersal capacity to long
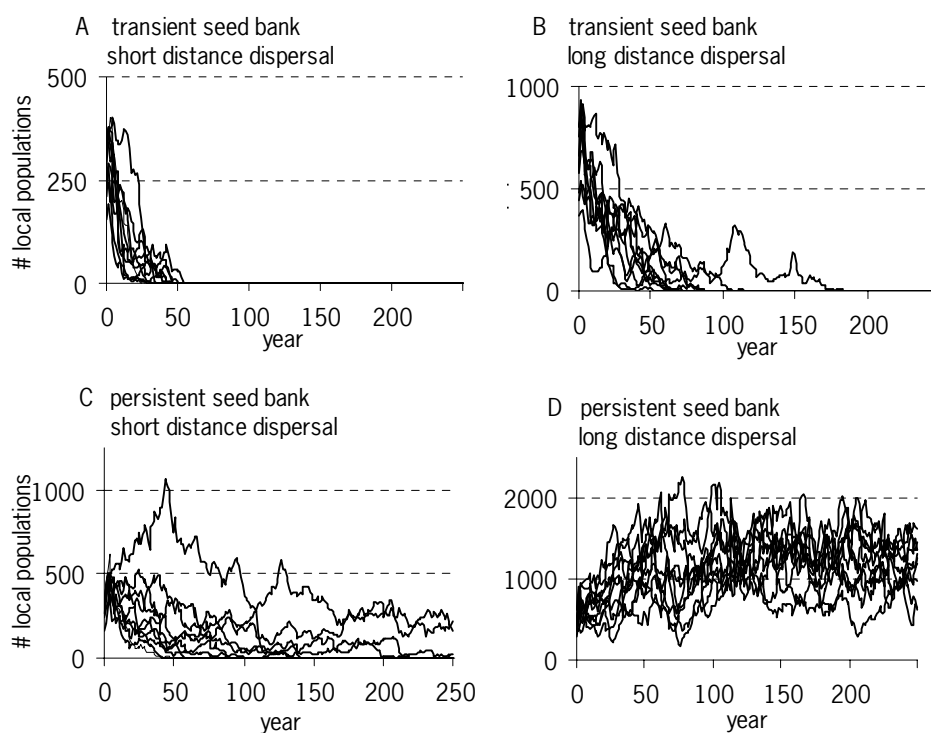

Figure 6.3 Examples of numbers of local population for each of the four model species during ten runs of a simulation in landscapes with high spatial continuity and intermediate temporal continuity.

distance dispersal increased the survival in the configurations with the highest temporal continuity (figure 6.4B). In landscapes with intermediate or low temporal continuity it did never survive up to 250 years. The model species with short distance dispersal and a persistent seed bank survived in 40% of the runs in landscapes with intermediate spatial continuity and high temporal continuity, but it did not survive when spatial fragmentation was further increased (figure 6.4C). It also survived in 30% of the runs in landscapes with high spatial continuity and intermediate temporal continuity, but did not survive when temporal continuity was further decreased. The species with persistent seeds and long distance dispersal had the highest survival percentages compared to the other model species for each landscape (figure 6.4D).

$T(ext)$ was determined for simulations in which the metapopulations in one or more of the runs went extinct within 250 years (figure 6.5). Decrease of spatial continuity and decrease of temporal continuity both decreased $T(ext)$ for the four model species. $T(ext)$ was shortest for the species with a transient seed bank and short distance dispersal (figure 6.5A).
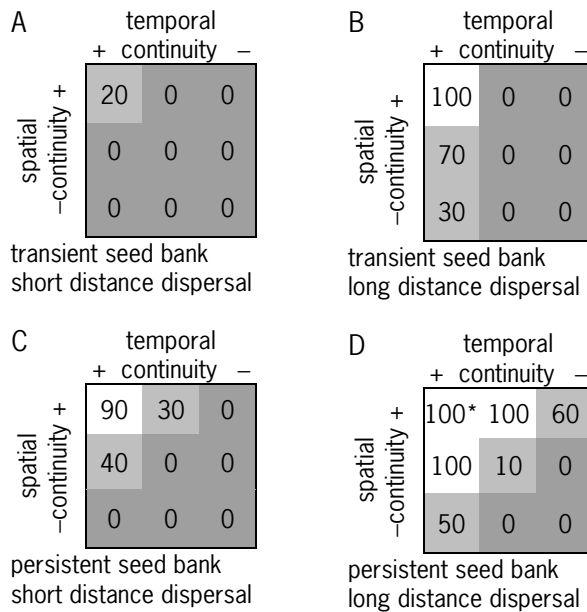

Figure 6.4 Results of simulation experiments: % of runs in which the metapopulation survived up to 250 years (10 runs per experiment, except *: 2 runs).
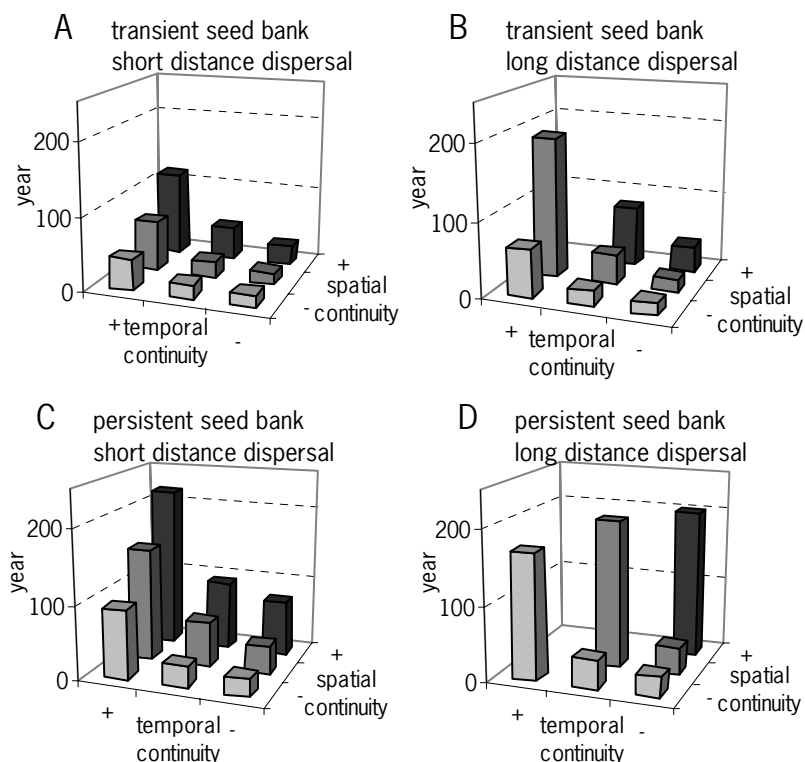
Figure 6.5 Median time to extinction,T(ext), for the four model species in runs that led to extinction within 250 years for different landscape parameters (see table 6.3).

The metapopulations persisted for a longer time when either the seed bank persistence or the dispersal distance was increased (figure 6.5B,C). Again, species with persistent seeds and long distance dispersal had the longest *T(ext)*.

       T(ext) was analyzed with analysis of variance in Genstat 5.4.2. (Lawes Agricultural Trust 2001). The Genstat procedure 'CENSOR' was used to estimate the missing values of *T(ext)* in runs in which the metapopulations survived longer than 250 years (Taylor 1973). The degrees of freedom of the Residual decreased because of the estimation of missing values. Table 6.5 gives the analysis of variance for the effect of temporal and spatial continuity and their interactions. The effects of temporal continuity and spatial continuity on *T(ext)* were statistically highly significant for all model species (p < 0.001, table 6.5). The effect of temporal continuity was much stronger than the effect of spatial continuity for species with transient seeds. For species with persistent seeds and long distance dispersal the effect of spatial continuity was stronger than the effect of temporal continuity.

Table 6.5 Analysis of variance of simulation results, dependent variables are *T(ext)* = extinction time metapopulation, *Npop* = mean number of local populations in final 50 years of simulations. *Npop* was only analyzed for model species with persistent seed bank and long distance dispersal, because the other model species had too many zeros.

source	T(ext)				Npop			
	df	S.S.	F-value	p	df	S.S	F-value	p
transien seed bank, short distance dispersal								
temporal continuity ($P_{uf} + P_{fu}$)	2	30.55	63.4	***	--			
spatial continuity (P_{uf}/P_{fu})	2	9.76	20.9	***				
temporal × spatial continuity	4	0.72	0.77	***				
Residual	80.7	18.93						
transient seed bank, long distance dispersal								
temporal continuity ($P_{uf} + P_{fu}$)	2	115.7	383.0	***	--			
spatial continuity (P_{uf}/P_{fu})	2	29.4	97.4	***				
temporal × spatial continuity	4	4.3	7.16	***				
Residual	68.5	12.2						
persistent seed bank, short distance dispersal								
temporal continuity ($P_{uf} + P_{fu}$)	2	40.5	101.6	***	--			
spatial continuity (P_{uf}/P_{fu})	2	32.7	82.1	***				
temporal × spatial continuity	4	0.2	0.3	n.s.				
Residual	72.9	16.13						
persistent seed bank, long distance dispersal								
temporal continuity ($P_{uf} + P_{fu}$)	2	74.97	210.6	***	2	115.5	544.7	***
spatial continuity (P_{uf}/P_{fu})	2	89.79	252.2	***	2	71.8	338.6	***
temporal × spatial continuity	4	13.94	19.6	***	1	12.6	118.9	***
Residual	50.7	14.41			28	3.0		

Npop, the number of local populations, was determined for simulations in which the metapopulations survived up to 250 years in at least one run (figure 6.6). The model species with transient seed banks and short distance dispersal had fewest local populations (figure 6.6A). Both a persistent seed bank and long distance dispersal increased the number of local populations (figure 6.6B,C). The species with a persistent seed bank and long distance dispersal had highest *Npop* compared to the other model species. For the species with a persistent seed bank and long distance dispersal an analysis of variance was used to test the effect of temporal and spatial continuity on *Npop*. (table 6.5). Temporal and spatial continuity and their interaction were highly significant (p < 0.001). For the other model species this analysis was omitted, because very few simulations had local populations left at the end of the runs (figures 6.4, 6.5, 6.6).
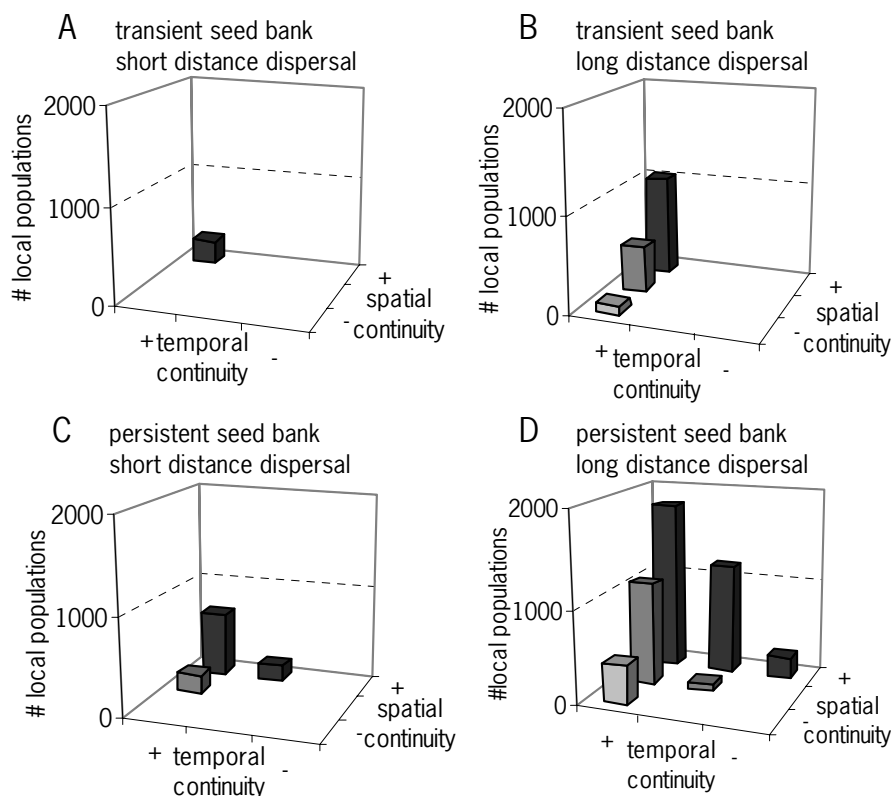
Figure 6.6 Mean number of local plant populations, Npop, for the four model species in the final 50 years for runs that survived up to 250 years for different landscape parameters (see table 6.3).

Local colonization and extinction, comparison with field data

In figure 6.7 we show the colonization and extinction rates of local populations for landscape - species combinations in the model. Only results of the four most extreme landscapes are shown, but the rates in the intermediate landscapes are intermediate for those of the extreme landscapes. Colonization rates as well as extinction rates increased with decreasing temporal continuity. Although less obvious, they also increased with decreasing spatial continuity. Extinction rates increased more than colonization rates with decreasing spatial or temporal continuity. The resulting difference between colonization and extinction was highest for the two species with transient seed banks in landscapes with the lowest temporal continuity.
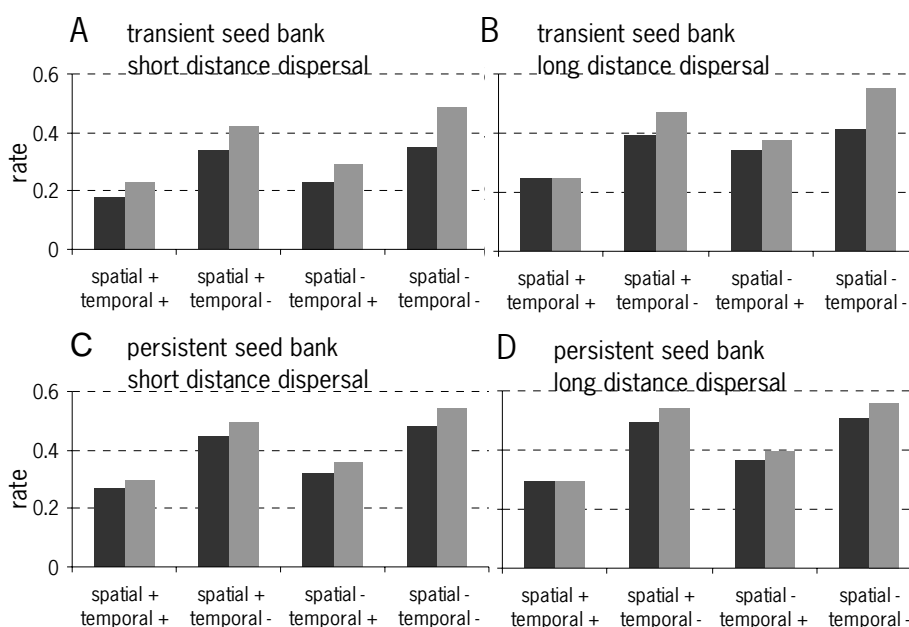
Figure 6.7 Colonization (■) and extinction (■) rates according to the model. Model values are based on the colonization rates in the final 50 years of the model runs for the four model species. The titles of the x-axes of the model graphs indicate spatial and temporal continuity of the landscapes (see table 6.3)

The model species with a transient seed bank and short distance dispersal had the lowest colonization and extinction rates and also the largest differences between the colonization and extinction rates (figure 6.7A). The colonization rates and the extinction rates increased when species have long distance dispersal, a persistent seed bank, or both. The differences between the colonization and extinction rates in the different simulation experiments were smaller for those three model species than for species with transient seed banks and short distance dispersal. Model species with persistent seed banks (figure 6.7C,D) have higher colonization rates than species with transient seed banks (figure 6.7A,B). These differences are most obvious in the landscapes with low temporal continuity. Species with long distance dispersal (figure 6.7B,D) also have higher colonization rates than species with short distance dispersal (figure 6.7A,C), especially when they have a transient seed bank.

The landscape in which the colonization and extinction rates were observed in the field was assumed to be of intermediate spatial continuity but

the dynamics of the landscape were not exactly known (see parameterization section). The model species in landscapes with intermediate temporal continuity and intermediate spatial continuity hardly survived, we therefore assume that a landscape with intermediate spatial continuity and high temporal continuity may be a better approximation of the field situation. The colonization and extinction rates of different model species were of the same order as the rates observed in the field (figure 6.8). However, the colonization and extinction rates observed in the field did vary considerably within dispersal and seed bank strategies and did not relate to the strategies of the species.
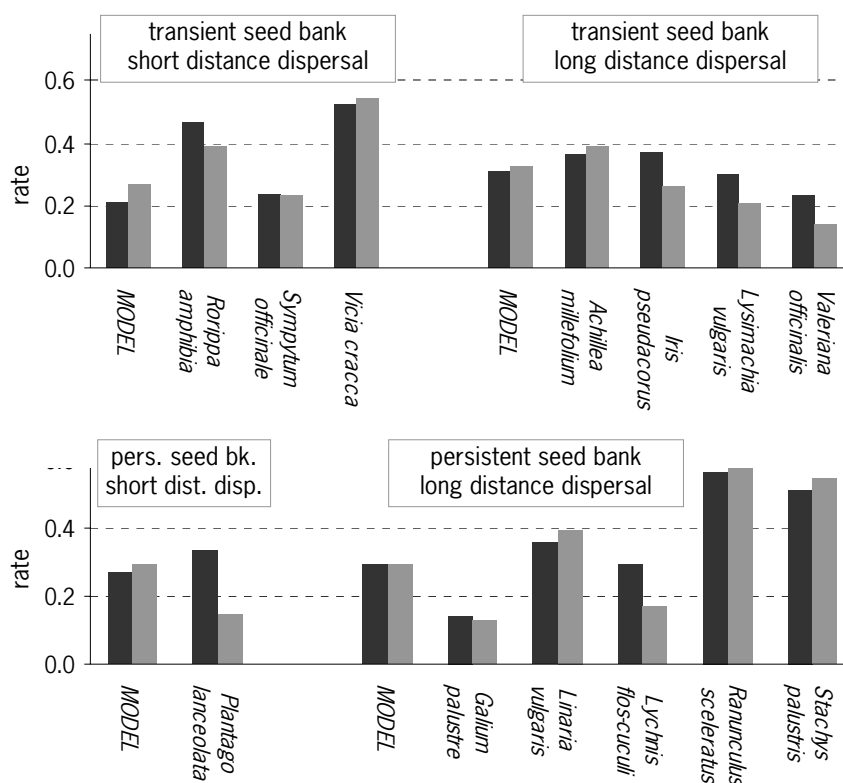

Figure 6.8 Colonization (■) and extinction (▇) rates according to the model and observed in the field in 1998-2000 for thirteen grassland species (chapter 4) representing similar seed bank and dispersal strategies as the four model species. Values are based on the colonization rates in the final 50 years of the model runs for the four model species in landscapes with high temporal continuity and intermediate spatial continuity.

The distribution of colonization events over the shortest distances to potential seed sources is given in figure 6.9. The number of colonization events exponentially decreased with distance, both in the model and in the field data and for all species strategies. Model species with either a persistent seed bank or long distance dispersal (or both) had colonization events at distances over 200 m. In the field data (not all data shown), most species had colonization events over 200 m.

Figure 6.10 depicts the distribution of extinction and persistence over the distances to nearest conspecific local populations for both model and field. Most local populations were located close to other local populations, therefore both distributions approach a negative exponential distribution. The local populations that persisted from one year to the next were found closer to other local populations than the local populations that went extinct. Isolated local populations more often became extinct than persisted. Comparable patterns were found in the field data. Differences between the strategies were not reflected in the model results or the field data. The high peaks of persistence and extinctions at the larger distances for model species with transient seed banks and short distance dispersal were an artefact of the simulations. These isolated local populations still reflect the distribution of seeds at the start of the simulation runs. At the start isolated local populations could arise for all model species. We assume that the other species were better able to colonize other patches, also adjacent ones, thus resulting in low numbers of isolated local populations.

Discussion

Spatial and temporal continuity

The survival, number of populations and time to extinction all decreased with decreasing spatial and temporal continuity for all four model species. The effect of temporal continuity on the survival statistics was larger than the effect of spatial continuity for three out of the four model species. Fahrig (1992) studied the effect of spatial continuity on survival of species (an organism without a seed bank) in a spatially explicit model by changing the isolation of patches while keeping the amount of suitable habitat constant. She found an even more pronounced effect of temporal scales of the landscape compared to spatial scales on the survival of in her model. A change of spatial continuity in
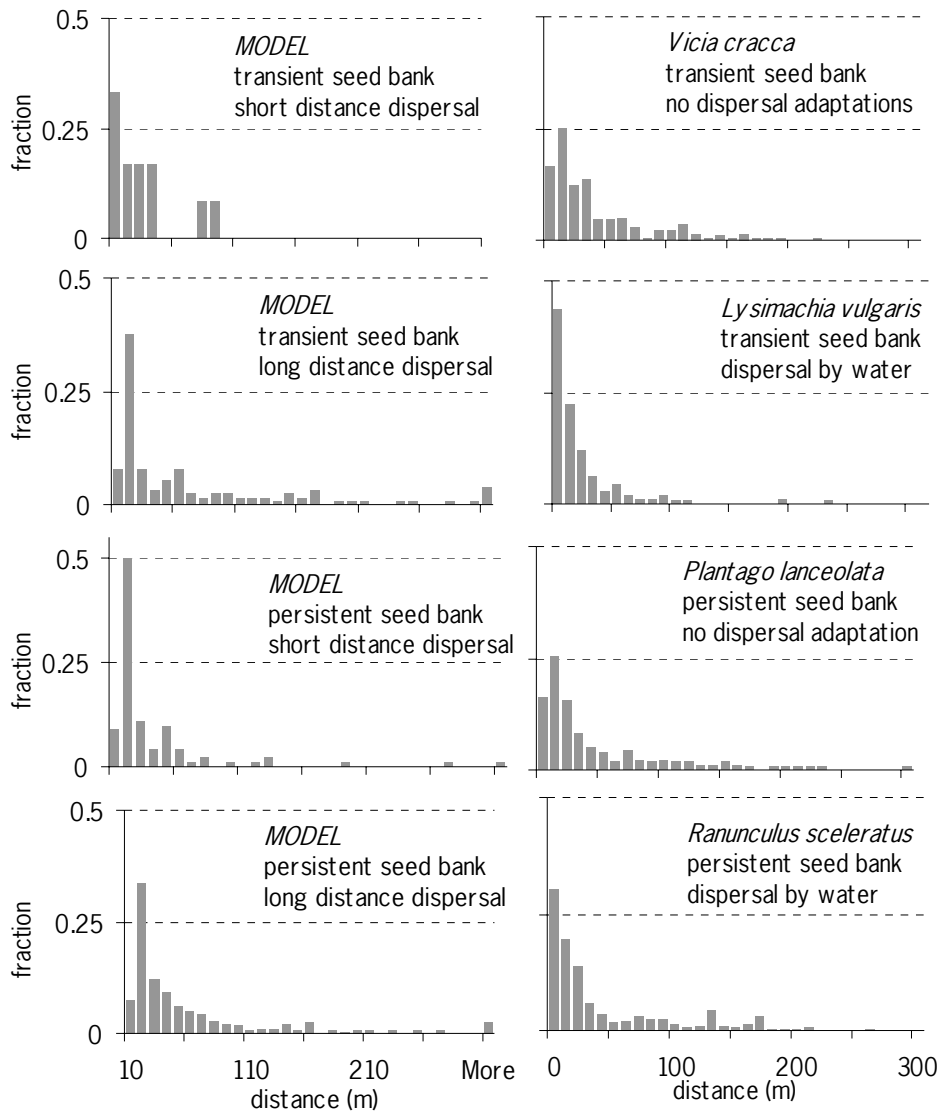
Figure 6.9 Fraction of colonizations (■) in year *t* related to distance to nearest populations in year *t-1* for four model species in the simulation study and for four species representing similar strategies in a field study. The fractions add up to 1. Model: years 11-15 in landscape with intermediate spatial continuity and high temporal continuity, field: based on field study in 1998-2000 (chapter 4).
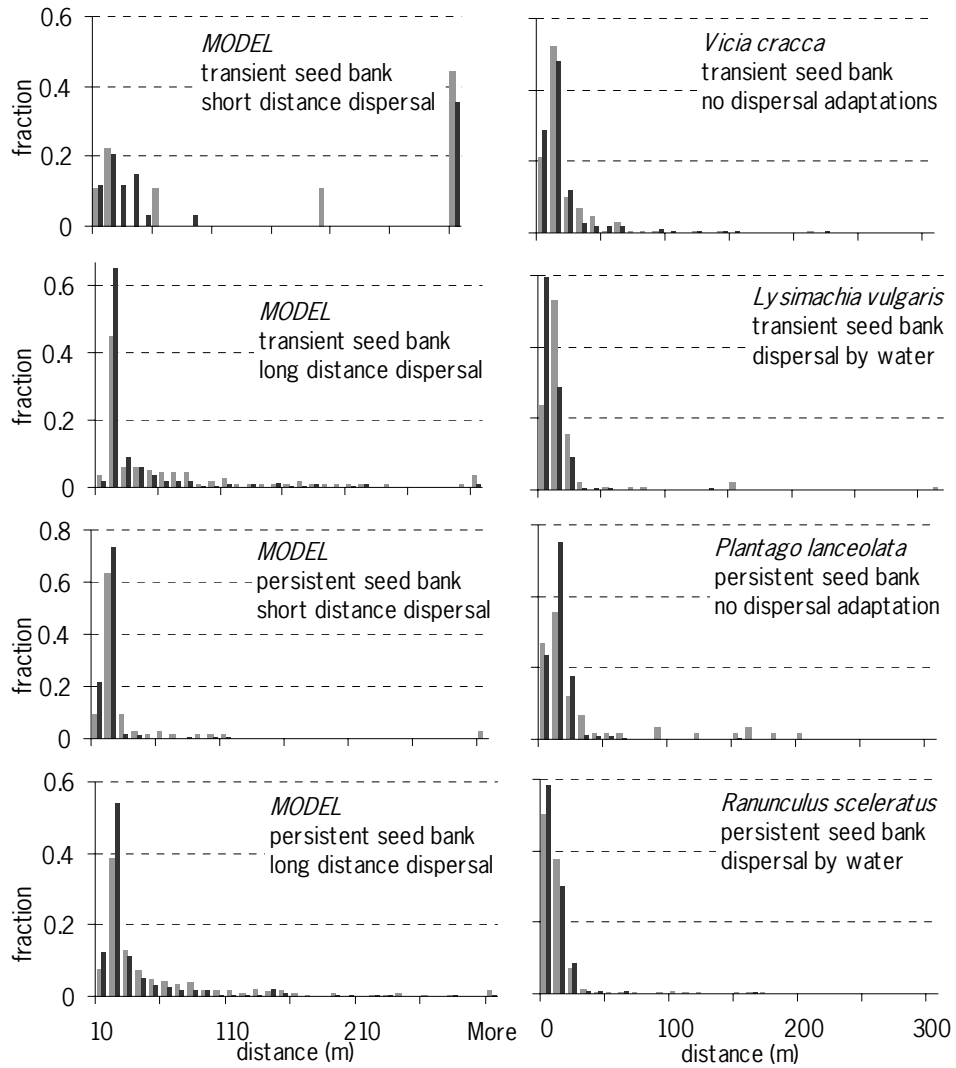
Figure 6.10 Fraction of extinct (▨) and persisting populations (■) in year *t* related to distance to nearest populations in year *t-1* for four model species in the simulation study and for four species representing similar strategies in a field study. The extinction fractions add up to 1 and the persistence fractions add up to 1. Model: years 11-15 in landscape with intermediate spatial continuity and high temporal continuity, field: based on field study in 1998-2000 (chapter 4).

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our study is a combination of both a change of the amount of habitat and a change of the distances between suitable habitats. This may explain the relative larger effect of spatial continuity in our study compared to the study of Fahrig (1992).

The effect of temporal and spatial continuity on the survival of the model species confirmed our hypothesis. Species with transient seed banks were more affected by a decrease of temporal continuity than species with persistent seed banks. Only model species with a persistent seed bank could survive until the end of the simulation runs in landscapes with intermediate or low temporal continuity. The strategy of persistent seeds thus appears to be a viable strategy for plants in dynamic landscapes. Species with short distance dispersal were more affected by a decrease of spatial continuity than species with long distance dispersal. However, a persistent seed bank also enabled species to survive in landscapes with lower spatial continuity. We assume more isolated local populations in landscapes with lower spatial continuity, so a persistent seed bank may indeed buffer the extinction risk of isolated populations.

Colonization and extinction

Colonization and extinction rates increased with increasing landscape dynamics. Extinction simply results from landscape dynamics as the probability that suitable habitat becomes unsuitable increases with increasing landscape dynamics. Increased colonization rates can be explained by an increased rate of 'birth' of new habitat when landscape dynamics increase. Similar results were found in other model studies of species with dispersal limitation in dynamic landscapes (Keymer *et al.* 2000). The probability that new habitat arises close to existing habitat increases with increasing landscape dynamics, thus isolated patches can become connected through space-time in dynamic landscapes. However, we expect that the positive effect of landscape dynamics on the colonization rates will be limited to a certain treshold value of habitat dynamics. Above this treshold value, the colonization rates will not increase anymore or even decrease. Extinction rates increase linearly with landscape dynamics, thus leading to lower survival rates in landscapes with higher dynamics. Small differences between colonization and extinction rates are a significant indication for the long term survival of the model species.

The colonization distances of species with long distance dispersal, a persistent seed bank or both, do not differ much from each other. The colonization events at large distances from source populations of species with

persistent seeds and short distance dispersal, must have originated from the seed bank. Caution is needed in field studies that try to infer dispersal distance from a comparison between former and present distribution patterns of plant species. Researchers should take notion of both the dispersal and seed bank strategies of the species studied.

The spatial patterns of the local colonizations and extinctions confirm the expected positive effect of neighbouring local populations on the survival of local populations. Most of the colonization events occur at distances within 30 m from potential source populations, both in the model and the field data. However, colonization events at distances over 150 m are no exception. The spatial distribution of the local populations, both in the model and in the field, is clustered. Local populations that persist from one year to the next were located closer to other local populations than populations that became extinct. This did not differ much between the strategies. These observations may be interpreted as evidence for the rescue effect by dispersing seeds.

It is striking that differences between the colonization strategies only appeared in the simulations at the long term. At the short term, differences between the colonization strategies were not apparent, neither in the field, nor in the simulation model. Whether or not the species will survive on the long term is hard to conclude from the field data. The data are based on only three years of observation and annual variation was quite high. This emphasizes the value of using model studies for the analysis of the long term persistence of plant populations in fragmented and dynamic landscapes. Long term model studies can be validated by comparison of areas with different spatial continuity of habitat and different histories. A comparison of the number of grassland species in agricultural areas of 1 km^2 with varying amounts of ditches (northern part of the Netherlands) revealed that areas with few ditches had fewer species present. Species with limited dispersal ability were found less often in areas with few ditches, which caused the lower species diversity in areas with relatively low spatial continuity of ditches (Schipperijn unpubl.).

The colonization and extinction rates and their distribution over distances to nearest conspecific local populations according to the model are of the same order as those observed in the field (chapter 4). Although not the total range of landscapes that were studied in the model could be compared with field data, the similarity of the results of the model and field data can be considered as a (partial) validation of the model.

Sensitivity to parameter estimations

The response of the species to the spatial and temporal continuity of the landscape in the present study might have been different when different landscape or species parameter values were used. We argued (see parameterization section) that the chosen landscape values were realistic estimations of the spatial and temporal continuity observed in the field. No other landscape parameter values were tested in the present study. The sensitivity of the model for the plant parameters was not tested. This is affordable because the aim of the study was to compare the effect of spatial and temporal continuity of landscapes on species that differed in colonization strategies. The other plant parameters were kept constant and were based on existing data (see parameterization section). The effect of two values for seed bank persistence combined with two values for dispersal distance were tested in the present study. More extreme values of seed bank and dispersal parameters might result in a more extreme effect of either spatial or temporal continuity.

Effects of simplifications of the real world

Of course a model does not equal reality. Several simplifications had to be made in this modelling study. For example: succession of the vegetation was not simulated; the suitability of the habitat in the ditches immediately followed the dynamics of the fields. In reality it takes some time before a new habitat patch is suitable for many perennial plant species (Kleijn *et al.* 2001). The period of unsuitability will thus be longer than assumed in the model. This means that the effect of landscape dynamics might have been underestimated and the number of local populations overestimated. Another important simplifacation is that perennial plants immediately respond to the decrease of habitat quality in our model. In reality perennial plants often show a delayed response to the deterioration of habitat (Grashof-Bokdam & Geertsema 1998). This simplication might have resulted in an underestimation of the number of populations. We do not know whether the effects of succession and delayed response balance each other in our model. A third simplification is that vegetative reproduction was not included in the model, whereas it can be a source of spatial expansion of plants. Vegetative reproduction operates on small spatial scales and is important for the local survival but not for the colonization of isolated patches.

chapter 7

Spatial and temporal habitat continuity increase effectivity of agri-environmental schemes

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Abstract

The botanical diversity of intensively managed farmland depends on networks of semi-natural landscape elements (Corbit *et al.* 1999; Opdam *et al.* 2000). Farmers may close contracts with the government for management activities that are assumed to protect biodiversity (Anonymous 1998, Potter 1998). However, the expected benefit to botanical diversity could not be shown in a pair-wise comparison with control fields (Kleijn *et al.* 2001). Likely causes that were suggested are: reduced fertilisation is inadequate for restoration of suitable habitat, and dispersal limitations hamper colonization (Kleijn *et al.* 2001). We add another possible cause: contract periods are too short to allow plant populations to respond to increased habitat quality (chapter 2). Here we explore which of these three causes has the strongest effect on the effectiveness of management activities using a metapopulation model for plant species in field margins in arable landscapes (chapter 6). This model was validated with field data (chapter 4; chapter 6). We compared the effectiveness of three options to change the conditions in management agreements: improving the quality of field margins, doubling the length of the contracts, and clustering the contracts in space. We show that, for four contrasting plant types, improving habitat quality with current contract periods was not effective, but longer contracts increase the effectiveness of the management contracts. The effectiveness of conservation contracts with farmers is best improved by spatial clustering.

Introduction

Landscape elements that are not used for food production are important habitat for wild plants in agricultural landscapes (Melman *et al.* 1988; Corbit *et al.* 1999; Opdam *et al.* 2000). Potentially, the landscape elements constitute a network of habitat through the landscape, but nowadays this network is highly fragmented (Merriam 1988; Opdam 1990; Hobbs & Saunders 1991; Fry 1994). An additional cause of the disappearance of plant species is the impact of agricultural activities on the adjacent fields (e.g. herbicide and fertilizer drift) (Van Strien *et al.* 1989; Kleijn & Verbeek 2000).

The survival probability of many plant species was expected to increase by adjusting management and by bufffering the deleterious impact of adjacent

land use (Moonen & Marshall 2001). Agri-environmental schemes have been developed based on this hypothesis (Anonymous 1998; Potter 1998; Kleijn *et al.* 2001). Farmers are contracted to adjust management on fields or field edges in such a way that better conditions are developed for a higher diversity of target species groups. In the Netherlands the current policy regarding management agreements resulted in random distribution of landscape elements under contract over the landscape. The contract periods are limited (minimum five years, usually six years in the Netherlands) (Anonymous 1995). When contracts are not extended, the result is a dynamic pattern of landscape elements with management agreements.

Recently, the biodiversity of plants, insects and birds for landscape elements with or without a management agreement was compared (Kleijn *et al.* 2001). Virtually no differences between the diversity of plants in field edges with or without a management contract were found. Other studies showed that not only habitat quality but also the spatial arrangement and dynamics of the habitat influences distribution patterns and survival probabilities of plant species in the landscape (chapter 2; Opdam 1990; Ouborg 1993; Grashof-Bokdam & Geertsema 1998). Spatially isolated habitat patches have lower colonization and occupation probabilities than patches located close to other habitat patches (chapter 4; Ouborg 1993; Marshall & Arnold 1995; Quintana-Ascencio & Menges 1996; Grashof-Bokdam & Geertsema 1998). Isolated populations also have higher extinction probabilities (chapter 4; Ouborg 1993; Quintana-Ascencio & Menges 1996). Habitat dynamics result in higher extinction probabilities for local populations, but if recolonizations balance local extinctions, a species can survive (chapter 2; Opdam 1990). However, many plant species have limited colonization ability, determined by the dispersal capacity and the longevity of soil seed bank (chapter 2; Bakker & Berendse 1999).

Here, we explore three potential solutions for increasing the nature value of farmers' contracts with a spatially explicit metapopulation model: spatial clustering, increasing the contract time and increasing the habitat quality of landscape elements. Such an analysis is not possible using existing monitoring data, because the samples do not include enough variation in conditions. Field experiments would need a long time before conclusive results could be obtained, not to mention the excessive amount of money and labour to carry out a landscape scale experiment over such a long time. Therefore an

experiment was conducted in a virtual landscape using the simulation model to evaluate the response of plant populations to changing the contract conditions.

We developed a spatially explicit simulation model of population dynamics of plants in fragmented and dynamic landscapes with habitat limited to a network of ditches. The model integrates the knowledge on the seed bank and dispersal characteristics at the landscape level (chapter 6). Dispersal and seed bank characteristics are key factors in the response of populations (chapter 2), therefore we used four model plant species that represent four combinations of dispersal and seed bank strategies: persistent (seed bank viable for five years) or transient seed bank (seed bank viable for one year) combined with short distance (mean dispersal distance 50 m) or long distance (mean dispersal distance 250 m) seed dispersal. The survival of the model plant species in three alternative scenarios was compared with the survival in a 'control' situation (table 7.1, figure 7.1). This control consists of conventional management agreements randomly distributed over the landscape with an average contract time of five years. The three scenarios are:

- scenario 1: 'high quality': increasing the habitat quality of the ditches by increased farming restrictions;
- scenario 2: 'long contract': increasing the contract time of conventional agreements from 5 to 10 years;
- scenario 3: 'cluster': clustering the conventional agreements in 22% of the landscape.

Table 7.1. Parameters that describe the scenarios. Parameter values that discriminate between scenarios are printed bold.

scenario	carrying capacity of management ditches	expected contract time (years)	part of landscape to which agreements are limited
'control'	10	5	100%
1 'high quality'	**14**	5	100%
2 'long contract'	10	**10**	100%
3 'cluster'	10	5	**22%**

Methods

Description of the model

A single-species spatially explicit stochastic simulation model was used for the present study (chapter 6). The model has been validated with field data of species in ditch banks along arable fields (chapter 4; chapter 6). The population dynamics of plants are simulated in a dynamic landscape. The model landscape consists of arable fields (total area approximately 7 km^2) and a network of ditches (total length approximately 45 km). The habitat of the plants is limited to the network of ditches (figure 7.1). The habitat quality of the ditches is determined in the landscape part of the model, which is a stochastic two-compartment model. The quality state of the two adjacent fields determines the habitat quality of the ditches. This results in three possible states for the suitability of the ditches. Because the quality of the fields is dynamic, the habitat quality of the ditches is also dynamic. Unsuitable, marginal and suitable ditches constitute the network of potential habitat for the plant species.

A stage-structured model for the plants and an age-structured model for the seed bank describe the population dynamics. Local populations can consist of a seed bank, seedlings and adult plants. The number of local populations in a ditch is limited by the minimum distance that is allowed between the populations (10 m). The number of adult plants in a local population is limited by the carrying capacity. The local populations are linked in space by
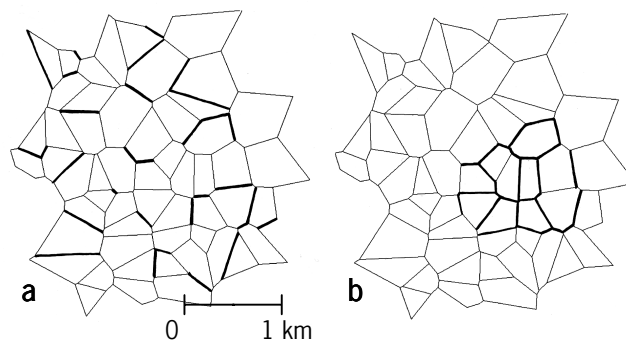

Figure 7.1 Possible location of the landscape elements with (bold lines) and without management agreements (normal lines) in one year. **a**, random allocation of management agreements in the landscape. **b**, clustered allocation management agreements

dispersing seeds. Dispersal of seeds is limited to the ditch network; seeds perform a self-avoiding random walk through the network.

The effect of the different scenarios was determined for four model species. The species differ in colonization strategy which is determined by the dispersal distance (mean of a negative exponential distribution, short = 50 m, long = 250 m) and the maximum age of the soil seed bank (transient = 1 year, persistent = 5 years). The different strategies were used in the simulations because the effects of landscape structure and dynamics depend on the colonization strategies of species (chapter 6).

The parameters that determined the population growth rate depended on the habitat suitability of the ditches. The local population growth rates of species with transient and persistent seed banks were (in absence of density dependence) 0.55 and 0.66 respectively in marginal habitat, and 1.17 and 1.28 respectively in suitable habitat and in ditches with a management agreement. The parameters for dispersal distance and seed bank persistence varied between the model species, but the demographic parameters remained constant.

The model landscape consisted of 180 ditches of which 32 were randomly assigned to management contracts, the 'management ditches'. The quality of these ditches is higher than the quality of suitable ditches, quantified by local population carrying capacity. The carrying capacity of sites is 10 adult plants in management ditches, 6 in suitable, 2 in marginal and 0 in unsuitable ditches. Each year the probability that a contract ended was 0.2, resulting in an average contract time of 5 years. At the same time new contracts were started, keeping the average amount of management ditches, suitable, marginal and unsuitable ditches constant.

Description of the scenarios

The parameters used for the control and the three scenarios are given in table 7.1. In the high quality scenario, the quality of the management agreements was increased by changing the carrying capacity of local populations to 14. In the long contract scenario, the probability of ending a contract was set to 0.1 (expected contract time = 10 years). The area to which the management contracts were limited determined the degree of clustering. In the control, the high quality and long contract scenarios this implied the total landscape (180 ditches). In the clustered scenario, this implied a selection of 22% of the landscape, consisting of 40 ditches. Within this network the 32 ditches with an agreement were randomly distributed (figure 7.1). The spatial distribution of

the management agreements is dynamic and the expected life-span of the agreements is five years, similar to the control and high quality scenario. The expected ditch length with unsuitable, marginal and suitable habitat and with management agreements remained constant over the simulations. The expected length of unsuitable ditches was 23.9 km, marginal ditches 13.2 km, suitable ditches 2.2 km and ditches with management agreements 6.1 km.

Simulations were run 20 times for each of the four model species in the control and the three scenarios. At the start of the runs, in 50% of the ditches 500 seeds were distributed per ditch. The runs lasted 25 years and the number of sites in the ditch network that was occupied by local populations in year 25 was used to quantify the effect of the four scenarios. The number of occupied sites was averaged for each species - scenario combination. The mean numbers of occupied sites in the four scenarios were compared (within each model species) with one-way Anova.

Results and discussion

The results for the four model species are shown in figure 7.2. We used the number of local populations in year 25 of the simulations (average for 20 runs) as a measure of effectiveness of the management scenarios.

It was expected that the increased carrying capacity in the high quality scenario would increase the size of local populations and therefore increase the persistence of the local populations (Fischer & Stöcklin 1997). A higher local persistence would result in higher numbers of occupied sites. However, this was not observed for any of the species: the number of occupied sites in the high quality scenario equaled the number of occupied sites in the control for each species (one-way Anova, $p > 0.05$). We explain this by assuming that the life span of the contracts is too short for local populations to profit from the higher carrying capacity. The average contract life-span is five years, in which period the larger local populations cannot build up. Indeed the size of the local populations in the 'high quality' scenario equaled the size of local populations in the control (figure 7.3). The number of plants in a local population appeared to be higher than the carrying capacity in some simulations, because the number of plants includes both adult plants and seedlings. The number of seedlings was not limited by a maximum carrying capacity in the model.
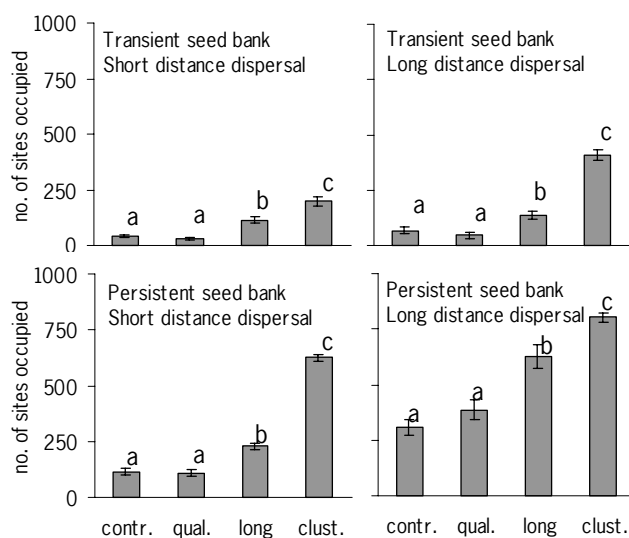
Figure 7.2 Number of sites in a ditch network that were occupied by local populations (mean ± s.e., n = 20) in year 25 of simulation runs in control and three scenarios for management agreements. Scenarios were run for four model species with different seedbank and dispersal characteristics. 'contr.' = control, 'qual.' = high quality scenario, 'long' = long contract scenario, 'clust.' = clustered scenario. Statistically significant differences (one-way Anova, p < 0.05) between the control and the scenarios are indicated by different characters.

Increasing the contract time from five to ten years had a statistically significant effect on the number of occupied sites in the habitat network (one-way Anova, p < 0.05). The number of occupied sites increased almost three times (species with a transient seed bank and long distance dispersal) or about two times (other species) compared to the control. Apparently an expected contract time of ten years enabled species to build up larger local populations (figure 7.3) and successfully colonize more sites in the habitat network (figure 7.2).

The effect of changing the spatial arrangement of the conventional management agreements (expected contract life-span of five years) was even stronger than doubling the contract time. The number of occupied sites of each model species was statistically significantly higher in the clustered scenario than in the control (one-way Anova, p < 0.05) (figure 7.2). The number of occupied sites increased more than twice (species with a persistent seed bank and long distance dispersal) to more than five times (other species). The size of the local populations was higher for species with persistent seed banks
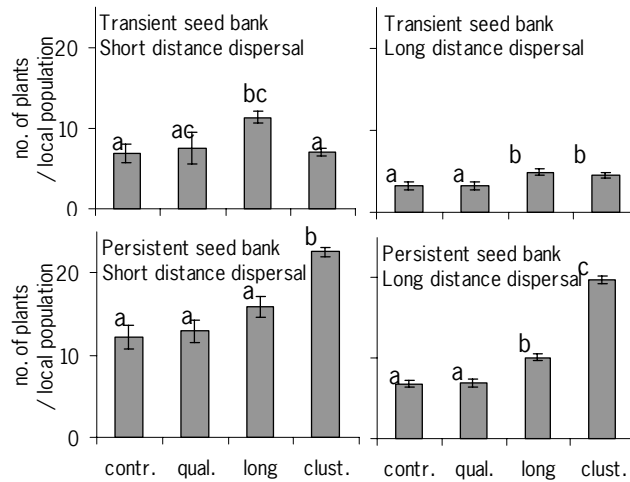
Figure 7.3 Size of local populations: number of plants per local population (mean ± s.e.) in year 25 of simulation runs in control and three scenarios for management agreements. Scenarios were run for four model species with different seedbank and dispersal characteristics. 'contr.' = control, 'qual.' = high quality scenario, 'long' = long contract scenario, 'clust.' = clustered scenario. Statistically significant differences (one-way Anova, $p < 0.05$) between the control and the scenarios are indicated by different characters.

compared to the control, but not for species with transient seed banks (figure 7.3). Apparently the increased number of local populations in this scenario was not always caused by larger local populations. Locating new management ditches close to existing management ditches is effective, because it increased the colonization probabilities from existing local populations, thus causing a higher number of local populations.

The effect of the clustering of management agreements was overwhelming, but the question is whether this effect depended on the dynamics of the spatial distribution of the management agreements. Therefore we wanted to know what the absolute effect of the spatial arrangement was. We compared two additional scenarios with random and clustered allocation of management agreements. In these aditional simulations, the locations of the management agreements were fixed and no contract terminated during the simulations. The contracts started in year one and we compared the number of local populations in the landscape in these two 'stable' scenarios in the fifth and the tenth year (20 runs per scenario for each species). These simulations also resulted in higher numbers of local populations in the landscapes of the

clustered scenario than in the random scenario, in both the fifth and the tenth year after the start of the management agreements for each model species (one-way Anova, $p < 0.05$, n = 20, data not shown). The conclusion concerning the positive effect of clustering on the survival of species therefore holds also for situations without dynamics in the distribution of the management agreements.

We conclude that the effectiveness of management agreements is best increased by concentration in one part of the landscape area. This is due to the limited colonization ability of plant species. The limited colonization ability of the species also accounts for the smaller, but still statistically significant effect of doubling the expected contract time. In habitat with a longer life span, the species are able to colonize more sites with larger populations (Fahrig 1992).

These conclusions are based on the findings for the survival of single species in a landscape. Processes that describe the interaction between species such as competition may influence the resulting species richness (Grubb 1977; Schipper 2000). However, species first have to colonize habitat patches (by seed dispersal or by a viable seed bank) before the interaction between species becomes relevant. Our results suggest that clustering of habitat will favour the development of more species-rich vegetations, because colonization limitation causes the lack of many target species in restored habitats.

The implication of these findings in management agreements calls for a landscape approach. Contracts should not apply to individual fields or field edges but to landscapes. Compared to contracting farmers individually, contracts with groups of farmers will be more effective, for instance with farmers working together in so-called nature co-operations. These farmer groups not only aim at improving the biodiversity values but also at improving other 'ecosystem services', such as cultural historical and esthetical values, water management, and recreation values. These functions also profit more from a landscape approach than an approach at the individual field or farm level.

chapter 8

Synthesis and perspectives

The research described in this thesis originated from the concern about the declining botanical diversity in modern agricultural landscapes. Measures that aimed at the development of environmental conditions that would protect the botanical diversity were not always successful. It was hypothesized that this lack of success and the decline of populations originate from the fragmented and dynamic distribution of suitable habitat in the landscape and the limited colonization ability of many of the target species. The limited colonization ability was expected to cause the decline of many species, as colonization rates could not balance local extinctions.

The hypothesis was tested in empirical and modelling studies. The effect of fragmentation and dynamics of the landscape was studied on the level of individual plants and seeds (chapter 5), local populations (chapters 3, 4, 6 and 7) and metapopulations (chapters 6 and 7).

Effect of landscape characteristics: fragmentation

Fragmentation of habitat can be quantified in different ways. Commonly used measures for fragmentation of plant habitat are area of individual habitat patches (Quintana-Ascencio & Menges 1996; Grashof 1997), total area of suitable habitat in (surrounding) landscapes (Fahrig 1992; Ouborg 1993; Grashof-Bokdam 1997), distance to nearest conspecific populations (Antonovics *et al.* 1994; Grashof & Geertsema 1998) or connectivity based on area of other habitat patches in the landscape, distance to the other patches and dispersal ability of the species (Quintana-Ascencio & Menges 1996). In the field studies I quantified fragmentation by distance to nearest conspecific populations, as this measure was expected to relate very well to the probability of a population or a patch to receive dispersed seeds. In the modelling study, fragmentation was quantified by the total length of suitable, marginal and unsuitable ditches. The suitable and marginal ditches were distributed randomly over the landscape. A decrease of the amount of suitable ditches and an increase of unsuitable ditches resulted therefore not only in less suitable habitat but also in larger distances between suitable habitats. Larger distances between suitable habitats also determined the fragmentation in the scenario studies: the distances between ditches that are managed for increased botanical diversity was larger when these managed ditches were randomly distributed in

the model landscape than when the distribution of the managed ditches was clustered in one part of the landscape.

The fragmentation measures used all had the expected effect on the plant species. In chapter 3, an increased occupation probability was observed with decreased distance to conspecific occupied patches. The colonization and persistence probabilities were higher and extinction probabilities lower at smaller distances to conspecific local populations in the field study and the modelling study (chapters 4 and 6). The species that were able to colonize the dispersal plots as described in chapter 5 often were also present within 5 m of the plots, especially the species without adaptations for long distance dispersal. In the modelling study the survival probabilities of the model species decreased with increasing fragmentation. The overwhelming effect of clustering the management agreements on the number of local populations in the scenario study also confirms the hypothesis of the negative effect of habitat fragmentation on the survival of plant populations (chapter 7).

In conclusion, the study of fragmentation shows that measures that aim at the protection of botanical diversity of agricultural landscapes will be more effective when these measures are concentrated in one part of the landscape, instead of randomly distributed in the landscape.

Effect of landscape characteristics: dynamics

In literature, habitat dynamics in landscape studies are quantified in different ways, e.g. by the intensity and predictability of disturbance (Grime & Hillier 1992), the habitat life-span (Fahrig 1992), the frequency of disturbance (Valverde & Silvertown 1997; Wu & Levin 1994), time since disturbance of individual patches (Quintana-Ascencio & Menges 1996), or the age of habitat (Grashof-Bokdam & Geertsema 1998). In this thesis, habitat dynamics indicated a change of habitat quality, which implied an improvement or a decline of habitat quality. Habitat dynamics in the study area of the empirical studies in this thesis were described by the age of the ditches (chapters 3 and 5). The young ditches were created in 1994-1996. From that time on, the habitat quality of the patches in the young ditches could change from unsuitable to marginal or suitable. In the model and scenario studies, the probability that the suitability of habitat quality changed, determined habitat dynamics (chapters 6 and 7).

Habitat dynamics had the expected effect on the distribution patterns for most of the species (chapter 3). The occupation probability of most of the species was higher in old, stable ditches than in young ditches. The old ditches had not experienced major disturbances for a few decades, resulting in a more stable environment as compared to the young ditches. The young ditches were created about 4 years before the field studies described in this thesis. Only a few species with persistent seeds were able to colonize young ditches, which was reflected by occupation probabilities of these species being similar in old and young ditches. However, the age of ditches was also related to habitat quality of the ditch banks, so it was not clear whether age or habitat quality was causing the differences in abundance between old and young ditches. The comparison of the seed bank of old and young ditches showed that species with short living seed banks are more abundant in the seed bank of stable, old ditches as compared to young ditches. Generally speaking, the dynamics of the ditches had a negative effect on the colonization ability of species with transient seed banks (chapter 5).

The age of the ditches in the field represents a single moment of change in the habitat quality. In the model I could study the effect of multiple changes of habitat quality: habitat patches could for example be suitable for a number of years, then be marginal for a number of years, then change to unsuitable and change to suitable again. Habitat dynamics resulted in lower survival probabilities of the species in the model and in the scenario study (lower numbers of local populations in metapopulations). The decline in survival of the metapopulations was particularly caused by an increase of the extinction probability of local populations. The colonization rates of local populations also increased with dynamics, because new habitat could appear close to existing habitat patches. The increase of colonization rates will be limited above a certain level of dynamics, but the local extinction rates continue to increase with habitat dynamics (chapter 6). The life-span of management contracts that aimed at increased botanical diversity in ditches, quantified the habitat dynamics in the scenario study. Longer contract time had a positive effect on the number of local populations in the scenario study, because a longer habitat life span enabled the plants to build up more and larger local populations (chapter 7).

In this thesis, dynamics implied large scale dynamics that destroyed large parts of the vegetation. Small scale disturbances or dynamics, which kill only small numbers of individual plants, are not studied in the thesis. These

small scale dynamics create gaps in the existing vegetation, which may favour the establishment of plants. The establishment probability of a species in a gap depends on a variety of species and gap characteristics, together defining the 'regeneration niche' (Grubb 1977).

In summary, dynamics of habitat had the expected negative effect on the distribution patterns and the survival of the plant species. In the former, I concluded that measures aiming to increase biodiversity will be more effective when these measures are clustered in the landscape. Here I conclude that the effectiveness of these measures also increases when they are applicable for more than six years (which is the minimal contract time nowadays for farmers in the Netherlands).

Effect of colonization strategy

The differences between the dispersal and seed bank strategies were less clear in the few years of observational studies than the effects of fragmentation and dynamics. Some differences were observed between the distribution patterns of species with different seed bank strategies (chapter 3). Species with persistent seed banks were more abundant in young ditches than species with a transient seed bank with either short or long distance dispersal. This indicated that a persistent seed bank is an important source of colonization after major disturbance and an adaptation to survive in dynamic landscapes. However, species with transient seeds are not favoured by large scale disturbances (chapter 5). Species with transient seeds will have to colonize by seed dispersal from other populations in the area. Because dispersal is often limited, prudence is called for in restoration projects that count on re-establishment of species rich grassland vegetations from the soil seed bank (Bekker *et al.* 2000).

I expected that species with adaptations for long distance dispersal would be less sensitive for spatial isolation than species without such adaptations. The distribution patterns of the species did differ, but these differences did not relate to the dispersal strategies of the species (chapter 3), neither did the differences between the colonization and extinction rates or patterns relate with the dispersal strategies of the species (chapter 4). It was argued that other dispersal mechanisms such as agricultural machinery might overrule the effect of the dispersal strategies. However, the spatial patterns of the colonization and extinction patterns according to the simulation model

showed similar patterns as observed in the field (chapter 6). The colonization probability exponentially decreased with distance to conspecific source populations in both approaches and isolated local populations had higher extinction probabilities than local populations closer (< ca. 50 m) to conspecific local populations. In the model, the dispersal distance of the species was solely determined by the dispersal strategy of the model species and no other dispersal mechanisms could overrule the effect of the dispersal strategy. The results of the model therefore cannot confirm the hypothesis that agricultural machinery functioned as a dispersal vector in the field.

I argue that by means of both a persistent seed bank and a long distance dispersal capacity species with different colonization strategies can end up with similar colonization, extinction and distribution patterns. This could explain the lack of a relation between the distribution patterns and the colonization strategies of the species observed in the field as described in chapter 3. However, it cannot explain why species without adaptations for long distance dispersal and with a transient seed bank can reach the long colonization distances observed in the field. Although the model results could not confirm the hypothesis that agricultural machinery or animals functioned as dispersal vectors, I conclude from the field data that agricultural machines or animals may have functioned as dispersal vectors. Alternative explanations can be that the longevity of the transient seed bank was underestimated, or that species have established from underground vegetative parts, which was not included in the field studies.

The advantage of the modelling approach was that the differences between species with contrasting colonization strategies could be monitored in the long term. In this approach the differences were obvious: both long distance dispersal and a persistent seed bank increase the survival probability of plants in dynamic and fragmented landscapes. This was observed in the modelling study (chapter 6) as well as the scenario study (chapter 7). Studies on the relation between the survival of species with contrasting dispersal and seed bank strategies and the degree of landscape fragmentation and dynamics are limited. In a preliminary study in which the diversity of species with long and short distance dispersal was related to the density of the network of ditches it appeared that species with short distance dispersal were more abundant in the areas with a high density of ditches per km^2 (Schipperijn, unpublished data). This study therefore confirms the observations of the modelling studies.

Both long distance dispersal and a persistent seed bank increased the survival probability in dynamic as well as fragmented landscapes. Species with transient seeds were relatively more sensitive for landscape dynamics. Less obvious was the sensitivity of species with short distance dispersal and a persistent seed bank for landscape fragmentation. Again, a persistent seed bank was an accurate adaptation for survival, not only in dynamic, but also in fragmented landscapes. I interpret this as an indication of the rescue-effect of the seed bank in isolated populations (Kalisz & McPeek 1993).

The survival probabilities of species with short or long distance dispersal and a transient or persistent seed bank all increase with decreasing habitat fragmentation and increasing habitat continuity in time. However, the species with a poor dispersal ability and a transient seed bank appeared to be the most sensitive for increased levels of fragmentation and dynamics. For those species it is even more important to protect existing populations and to keep the dynamics and fragmentation of habitat at the lowest level as possible. Species with a poor dispersal ability and a transient seed bank are poor colonizers, but can have other characteristics that enable them to survive in stable, non-isolated habitats. These characteristics can be very diverse, for example a long life-span of adult plants, vegetative reproduction, or they enable species to survive in extreme conditions (very dry, wet or nutrient poor soils) where other species cannot survive (Grubb 1977).

Perspectives

Measuring and modelling dispersal

The dispersal strategies had little effect on observed differences in the distribution patterns and colonization and extinction distances between species, but a large effect on differences in long term survival. The question remains how the processes of dispersal and establishment relate to seed characteristics and how dispersal and establishment influence the long term survival.

The most direct measurement of dispersal distance of seeds is to observe the dispersal of individual seeds (Jongejans & Telenius 2001). An alternative way is the observation of the seed rain using seed traps. By placing seed traps at different distances of a source plant or populations, a dispersal curve can be calculated (Bullock & Clarke 2000). Genetic analysis can increase our knowledge of dispersal distances by quantifying the genetic difference between

populations that results from seed and pollen dispersal (Grashof-Bokdam *et al.* 1998; Ouborg *et al.* 1999). However, it remains difficult to accurately observe and quantify the long distance dispersal, in particular the tail of the dispersal curve that represents the rare events of very long dispersal distances. It has been argued that this tail is very important for explaining biogeographical distribution patterns of plant species (Cain *et al.* 1998; Higgins & Richardson 1999). I define long distance dispersal as the distance that is crossed by a small, but significant part of the dispersing seeds. Long distance dispersal determines whether relatively remote local populations or habitat patches may be able to receive seeds from other populations. The dispersal curves that fitted the direct observations of dispersal often fail to explain realized distribution patterns of species. For example Van Dorp *et al.* (1996) observed a maximum dispersal distance of 20-30 m at windspeeds of 14 m s^{-1} for species with light seeds, whereas we found several colonizations at distances over 150 m for species with wind dispersed seeds (chapter 4).

I therefore advise against an increased effort in direct measurement of long distance dispersal. The probability of observing the rare events of long distance dispersal is too low to justify the effort. A better method would be the combination of mechanistic modelling of dispersal and establishment and validation of the resulting distribution patterns of species in the field. The observation of distribution patterns over a few consecutive years can give especially valuable information. Of course one should always bear in mind the possibility of establishment from the soil seed bank. The importance of the soil seed bank could be studied separately or be eliminated experimentally (as in chapter 5). Field studies of primary succession patterns of new habitat where one can be sure that no seed bank was present also deliver valuable insight into the role of dispersal processes (e.g. Nip-Van der Voort *et al.* 1979: colonization of new polders, or Wood & Moral 2000: colonization after volcanic eruptions).

The value of combining empirical and modelling approaches
The value of the combined approach of empirical and modelling studies was emphasized in the previous sections. I used a model to study large scale and long term processes of population dynamics in a range of landscapes. An empirical study of the same processes was impossible. However, a model will never represent the full complexity of reality. But field experiments represent a simplified world as well, since a limited number of explanatory variables are included in experiments, keeping the other variables constant between

treatments. Therefore, the results of models and experiments that study processes on landscape scales should always be evaluated with large scale observational field data that include as much variation as possible. The results of the simulation model were well in line with the results of the observational field studies in this thesis. When the results of models diverge from observations in the field, new hypotheses of the modelled system can be formulated. Using these new hypotheses, the model should be adjusted and tested again. This iterative use of modelling and empirical research enables scientists to better quantitative understanding of the studied systems than the separate use of both approaches (Verboom *et al.* 1991; Foppen 2001).

The model that was used in this thesis gives results for the survival of single species on the landscape scale. Interaction between species was explicitly included. A multi-species model is closer to reality. An important additional process in a multi-species model will be the competition between species (e.g. Schippers 2000). Competition influences all life-stages of the individual plants, from the germination and establishment to the survival of adult plants. A multi-species model is more complex, so inevitably more assumptions on the value of model parameters will have to be made. The question is whether the results of the single-species model would be very different when algorithms for competition between species would have been included in the model. This is not expected to be the case. Firstly, because competition is only possible when species are present at a site. So competition is only relevant when species are able to colonize a patch. Secondly, because competition was already implicitly included in the models by the effect of habitat quality on the demographic parameters for local population dynamics. In the simulation model, nutrient poor soil conditions were assumed to represent suitable growing conditions for the target species of species rich grassland vegetations. These conditions prevent the dominance of single species that may outcompete less competitive species (Schippers 2000).

Ecological profiles

Plant species were classified in a two by two matrix of dispersal and seed bank characteristics in this study. The classification was a useful tool to study the effect of fragmentation and dynamics of habitat on the distribution and the survival of plant species. It allows a comparative approach in the study of species groups, without the need to go into detail on the differences between individual species (Grubb 1985; Lavorel *et al.* 1997). The challenge is to

integrate the findings described in this thesis in quantitative rules for design and evaluation of landscape plans that aim at an increase of the survival of plant species. Vos *et al.* (2001) used the concept of ecological profiles to group species according to characteristics that determine their response to landscape changes. They integrated the species and landscape characteristics to develop ecologically scaled landscape indices ('*ESLI's*'), which can be used for the evaluation of landscape plans.

Vos *et al.* (2001) proposed two ecologically scaled landscape indices: average patch carrying capacity and average patch connectivity. Are these ecologically scaled landscape indices relevant for the plants that I have studied? Average patch connectivity (based on dispersal capacity of species and isolation of patches) is important for plants as well. I found differences in dispersal capacity between species, which implies that the absolute distance between patches means quite a different (ecologically scaled) distance to species with different dispersal strategies. The other ESLI, patch carrying capacity, is less useful to characterize species responses to landscape changes. However, it has been shown that the size of local plant populations, which is often related to carrying capacity, is important for the survival of plants as well (Fischer & Stocklin 1997), but it is not so clear whether this population size is directly related to the size of a patch.

The important role of patch dynamics to plant survival is apparent from my study. I suggest that the spatial dynamics of habitat at the landscape level is a third characteristics of the landscape that should be scaled ecologically. For example, more species of forest habitats have a transient seed bank and short distance dispersal compared to species of grassland vegetations (chapter 2, figure 2.4). It takes decades before forest habitat is suitable for typical forest herbs (Grashof-Bokdam & Geertsema 1998). Therefore, time has a different ecological scale for forest species than for grassland species.

Beyond biodiversity

In densely populated countries as the Netherlands, the agricultural landscape is becoming increasingly important for other functions than agriculture or nature functions. Some of these other functions are recreation, water management, aesthetic or cultural values and the increasing number of people who move from the urban to the rural areas for living. These functions profit from a higher biodiversity. An increasing number of farmers in the Netherlands provide

facilities for recreation (camping sites and footpaths) or services for water management (Migchels *et al.* 2000).

Improvement of other functions may also conflict with measures to protect biodiversity as the other functions also compete for space and money with biodiversity. Therefore landscape plans seldom only aim at a better protection of biodiversity. They try to increase the conditions for as many functions as possible. Landscape planners should therefore represent different disciplines and co-operate in order to balance the interests of the different functions (Fry 2001; Tress & Tress 2001). The application of landscape indices that quantify the needs for other functions as well, will improve the value of a landscape for several functions (Opdam *et al.* 2000).

References

Anonymous. (1995). Regeling beheersovereenkomsten en natuurontwikkeling. Ministerie van Landbouw, Natuurbeheer en Visserij, Den Haag.

Anonymous (1998). DGVI Commission Working Document *'State of application of regulation (EEC) no. 2078/92. Evaluation of agri-environmental programmes'*. VI/7655/98.

Antonovics, J., Thrall, P., Jarosz, A. and Stratton, D. (1994). Ecological genetics of metapopulations: the Silene-Ustilago plant-pathogen system. In: Real, L.A. (ed.), Ecological genetics. Princeton University Press. Princeton, New Jersey, pp. 146-170.

Bakker, J.P (1989). Nature management by grazing and cutting. Geobotany 14. Kluwer Academic Publishers, Dordrecht.

Bakker, J.P. & Berendse, F. (1999). Constraints in the restoration of ecological diversity in grassland and heathland communities. Trends in Ecology and Evolution 14: 63-68.

Bakker, J.P. & De Vries, Y. (1988). Seed dispersal by hay-making machines and large herbivores. De Levende Natuur 89: 173-176.

Bakker, J.P., Poschlod, P., Strykstra, R.J., Bekker, R.M. & Thompson, K. (1996). Seed banks and seed dispersal: important topics in restoration ecology. Acta Botanica Neerlandica 45: 461-490.

Barbaro, L., Dutoit, T. & Cozic, P. (2001). A six-year experimental resotration of biodiversity by shrub-clearing and grazing in calcareous grasslands of the French Prealps. Biodiversity and Conservation 10: 119-135.

Barends, S. (1989). Percelen in Nederland. Veranderingen in de percelering tussen 1900 en nu. Reeks Landschapsstudies 14, Pudoc, Wageningen.

Baudry, J. & Tatoni, T. (1993). Changes in landscape patterns and vegetation dynamics in Provence, France. Landscape and Urban Planning 24: 153-159.

Baudry, J., and Burel, F. (1997). Agricultural landscape dynamics: implications for species movements. In: A. Cooper, A. & Power, J. (eds.). Species dispersal and land use processes, Proceedings IALE UK conference 1997, pp. 3-10.

Baveco, J. M. and Smeulders, A. W. M. (1994). Objects for simulation: Smalltalk and ecology. Simulation 62: 42-57.

Bekker, R. M. (1998). The ecology of soil seed banks in grassland ecosystems. PhD Thesis University of Groningen.

Bekker, R.M., Verweij, G.L., Bakker, J.P. & Fresco, L.F.M. (2000). Soil seed bank dynamics in hayfield succession. Journal of Ecology 88: 594-607.

Bignal, E.M. & McCracken, D.I. (1996). Low-intensity farming systems in the conservation of the countryside. Journal of Applied Ecology 33: 413-424

Boatman, N. (ed.) (1994). Field margins: integrating agriculture and conservation. British Crop Protection Council, Monograph No 58, Surrey.

Boatman, N.D., Davies, D.H.K., Chaney, K., Feber, R., De Snoo, G.R. & Sparks, T.H. (eds.) (1999). Field margins and buffer zones: ecology, management and policy. Aspects of Applied Biology 54.

Brandt, J., Tress, B. & Tress, G. (eds.) (2000). Multifunctional Landscapes: Interdisciplinary approaches to landscape research and management. Conference material for the conference on "multifunctional landscapes", Centre for Landscape Research, Roskilde.

Brown, J.H. & Kodric-Brown, A. (1977). Turnover rates in insular biogeography: effect of immigration on extinction. Ecology 58: 445-449.

Bruggink, M. & Buitink, G. (1995). Experiment randenbeheer. In: De Snoo, G.R., Rotteveel, A.J.W. & Heemsbergen H. (eds.). Akkerranden in Nederland, Werkgroep Akkerranden, Wageningen/Leiden, pp. 133-142.

Bulle, B., Van Groenendael, J. & Jurgens, C. (1994). Helophytes in 'het Wageningse Binnenveld' Their distribution related to their dispersal characteristics. Landschap 11: 19-28.

Bullock, J.M. & Clarke, R.T. (2000). Long distance seed dispersal by wind: measuring and modelling the tail of the curve. Oecologia 24: 506-521.

Bunce, R.G.H. & Hallam, C.J. (1993). The ecological significance of linear features in agricultural landscapes in Britain. In: Bunce, R.G.H., Ryszkowski, L. & Paoletti, M.G. (eds.), Landscape Ecology and agroecosystems. Lewis Publishers, Boca Raton, pp. 11-19.

Bunce, R.G.H., Ryszkowski, L. & Paoletti, M.G. (eds.) (1993). Landscape Ecology and agroecosystems. Lewis Publishers, Boca Raton.

Burel, F. & Baudry, J. (1995). Species biodiversity in changing agricultural landscapes: A case study in the Pays d'Auge, France. Agriculture, Ecosystems and Environment 55: 193-200.

CBS (Centraal Bureau voor de Statistiek) (1993). Botanisch Basis Register. Voorburg.

Cain, M. L., Milligan, B. G. & Strand, A. E. (2000). Long-distance seed dispersal in plant populations. American Journal of Botany 87: 1217-1227.

Corbit, M., Marks, P.L. & Gardescu, S. (1999). Hedgerows of habitat corridors for forest herbs in central New York, USA.. Journal of Ecolology 87: 220-232.

Coulson, S.J., Bullock, J.M., Stevenson, M.J. & Pywell, R.F. (2001). Colonization of grassland by sown species: dispersal versus microsite limitation in responses to management. Journal of Applied Ecology 38: 203-216.

Danvind, M. & Nilsson, C. (1997). Seed floating ability and distribution of alpine plants along a northern Swedish river. Journal of Vegetation Science 8: 271-276.

De Snoo, G.R. & Van der Poll, R.J. (1999). Effect of herbicide drift on adjacent boundary vegetation. Agriculture, Ecosystems and Environment 73: 1-6.

Deffontaines, J.P., Thenail, C. & Baudry, J. (1995). Agricultural systems and landscape patterns: how can we build a relationship? Landscape and Urban Planning 31: 3-10.

Dzwonko, Z. (1993). Relation between the floristic composition of isolated young woods and their proximity to ancient woodland. Journal of Vegetation Science 4: 693-698.

Elberse, W.Th., Van den Berg, J.P. & Dirven, J.G.P. (1983). Effect of use and mineral supply on the botanical composition and yield of old grassland on heavy-clay soil. Netherlands Journal of Agricultural Sciences 31: 63-88.

Eriksson, O. (1996). Regional dynamics of plants: a review of evidence for remnant, source-sink and metapopulations. Oikos 77: 248-258.

Eriksson, O. (1997). Colonization dynamics and relative abundance of three plant species (*Antennaria dioica, Hieracium polosella* and *Hypochoeris maculata*) in dry semi-natural grasslands. Ecography 20:559-568.

ESRI (2000). ArcView GIS 3.2a. Environmental Systems Research Institute, Inc., Redlands, USA.

Fahrig, L. (1992). Relative importance of spatial and temporal scales in a patchy environment. Theoretical Population Biololgy 41: 300-314.

Falinska, K. (1991). Plant demography in vegetation succession. Kluwer Academic Publishers, Dordrecht.

Falinska, K. (1999). Seed bank dynamics in abandoned meadows during a 20-year period in the Bialowieza National Park. Journal of Ecology 87: 461-475.

Fenner, M. (1985). Seed Ecology. Chapman and Hall, New York.

Fischer, M. & Stöcklin, J. (1997). Local extinctions of plants in remnants of extensively used calcareous grasslands 1950-1985. Conservation Biology 11: 727-737.

Fischer, S.F., Poschlod, P. & Beinlich, B. (1996). Experimental studies on the dispersal of plants and animals on sheep in calcareous grasslands. Journal of Applied Ecology 33: 1206-1222.

Foppen, R.P.B. (2001). Bridging gaps in fragmented landscapes. Applying landscape ecology for bird conservation. Alterra Scientific Contributions 4. Alterra Green World Research, Wageningen.

Frank, K. & Wissel, C. (1998). Spatial aspects of metapopulation survival - from model results to rules of thumb for landscape management. Landscape Ecology: 13: 363-379.

Fröborg, H. & Eriksson, O. (1997). Local colonization and extinction of field layer plants in a deciduous forest and their dependence upon life history features. Journal of Vegetation Science 8: 395-400.

Fry, G. L. A. (1994). The role of field margins in the landscape. - In: Boatman, N. (ed.), Field margins: integrating agriculture and conservation. British Crop Protection Council, Monograph No 58, Surrey, pp. 31-40.

Fry, G.L.A. (2001). Multifunctional landscapes - towards transdisciplinary research. Landscape and Urban Planning 57: 159-168.

Goossen, C.M., Langers, F. & Lous, J.F.A. (1997). Indicatoren voor recreatieve kwaliteiten in het landelijk gebied. Rapport 584 Staring Centrum, Wageningen.

Grashof-Bokdam, C. J. & Geertsema, W. (1998). The effect of isolation and history on colonization patterns of plant species in secondary woodland. Journal of Biogeography 25: 837-846.

Grashof-Bokdam, C.J. (1997). Forest species in an agricultural landscape in the Netherlands: effects of habitat fragmentation. Journal of Vegetation Science 8: 21-28.

Grashof-Bokdam, C.J., Jansen, J. & Smulders, M.J.M. (1998). Dispersal patterns of Lonicera periclymenum determined by genetic analysis. Molecular Ecology 7: 165-174.

Greene, D.F. & Johnson, E.A. (1989). A model of wind dispersal of winged or plumed seeds. Ecology 70: 339-347

Grime, J.P. & Hillier, S.H. (1992). The contribution of seedling regeneration to the structure and dynamics of plant communities and larger units of landscape. In: Fenner, M. (ed.) Seeds, the ecology of regeneration in plant communities, CAB International Wallington UK, pp 349-364.

Grime, J.P., Hodgson, J.G. & Hunt, R. (1988). Comparative plant ecology: a functional approach to common British species. Unwin Hyman, London.

Grubb, J.P. (1977). The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biological Reviews 52: 107-145.

Grubb, J.P. (1985). Plant populations and vegetation in relation to habitat, disturbance and competition: problems of generalization. In: White, J. (ed.). The population structure of vegetation. Dr. W. Junk Publishers, Dordrecht.

Hanski, I. (1985). Single-species dynamics may contribute to long-term rarity and commonness. Ecology 66: 335-343.

Harrison, S., Maron, J. & Huxel, G. (2000). Regional turnover and fluctuation in populations of five plants confined to serpentine seeps. Conservation Biology 14: 769-779.

Harvey, C.A. (2000). Windbreaks enhance seed dispersal into agricultural landscapes in Monteverde, Costa Rica. Ecological Applications 10: 155-173.

Haughton, A.J., Wilcox, A., Chaney, K., Cooper, S.E. & Boatman, N.D. (1998). Spray drift into field margins: the effect of width of buffer strip and plant species on the interception of spray drift. The 1998 Brighton Conference – Pests and Diseases, pp.285-290.

Haydon, D. T. & Pianka, E. R. (1999). Metapopulation theory, landscape models, and species diversity. Ecoscience 6: 316-328.

Hensen, I. & Müller, C. (1997). Experimental and structural investigations of anemochorous dispersal. Plant Ecology 133: 169-180.

Hess, G.R., Campbell, C.L., Fiscus, D.A., Hellkamp, A.S., McQuaid, B.F., Munster, M.J., Peck, S.L. & Shafer, S.R. (2000). A conceptual model and indicators for assessing the ecological condition of agricultural lands. Journal of Environmental Quality 29: 728-737.

Higgins, S.I. & Richardson, D.M. (1999). Predicting plant migration rates in a changing world: the role of long-distance dispersal. The American Naturalist 153(3): 464-475.

Hobbs, R.J. & Saunders, D.A. (1991). Re-integrating fragmented landscapes - a preliminary framework for the Western Australian wheatbelt. Journal of Environmental Management 33: 161-167.

Hodge, I. (2001). Beyond agri-environmental policy: towards an alternative model of rural environmental governance. Land Use Planning 18: 99-111.

Hodgson, J.G. & Grime, J.P. (1990). The role of dispersal mechanisms, regenerative strategies and seed banks in the vegetation dynamics of the British landscape. In: Bunce, R.G.H. & Howard, D.C. (eds.) Species dispersal in agricultural habitats. Belhaven Press, London, pp 65-81.

Hodgson, J.G., Grime, J.P, Hunt, R. & Thompson, K. (1995). The electronic comparative plant ecology. Chapman & Hall, London.

Horlings, I. (1996). Duurzaam boeren met beleid: innovatie groepen in de landbouw. PhD thesis, Katholieke Universiteit Nijmegen.

Howe, H.F. & Smallwood, J. (1982). Ecology of seed dispersal. Annual Review of Ecology and Systematics 13: 201-228.

Hughes, L., Dunlop, M., French, K., Leishman, M.R., Rice, B., Rodgerson, L. & Westoby, M. (1994). Predicting dispersal spectra: a minimal set of hypotheses based on plant attributes. Journal of Ecology 82: 933-950.

Husband, B.C. & Barrett, S.C.H. (1996). A metapopulation perspective in plant population biology. Journal of Ecology 84: 461-467.

Husband, B.C. & Barrett, S.C.H. (1998). Spatial and temporal variation in population size of *Eichhornia paniculata* in ephemeral habitats: implications for metapopulation dynamics. Journal of Ecology 86: 1021-1031.

Hutchings, M.J. & Booth, K.D. (1996a). Studies on the feasibility of re-creating chalk grassland vegetation on ex-arable land. I. The potential roles of the seed bank and seed rain. Journal of Applied Ecology 33:1171-1181.

Hutchings, M. J. & Booth, K. D. (1996b). Studies on the feasibility of re-creating chalk grassland vegetation on ex-arable land. II. Germination and early survivorship of seedlings under different management regimes. Journal of Applied Ecology 33:1182-1190.

Joenje, W. & Kleijn, D. (1994). Plant distribution across arable field ecotones in the Netherlands. In: Boatman, N. (ed.). Field margins: integrating agriculture and conservation. British Crop Protection Council, Monograph No 58, Surrey, pp. 323-328.

Jongejans, E. & Schippers, P. (1999). Modeling seed dispersal by wind in herbaceous species. Oikos 87: 362-372.

Jongejans, E. & Telenius, A. (2001). Field experiments on seed dispersal by wind in ten umbelliferous species (Apiaceae). Plant Ecology 152: 67-78.

Kalisz, S & McPeek, M. A. (1993). Extinction dynamics, population growth and seed banks. Oecologia 95: 314-320.

Keen, A. & Engel, B. (1998). Procedure IRREML. In: Goedhart, P.W. & Thissen, J.T.N.M. (eds.), CBW Genstat Procedure Library Manual Release 4.1. Centre for Biometry Wageningen, Wageningen, The Netherlands.

Keymer, J. E., Marquet, P. A., Velasco-Hernández, J. X. & Levin, S. A. (2000). Exinction thresholds and metapopulation persistence in dynamic landscapes. American Naturalist 156: 478-494.

Kiss, J., Penksza, K., Tóth, F. & F. Kádár. (1997). Evaluation of fields and field margins in nature production capacity with special regard to plant protection. Agriculture, Ecosystems and Environment 63: 227-232.

Kleijn, D. & Verbeek, M. (2000). Factors affecting the species composition of arable field boundary vegetation. Journal of Applied Ecology 37: 256-266.

Kleijn, D. (1997). Species richness and weed abundance in the vegetation of arable field boundaries. PhD Thesis Wageningen Agricultural University.

Kleijn, D., Berendse, F., Smit, R. & Gilissen, N. (2001). Agri-environmental schenes do not effectively protect biodiversity in Dutch agricultural landscapes. Nature 413:723-725.

Kleijn, D., Joenje, W. & Kropff, J.M. (1997). Patterns in species composition of arable field boundary vegetation. Acta Botanica Neerlandica 46: 175-192.

Kleijn, D., Joenje, W. Le Coeur, D. & Marshall, E.J.P (1998). Similarities in vegetation development of newly established herbaceous strips along contrasting European field boundaries. Agriculture, Ecosystems and Environment 68: 13-26.

Kleyer, M. (1999). Distribution of plant functional types along gradients of disturbance intensity and resource supply in an agricultural landscape. Journal of Vegetation Science 19: 697-708.

Lamont, B.B. & Klinkhamer, P.G.L. (1993). Population size and viability. Nature 362: 211.

Lavorel, S., McIntyre, S., Landsberg, J. & Forbes, T.D.A. (1997). Plant functional classifications: from general groups to specific groups based on response to disturbance. Trends in Ecology and Evolution 12: 474-478.

Lavorel, S., Touzard, B., Lebreton, J.-D. & Clément, B. (1998). Identifying functional groups for response to disturbance in an abandoned pasture. Acta Oecologia 19: 227-240.

Lawes Agricultural Trust (Rothamsted Experimental Station) (2001). GenStat Release 4.2 (Fifth Edition) (PC/Windows 2000).

Le Coeur, D., Baudry, J. & Burel, F. (1997). Field margins plant assemblages: variation partitioning between local and landscape factors. Landscape and Urban Planning 37: 57-71.

Levins, R. (1969). Some demographic and genetic consequences of environmental heterogeneity for biological control. -Bulletin of the Entomological Society of America 15: 237-240.

Levins, R. (1970). Extinctions. Some mathematical questions in biology. In: Gerstenhaber, R (ed.). Lectures on mathematics in life sciences 2. The American Mathematical Society, Providence, RI, pp. 77-107.

Marks, P.L. & Mohler, C.L. (1985). Succession after elimination of buried seeds from a recently plowed field. Bulletin of the Torrey Botanical Club 112: 376-382.

Marshall, E.J.P. (1989). Distribution patterns of plants associated with arable field edges. Journal of Applied Ecology 26: 247-257.

Marshall E.J.P. & Arnold, G.M. (1995). Factors affecting field weed and field margin flora on a farm in Essex, UK. Landscape and Urban Planning 31: 205-216.

McLaughlin, A. & Mineau, P. (1995). The impact of agricultural practices on biodiversity. Agriculture, Ecosystems and Environment 55: 201-212.

Meeus, J.H.A. (1993). The transformation of agricultural landscapes in Western Europe. The Science of the Total Environment 129: 171-190.

Melman, Th.C.P., Clausman, P.H.M.A. & Van Strien, A.J. (1988). Ditch banks in the western Netherlands as connectivity structure. In: Schreiber, K.-F. (ed.). Connectivity in Landscape

Ecology, Proceedings of the 2nd International Seminar of IALE. Munstersche Geografische Arbeiten 29, Munster, pp. 157-161.

Merriam, G. (1988). Landscape dynamics in farmland. Trends in Ecology and Evolution 3: 16-20.

Meyer, A. H. & Schmid, B. (1999). Seed dynamics and seedling establishment in the invading perennial *Solidago altissima* under different experimental treatments. Journal of Ecololgy 87: 28-41.

Middleton, J. & Merriam, G. (1983). Distribution of woodland species in farmland woods. Journal of Applied Ecology 20: 625-644.

Migchels, G., Gaasbeek, N.H., Cools, N. & Scholtz, D.R.M. (2000). Handboek Programma Beheer voor particulieren en gemeenten. SBNL, Wijk bij Duurstede.

Ministry of Agriculture, Nature Conservation and Fisheries. (2000a). Natuur voor mensen, mensen voor natuur. Nota natuur, bos en landschap in de 21e eeuw.

Ministry of Agriculture, Nature Conservation and Fisheries. (2000b). Voedsel en Groen, het Nederlandse agro-foodcomplex in perspectief.

Moloney, K. A. and Levin, S. A. (1996). The effects of disturbance architecture on landscape-level population dynamics. Ecology 77(2): 375-394.

Moonen, A.C. & Marshall, E.J.P. (2001). The influence of sown margin strips, management and boundary structure on herbaceous field margin vegetation in two neighbouring farms in southern England. Agriculture, Ecosystems and Environment 86: 187-202.

Mountford, J.O., Parish, T & Sparks, T.H. (1994). The flora of field margins in relation to land use and boundary features. In: Boatman, N. (ed.). Field margins: integrating agriculture and conservation. British Crop Protection Council, Monograph No 58, Surrey, pp. 105-110.

Nathan, R. & Muller-Landau, H.C. (2000). Spatial patterns of seed dispersal, their determinants and consequences for recruitment. Trends in Ecology and Evolution 15: 278-285.

Nip-Van der Voort, J., Hengeveld, R. & Haeck, J. (1979). Immigration rates of plant species in three Dutch polders. Journal of Biogeography 6: 301-308.

Noble, I.R. & Gitay, H. (1996). A functional classification for predicting the dynamics of landscapes. Journal of Vegetation Science 7: 329-336.

Olff, H. & Bakker, J.P. (1991). Long-term dynamics of standing crop and species composition after the cessation of fertilizer application to mown grassland. Journal of Applied Ecology 28:1040-1052.

Opdam, P. (1990). Dispersal in fragmented populations: the key to survival. In: Bunce, R.G.H. & Howard, D.C (eds.). Species dispersal in agricultural habitats Belhaven Press, London, New York, pp. 3-17.

Opdam, P. (In press). Assessing the conservation potential of habitat networks. In: Gutzwiller, K. J. (ed.). Concepts and application of landscape ecology in biological conservation. Springer Verlag, New York .

Opdam, P., Grashof C. & Van Wingerden, W. (2000). Groene dooradering, een ruimtelijk concept voor functiecombinaties in het agrarisch landschap. Landschap 17: 45-51.

Opdam, P., Vos, C., & Foppen, R. (In press). Bridging the gap between ecology and spatial planning. Landscape Ecology.

Ouborg, N. J. (1993). Isolation, population size and extinction: the classical and metapopulation approaches applied to vascular plants along the Dutch Rhine-system. Oikos 66: 298-308.

Ouborg, N.J., Piquot, Y. & Van Groenendael, J.M. (1999). Population genetics, molecular markers and the study of dispersal in plants. Journal of Ecology 87: 551-568.

Pakeman, R.J., Attwood, J.P. & Engelen, J. (1998). Sources of plants colonizing experimentally disturbed patches in an acidid grassland, in eastern England. Journal of Ecology 86: 1032-1041.

Parr, T.W. & Way, J.M. (1988). Management of roadside vegetation: the long-term effects of cutting. Journal of Applied Ecology 25: 1073-1087.

Perry, J. N. & Gonzalez-Andujar, J. L. (1993). Dispersal in a metapopulation neighbourhood model of an annual plant with a seedbank. Journal of Ecology 81: 453-463.

Perry, N.H., Chaney, K., Wilcox, A. & Boatman, N.D. (1996). The effect of fertiliser and herbicide application on herbaceous field margin communities. In: Marshall, E.J.P., Morgan, J.L. & Willoughby, L. (eds.). Vegetation management in forestry, amenity and conservation areas: Managing for multiple objectives, Aspects of Applied Biology 44, pp. 339-344.

Poschlod, P. & Bonn, S. (1998). Changing dispersal processes in the central European landscape since the last ice age: an explanation for the actual decrease of plant species richness in different habitats? Acta Botanica Neerlandica 47: 27-44.

Potter, C. (1998). Against the Grain, Agri-Environmental Reform in the United States and the European Union. CAB International, Wallingford.

Power, J. & Cooper, A. (1995). Vegetation and land use change in north-eastern Ireland. Landscape and Urban Planning 31: 195-203.

Primack, R.B. & Miao, S.L. (1992). Dispersal can limit local plant distribution. Conservation Biology 6: 513-519.

Prins, A. H., Dijkstra, G. A. & Bekker, R. M. (1998). Feasibility of target communities in a Dutch brook valley system. Acta Botanica Neerlandica 47: 71-88.

Putwain, P.D. & Gillham, D.A. (1990). The significance of the dormant viable seed bank in the restoration of heathlands. Biological Conservation 52: 1-16.

Quintana-Ascencio, P.F. & Menges, E.S. (1996). Inferring metapopulation dynamics from patch-level incidence of Florida scrub plants. Conservation Biology 10: 1210-1219.

Rademaker, M. C. J. & De Jong, T. J. (1999). The shape of the female fitness curve for *Cynoglossum officinale*: Quantifying seed dispersal and seedling survival in the field. Plant Biology 1: 351-356

Richards, C.M. (2000). Inbreeding depression and genetic rescue in a plant metapopulation. American Naturalist 155: 383-394.

Robinson, G.R. & Quinn, J.F. (1988). Extinction, turnover and species diversity in an experimentally fragmented California annual grassland. Oecologia 76: 71-82.

Sarlöv Herlin, I.L. & Fry, G.L.A. (2000). Dispersal of woody plants in forest edges and hedgerows in a Southern Swedish agricultural area: the role of site and landscape structure. Landscape Ecology 18: 229-242.

Schaminée, J.H.J., Stortelder, A.H.F. & Weeda, E.J. (1996). De Vegetatie van Nederland 3. Opulus Press, Uppsala.

Schaminée, J.H.J., Weeda, E.J. & Westhoff, V. (1998). De Vegetatie van Nederland 4. Opulus Press, Uppsala.

Schippers, P. (2000). Dynamics of plant communities in field boundaries, restoration of biodiversity. PhD Dissertation Wageningen University.

Schippers, P., Ter Borg, S.J., Van Groenendael, J.M. & Habekotte. (1993). What makes *Cyperus esculentus* (Yellow nutsedge) an invasive species? - A spatial model approach. Brighton crop protection conference Weeds 5A-2: 495-504.

Silvertown, J. W. (1982). Introduction to plant population ecology. Longman, London.

Smeding, F.W. & Joenje, W. (1999). Farm-Nature Plan: landscape ecology based farm planning. Landscape and Urban Planning 46:109-115.

Stortelder, A.F.H., Schaminée, J.H.J. & Hommel, P.W.F.M. (1999). De vegetatie van Nederland 5. Opulus Press, Uppsala.

Strykstra, R.J., Bekker, R.M. & Verweij, G.L. (1996). Establishment of *Rhinanthus angusitfolius* in a successional hayfield after seed dispersal by mowing machinery. Acta Botanica Neerlandica 45: 557-562.

Taylor, J. (1973). The analysis of designed experiments with censored observations. Biometrics 29, 35-43.

Ter Heerdt, G.N.J., Verweij, G.L., Bekker, R.M. & Bakker, J.P. (1996). An improved method for seed-bank analysis: seedling emergence after removing the soil by sieving. Functional Ecology 10: 144-151.

Ter Heerdt, G.N.J., Schutter, A. & Bakker, J.P. (1999). The effect of water supply on seed-bank analysis using the seedling-emergence method. Functional Ecology 13: 428-430.

Thies, C. & Tscharntke, T. (1999). Landscape structure and biological control in agroecosystems. Science 285: 893-895

Thompson, K., Bakker, J. P. & Bekker, R. M. (1997). Soil seed banks of NW Europe: methodology, density and longevity. Cambridge University Press.

Tilman, D. (1993). Species richness of experimental productivity gradients: how impirtant is colonizatin limitation? Ecology 74: 2179-2191.

Tilman, D. (1997). Community invasibility, recruitment limitation and grassland biodiversity. Ecology 78: 81-92.

Tress, B. & Tress, G. (2001). Capitalising on multiplicity: a transdisciplinary systems approach to landscape research. Landscape and Urban Planning 57: 143-157.

Valverde, T. & Silvertown, J. (1997). A metapopulation model for *Primula veris*, a temperate forest understorey herb. Journal of Ecology 85: 193-210.

Van der Meijden, E., Klinkhamer, P.G.L., De Jong, T.J. & Van Wijk, C.A.M. (1992). Metapopulation dynamics of biennial plants: how to exploit temporary habitats. Acta Botanica Neerlandica 41: 249-270.

Van der Meijden, R. (1996). Heukels' flora van Nederland. Wolters-Noordhoff, Groningen.

Van der Pijl, L. (1982). Principles of dispersal in higher plants. Springer-Verlag, Berlin.

Van Dorp, D. (1996). Seed dispersal in agricultural habitats and the restoration of species-rich meadows. PhD thesis Wageningen Agricultural University.

Van Dorp, D., Schippers, P. & Van Groenendael, J. M. (1997). Migration rates of grassland plants along corridors in fragmented landscapes assessed with a cellular automation model. Landscape Ecol. 12: 39-50.

Van Dorp, D., Van den Hoek, W.P.M. & Daleboudt, C. (1996). Seed dispersal capacity of six perennial grassland species measured in a windtunnel at varying wind speed and height. Canadian Journal of Botany 74: 1956-1963.

Van Groenendael, J., Ehrlén, J. & Svensson, B.M. (2000). Dispersal and persistence: population processes and community dynamics. Folia Geobotanica 35: 107-114.

Van Strien, A.J., Van der Linden, J., Melman, Th.C.P. & Noordervliet, M.A.W. (1989). Factors affecting the vegetation of ditch banks in peat areas in the Western Netherlands. Journal of Applied Ecology 26: 989-1004.

Verboom, J., Lankester, K. & Metz, J.A.J. (1991). Linking local and regional dynamics in stochastic metapopulation models Biological Journal of the Linnean Society 42: 39-55.

Verboom, J., Metz, J.A.J. & Meelis, E. (1993). Metapopulation models for impact assessment of fragmentation. In: Vos, C. & Opdam, P. (ed.). Landscape ecology of a stressed environment. Chapman and Hall, London, pp. 172-191.

Vermeer, J.G. & Berendse, F. (1983). The relationship between nutrient availability, shoot biomass and species richness in grassland and wetland communities. Vegetatio 53:121-126.

Vos, C.C. & Stumpel, A.H.P. (1996). Comparison of habitat-isolation parameters in relation to fragmented distribution patterns in the tree frog (*Hyla arborea*). Landscape Ecology 11: 203-214.

Vos, C.C., Verboom, J., Opdam, P.F.M. & Ter Braak, C.J.F. (2001). Toward ecologically scaled landscape indices. American Naturalist 157: 24-51.

Vos, C.C. & Zonneveld, J.I.S. (1993). Patterns and processes in a landscape under stress: the study area. In: Vos, C.C. & Opdam, P. (eds.). Landscape ecology of a stressed environment. Chapman & Hall. London, pp. 1-27.

Wieberdink, G.L. (1990). Historische Atlas Drenthe. Robas Producties. Den Ilp.

Willson, M. F. (1993). Dispersal mode, seed shadows and colonization patterns. Vegetatio 107/108: 261-280.

Willson, M.F., Rice, B.L. & Westoby, M. (1990). Seed dispersal spectra: a comparison of temperate plant communities. Journal of Vegetation Science 1: 547-562.

Wood, D.M. & Del Moral, R. (2000). Seed rain during early primary succession on Mount St. Helens, Washington. Madrono 47(1): 1-9

Wolf, A. & Harrison, S.P. (2001). Effects of habitat size and patch isolatin on reproductive success of the serpentine morning glory. Conservation Biology 15: 111-121.

Wolf, A., Brodmann, P.A. & Harrison, S. (1999). Distribution of the rare serpentine sunflower, *Helianthus exilis* (Asteraceae): the roles of habitat availability, dispersal limitation and species interactions. Oikos 84:69-76.

Wu, J. and Levin, S. A. (1994). A spatial patch dynamic modeling approach to pattern and process in an annual grassland. Ecological Monographs 64: 447-464

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Summary

Landscape elements that are not used for food production are of major importance to the survival of many plant species in agricultural landscapes of North Western Europe, parts of North America and Australia. These species cannot survive in the intensively used fields but are still present in the networks of semi-natural vegetation types in ditch banks, road verges, hedgerows and forest patches. The intensification of agricultural production systems in the second half of the 20th century involved the removal of many of the landscape elements and resulted in a decrease of the habitat quality of the remaining landscape elements for many plant species. This caused a decrease of the diversity of plants in agricultural landscapes.

Concern about the conservation of agricultural landscapes led to measures to protect the botanical diversity of agricultural landscapes. However, these measures did not always result in the expected increase of botanical diversity. Landscape ecological research indicated that the survival of species in a landscape is not only determined by the quality of the local habitat patches, but also by the fragmentation and dynamics of the habitat. In fragmented habitats, species are divided into local populations. The habitat in non-productive landscape elements in agricultural landscapes is typically dynamic due to the agricultural activities on the adjacent fields. Species can become locally extinct, but new habitat patches can be colonized. The colonization capacity of species is a key factor in the survival probability of species in fragmented and dynamic landscapes. Seed dispersal and the persistence of the soil seed bank determine the colonization capacity of plant species.

The research described in this thesis aimed at increasing the knowledge of the relation between the survival probability of plant species and the fragmentation and dynamics of the habitat network in agricultural landscapes. I wanted to know if species with different dispersal and seed bank characteristics respond differently to the spatial and temporal arrangement of the habitat. This knowledge is needed to increase the effectiveness of measures that are taken to increase the botanical diversity of agricultural landscapes.

Therefore, I studied the relation between the survival of plant species with contrasting colonization strategies and the arrangement of habitat in space and time by combining empirical and modelling approaches.

In chapter 2 a conceptual model is proposed. Field studies of plant species in a network of ditch banks in an agricultural area in the province of Drenthe are described in chapters 3-5. The modelling studies are described in chapters 6 and 7.

The conceptual model that I propose in chapter 2 is the starting point for the empirical and modelling studies described in the other chapters of the thesis. The conceptual model relates plant population dynamics to habitat quality, configuration and dynamics. Based on dispersal and seed bank characteristics, four plant strategies are distinguished: species having either long (>100 m) or short (< 100 m) distance dispersal and either a long (> 5 yr.) or short (< 5 yr.) term persistent seed bank. It was hypothesized that species with contrasting strategies have different survival probabilities in landscapes with contrasting habitat arrangement in space and time. I found few published empirical data suitable for testing these hypotheses. An iterative process of empirical and modelling research was proposed to determine this relation and to define management options for multifunctional farms in which biodiversity is one of the land use aims.

The field studies described in chapters 3-5 were carried out in a study area in the province of Drenthe in the north of the Netherlands. The study area consisted of arable fields intersected by a network of ditches. The study area was selected because the vegetation types in the ditch banks showed a large variation in habitat quality. Several herbaceous plant species with contrasting dispersal and seed bank strategies occurred as fragmented populations in the ditch banks. I focussed on the distribution patterns of thirteen perennial herbaceous plant species with contrasting dispersal and seed bank strategies.

In chapter 3 I describe the relationship between the distribution patterns of the thirteen plant species in the network of ditches and habitat quality, spatial isolation and age of habitat patches. Habitat patches were defined as 10m-long segments of the ditch banks. The distribution patterns of the plant species were mainly determined by habitat quality and the presence of seed sources at short distances (< 25 m). This conclusion was independent of the dispersal characteristics of the species. Most species had higher occupation frequencies in older than younger ditch banks. Only species with persistent seeds had almost equal occupation probabilities in older and younger habitat patches, indicating the importance of the soil seed bank as a source for colonization after large-scale disturbances.

The distribution patterns of the thirteen species were monitored during three years. In chapter 4 the dynamics of the distribution patterns were analyzed. All species frequently colonized empty patches and occupied patches frequently became extinct. The fraction of the occupied patches that had been colonized in the current year was more than 0.3 (mean over the species). The

mean fraction of local populations that became extinct from one year to the next was slightly lower. Spatial isolation correlated positively with extinction probabilities and negatively with colonization probabilities of the species. This indicated that all species had characteristics of metapopulation dynamics. Most colonization events were found within 50 m of conspecific local populations in the preceding year, but colonization events at more than 200 m were also observed. There was no relation between colonization distances and dispersal characteristics of the species. Species with a persistent seed bank had longer colonization distances than species with a transient seed bank. The differences between the colonization patterns of species with persistent and transient seed banks may have been caused by the cumulative result of the seed rain of several years of species with persistent seed banks.

The local colonizations discussed in chapter 4 are the combined result of seed dispersal and seed bank persistence. In chapter 5 the separate role of seed dispersal and the seed bank in the colonization of all plant species in the ditch banks in the study area was analyzed using an experimental approach. I first measured floating and drop time of seeds of ten species to evaluate the existing classification of water and wind dispersed species. The measurements confirmed the classification. Next, plots were created in ditch banks to monitor colonization by dispersal. These 'dispersal plots' were created by replacing the top layer of the soil (including the soil seed bank) by sterile soil (without any seed bank). The number of species that colonized the dispersal plots was lower than the number of species present in the surrounding vegetation. Species that colonized the dispersal plots were often also present in the surrounding vegetation, especially species without adaptations for long distance dispersal. The soil seed bank was studied by monitoring germination from soil samples. The number of species that were found in the soil seed bank was higher than the number of species in the surrounding vegetation. The number of species with a transient seed bank was higher in the seed bank of old ditches than in young ditches. This could be explained by the fact that the presence of transient seeds in the soil seed bank follows rather than determines the above ground vegetation. Species with transient seeds depend on colonization by dispersal and did not colonize the young ditches to the same extent as species with persistent seeds.

Chapter 6 presents the spatially explicit, individual-based single-species model that was developed to study the relationship between plant species survival and the dynamics and fragmentation of habitat. I studied the survival

of four model species with contrasting dispersal (short or long distance) and seed bank (transient or persistent) characteristics in a network of ditches with varying spatial and temporal continuity. The survival of the four model species decreased statistically significant when spatial or temporal continuity decreased. Differences between the survival of species with contrasting colonization strategies was very clear when taking long-term population dynamics into account (250 years), however when data of only a few years are taken into account, these differences do not emerge. I validated the model by comparing the rates and spatial distribution of colonization and extinction events according to the model with field data. For this comparison the results of the three-year distribution pattern study (chapter 4) were compared with the results of five consecutive years in the model. These short term results of the model and the field data were rather similar: colonization probabilities increased and extinction probabilities decreased with spatial isolation and no obvious differences between the colonization and extinction patterns were observed for species with contrasting dispersal and seed bank characteristics.

In chapter 7 the simulation model is used in a scenario study for alternative ways of implementing management agreements with farmers. I wanted to explore different explanations for the reported failing success of Dutch management agreements. Likely causes that were suggested are: reduced fertilisation is inadequate for restoration of suitable habitat, and dispersal limitations hamper colonization. In this chapter another explanation is explored: contract periods are too short to allow plant populations to respond to increased habitat quality. The simulation model described in chapter 6 was adjusted for the scenario study. The effectiveness of three ways of changing the conditions in management agreements was compared: improving the habitat quality of field margins, doubling the length of the contract or clustering the contracts in space. For four plant types, the effectiveness of conservation contracts with farmers was best improved by clustering as quantified by an increased number of local populations in the landscapes. The number of local populations in the landscape also increased when the contract time was increased to ten years instead of five years. However, the number of local populations in the 'high quality' scenario did not differ from the scenario with standard habitat quality, because the standard contract time of five years was too short to enable the species to profit from the higher habitat quality.

In chapter 8 I presented a synthesis of the results and formulated perspectives for further research. I conclude that the fragmentation and

dynamics of habitat had the expected negative effect on the distribution patterns and the survival of plant species. The differences between species with contrasting dispersal and seed bank characteristics were not very clear in the field situation, but in the model simulations the long-term effects on the survival of plants with different strategies were obvious. The combination of empirical and modelling approaches appeared to be a useful strategy to study the effects of fragmentation and dynamics of habitat on the survival of plants in agricultural landscapes. I argued that long distance dispersal of plant species should also be studied by a combination of modelling and empirical studies, because direct observations of seed dispersal often underestimate the potential of long distance dispersal. The challenge for further research is how to integrate our knowledge of the relation between the survival of plants and the role of the plant strategies and landscape characteristics into quantitative rules for landscape management. I concluded that the suitability of landscapes for the survival of plants should be judged on the spatial arrangement of suitable habitat and the dynamics of the habitat related to the colonization strategies of plant species.

Samenvatting

Landschapselementen die niet worden gebruikt voor de voedselproductie zijn van groot belang voor de overleving van veel plantensoorten in agrarische landschappen in Noordwest Europa en delen van Noord-Amerika en Australië. Deze plantensoorten kunnen niet overleven in de intensief beheerde akkers en graslanden, maar zijn nog wel aanwezig in netwerken van half-natuurlijke vegetaties in sloten, wegbermen, houtwallen en kleine bosjes. De intensivering van de landbouw gedurende de tweede helft van de 20ste eeuw leidde tot het verwijderen van grote delen van die landschapselementen. Ook leidde het tot verslechtering van de habitatkwaliteit in de overgebleven landschapselementen voor grote aantallen plantensoorten. Het resultaat was een afname van de diversiteit van planten in agrarische landschappen.

Om de biodiversiteit van agrarische landschappen beter te beschermen, zijn maatregelen in het leven geroepen die er onder andere op gericht zijn de afname van de diversiteit van plantensoorten tegen te gaan. Deze maatregelen leidden echter lang niet altijd tot het gewenste resultaat. Op veel plaatsen bleef een verwachte toename van de plantendiversiteit uit. Landschapsecologisch onderzoek heeft aangetoond dat de overleving van planten- en diersoorten in een landschap niet alleen afhangt van de kwaliteit van de plekken waar de soorten kunnen voorkomen (habitatplekken), maar ook van de fragmentatie en de dynamiek van habitat op landschapsschaal. Wanneer habitat versnipperd is in diverse kleinere plekken, zullen ook de individuen van een soort verdeeld zijn over verschillende kleine lokale populaties. De kwaliteit van habitat in netwerken van landschapselementen in agrarische landschappen is dynamisch, onder andere door de invloed van landbouwactiviteiten in de aangrenzende percelen. Soorten kunnen lokaal uitsterven (extinctie), terwijl nieuwe, lege habitatplekken kunnen worden gekoloniseerd (uit zaad dat uit andere lokale populaties komt of dat al in de grond aanwezig was). Alleen wanneer de kolonisaties vaker vóórkomen dan de extincties kunnen soorten overleven in een landschap. Het kolonisatievermogen van plantensoorten is daarmee een sleutelfactor in de overlevingskans van soorten in gefragmenteerde en dynamische landschappen. Het verspreidingsvermogen van zaden (zaaddispersie) en de overlevingsduur van de zaden in de grond (de zaadbank) bepalen het kolonisatievermogen van plantensoorten.

Het onderzoek dat beschreven is in dit proefschrift heeft tot doel de kennis over de relatie tussen de overlevingskansen van plantensoorten en de fragmentatie en de dynamiek van het habitatnetwerk in agrarische landschappen te vergroten. Ik wilde weten of die relatie van soorten met de

rangschikking van habitat in ruimte en tijd afhing van de dispersie- en zaadbankeigenschappen van die soorten. Deze kennis is nodig om de effectiviteit van de maatregelen ter bescherming van de diversiteit van planten in agrarische landschappen te vergroten.

Om dat te bereiken, heb ik de relatie tussen de overleving van plantensoorten met verschillend kolonisatievermogen en de rangschikking van habitat in ruimte en tijd bestudeerd. Die relatie heb ik onderzocht met behulp van een combinatie van veldwerk en een computermodel. In hoofdstuk 2 wordt een conceptueel, theoretisch model beschreven dat is gebaseerd op een literatuurstudie. Verschillende veldstudies van planten in een netwerk van slootkanten in een agrarisch gebied in Drenthe worden beschreven in de hoofdstukken 3-5. Het werk dat met het computermodel is gedaan wordt beschreven in de hoofdstukken 6 en 7.

Het conceptuele model dat ik in hoofdstuk 2 beschrijf, is het startpunt voor zowel het veld- als het modellenwerk dat in de andere hoofdstukken is beschreven. Het conceptuele model beschrijft de relaties tussen de populatiedynamiek van planten en de kwaliteit, ruimtelijke rangschikking en dynamiek van het habitat. Op basis van het dispersievermogen van de zaden en de levensduur van de zaadbank worden vier kolonisatiestrategieën onderscheiden: soorten met òf lange (> 100 m) òf korte (< 100 m) afstand dispersie gecombineerd met òf een kortlevende (< 5 jaar) òf een langlevende (> 5 jaar) zaadbank. De hypothese die uit het conceptuele model voortkwam, was dat de overlevingskans van soorten enerzijds afhangt van hun kolonisatiestrategie en anderzijds van de de ligging van habitatplekken in het landschap en de dynamiek van de habitatplekken. Er waren slechts weinig gepubliceerde gegevens beschikbaar waarmee deze hypothese getest kon worden. Om de relatie tussen planten en landschappen te onderzoeken kan het beste een methode gebruikt worden waarin veldstudies en modelstudies op elkaar ingrijpen.

De veldstudies die beschreven zijn in de hoofdstukken 3-5 zijn uitgevoerd in een studiegebied in Drenthe. Het studiegebied bestond uit akkers die door een netwerk van sloten van elkaar zijn gescheiden. Dit studiegebied was gekozen omdat de vegetatie van de slootkanten veel variatie in kwaliteit vertoonde. Verschillende plantensoorten met contrasterende dispersie (korte of lange afstandsdispersie) en zaadbank (kort of lang levend zaad) eigenschappen kwamen in gefragmenteerde populaties in de slootkanten voor. Ik heb me

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vooral gericht op een selectie van dertien meerjarige kruidachtige plantensoorten met contrasterende zaadbank en dispersie-eigenschappen.

In hoofdstuk 3 beschrijf ik de relatie tussen de aanwezigheid van de dertien aandachtssoorten en de kwaliteit, ruimtelijke isolatie en leeftijd van habitatplekken. Habitatplekken waren gedefinieerd als stukken slootkant van 10 m lang. Of een soort wel of niet aanwezig was in een habitatplek werd vooral bepaald door de habitatkwaliteit en de aanwezigheid van dezelfde soort op korte afstanden van onderzochte plekken (< 25 m). Deze conclusie werd niet beïnvloed door de dispersie-eigenschappen van de soorten. De meeste soorten waren vaker aanwezig in oude dan in jonge sloten. Alleen soorten die een langlevende zaadbank hadden, werden ongeveer even vaak in jonge als in oude sloten gevonden. Dit geeft het belang van de zaadbank aan als bron van kolonisatie na grootschalige verstoringen.

De verspreidingspatronen van de dertien soorten werden gedurende drie opeenvolgende jaren bestudeerd. In hoofdstuk 4 wordt de dynamiek van die verspreidingspatronen geanalyseerd. Alle soorten koloniseerden regelmatig lege plekken van het ene op het andere jaar en bezette plekken raakten regelmatig leeg van het ene op het andere jaar door lokale extinctie. Ongeveer een derde van de bezette plekken in een bepaald jaar was in het afgelopen jaar gekoloniseerd (gemiddeld van de dertien soorten). De gemiddelde fractie van de bezette plekken dat uitstierf van het ene op het andere jaar was iets kleiner dan een derde. De kans dat een lokale populatie uitstierf, werd groter naarmate deze lokale populatie meer geïsoleerd lag (op een grotere afstand van andere lokale populaties van die soort). De kolonisatiekans nam juist af bij toenemende isolatie. De meeste kolonisaties werden gevonden binnen een afstand van 50 m tot een lokale populatie van de soort in het voorgaande jaar, maar regelmatig werden ook kolonisaties gevonden op afstanden van meer dan 200 m tot een andere populatie van de soort. Er was geen relatie tussen die kolonisatieafstanden en de dispersie-eigenschappen van de soorten. Voor soorten met een langlevende zaadbank werden langere kolonisatieafstanden gevonden dan voor soorten met een kortlevende zaadbank. De verschillen tussen de kolonisatiepatronen van soorten met een langlevende en kortlevende zaadbank kunnen het gevolg zijn van de jarenlange opeenhoping van de verspreide zaden van soorten met langlevende zaden.

De lokale kolonisaties die beschreven zijn in hoofdstuk 4 zijn het gecombineerde resultaat van zaadverspreiding en overleving van zaad in de grond. In hoofdstuk 5 worden zaadverspreiding en de zaadbank afzonderlijk

bestudeerd. Hiervoor is een aantal experimenten uitgevoerd. Allereerst is het vermogen van zaden om te drijven op water en de snelheid waarmee ze in de lucht naar beneden vallen gemeten. Met deze metingen was een bestaande indeling (in de literatuur) van soorten in groepen die door water of door wind verspreid worden te testen. De bestaande indeling bleek goed te voldoen. Vervolgens werden in het veld plots aangelegd waarin kolonisatie door zaadverspreiding bestudeerd kon worden. Deze 'dispersieplots' werden aangelegd in de slootkanten door de bovenste laag van de grond (met daarin de zaadbank) over een oppervlakte van 1 m^2 te vervangen door steriele grond (zonder zaadbank). Er werden minder soorten in de dispersieplots gevonden dan in de vegetatie rondom de plots. Soorten die een plot hadden gekoloniseerd, waren meestal ook aanwezig in de vegetatie rondom het plot, vooral soorten zonder aanpassingen voor lange afstandsdispersie. De zaadbank werd bestudeerd door te kijken welke soorten kiemden vanuit bodemmonsters. De bodemmonsters waren vlak naast de dispersieplots verzameld. Er werden meer soorten in de bodemmonsters gevonden dan in de vegetatie van de plek waar de monsters waren verzameld. Het aantal soorten met kortlevende zaden was groter in de monsters van oude sloten dan in die van jonge sloten. Dit komt doordat de aanwezigheid van die soorten in de zaadbank wordt bepaald door de aanwezigheid van die soorten in de bovengrondse vegetatie. Ze komen minder vaak voor in de vegetatie van jonge sloten vergeleken met oude sloten, waarschijnlijk door beperkte kolonisatie door dispersie, hetgeen ook de beperktere aanwezigheid van die soorten in de zaadbank van jonge sloten kan verklaren.

In hoofdstuk 6 wordt het computermodel beschreven. Het is een ruimtelijk expliciet model waarin de overleving van de populaties van een plantensoort in dynamische en gefragmenteerde landschappen wordt gesimuleerd. Het model is individu-gebaseerd, wat betekent dat ieder zaadje en iedere plant apart worden doorberekend. Ik heb met behulp van het model de overleving van vier model-soorten met contrasterende dispersie (korte of lange afstandsdispersie) en zaadbank (kort of lang levend zaad) eigenschappen bestudeerd in een netwerk van sloten met variërende fragmentatie en dynamiek van habitat. De overleving van de vier model-soorten nam statistisch significant af wanneer de fragmentatie en dynamiek van habitat toenamen. De verschillen tussen de overleving van de soorten met de verschillende kolonisatiestrategieën waren erg duidelijk voor de lange termijn ontwikkeling van de populaties (250 jaar). Maar wanneer naar de resultaten over een kortere

termijn, slechts 5 jaar, van de simulatieruns gekeken werd, waren de verschillen niet duidelijk. Ik heb de geldigheid van het model getest door kolonisatie- en extinctiekansen van lokale populaties en de ruimtelijke patronen van lokale kolonisaties en extincties volgens het model en het veldwerk met elkaar te vergelijken. Hiervoor werden de resultaten gedurende 5 opeenvolgende jaren volgens het model vergeleken met de resultaten van de tijdreeks van 3 jaar veldstudie (beschreven in hoofdstuk 4). Deze korte termijn resultaten van het model en de veldstudie kwamen goed overeen: kolonisatiekansen namen af en extinctiekansen namen toe wanneer de ruimtelijke isolatie toenam. Ook waren er geen duidelijke verschillen tussen de kolonisatie- en extinctiepatronen van soorten met verschillende kolonisatiestrategieën te zien.

In hoofdstuk 7 wordt het simulatiemodel gebruikt voor een scenario studie. In deze scenario studie worden verschillende alternatieven voor de uitvoering van beheersovereenkomsten, gericht op het verhogen van de plantendiversiteit in perceelranden, vergeleken. Ik wilde mogelijke verklaringen voor het uitblijven van het effect van beheersovereenkomsten op de plantendiversiteit testen. Andere onderzoekers stelden dat de afname van bemestingsdruk onvoldoende was voor het herstel van geschikt habitat voor soortenrijke vegetaties en dat het dispersievermogen van planten te klein is om de nieuwe habitatplekken te bereiken. In dit hoofdstuk wordt nog een andere verklaring voorgesteld: een 6-jarige contractduur voor beheersovereenkomsten is te kort om planten de gelegenheid te geven te profiteren van de betere habitatkwaliteit. Het simulatiemodel dat in hoofdstuk 6 was gebruikt, is enigszins aangepast voor de scenario studie. De effectiviteit van drie alternatieve scenario's voor de toepassing van beheersovereenkomsten werd vergeleken met die van standaard beheersovereenkomsten. Het standaard scenario was de willekeurige verspreiding van een aantal sloten met een beheersovereenkomst in het landschap. De overeenkomsten hadden een gemiddelde contractduur van 5 jaar. De drie alternatieve scenario's waren: verhogen van de habitatkwaliteit, verdubbeling van de gemiddelde contractduur naar 10 jaar en het clusteren van de sloten met beheersovereenkomsten in één deel van het landschap. De effectiviteit werd getest voor vier model-soorten met contrasterende dispersie- en zaadbankeigenschappen. Als maat voor de effectiviteit werd het aantal lokale populaties na 25 jaar genomen. Het scenario waarin de beheersovereenkomsten werden geclusterd was het meest effectief. Het aantal lokale populaties ten

opzichte van het standaard scenario nam ook toe wanneer de contractduur verdubbeld werd. Een verhoging van de habitatkwaliteit had echter vrijwel geen effect, omdat een gemiddelde contractduur van 5 jaar te kort was om de populaties in staat te stellen te profiteren van de verhoogde kwaliteit.

In hoofdstuk 8 wordt een synthese van de resultaten gegeven en worden voorstellen gedaan voor verder onderzoek. Ik concludeer dat fragmentatie en dynamiek van habitat het verwachte negatieve effect hadden op de overleving van plantensoorten. De verschillen tussen soorten met verschillende dispersie- en zaadbankeigenschappen waren niet altijd duidelijk in de veldstudies, maar in de modelsimulaties waren wel degelijk de lange termijn effecten voor de overleving van de verschillende soortgroepen te zien. De combinatie van veldwerk en modelstudies bleek een bruikbare methode te zijn om de effecten van fragmentatie en dynamiek van habitat op de overleving van plantensoorten in agrarische landschappen te bestuderen. Ik stel dat lange afstandsdispersie van planten ook het best bestudeerd kan worden met een combinatie van veldwerk en modelstudies, omdat potentiële dispersie afstanden vaak onderschat worden bij directe waarnemingen van zaaddispersie. Het is een uitdaging om in vervolgonderzoek de kennis van de relatie tussen overleving van plantensoorten en hun kolonisatiestrategieën en de landschapskenmerken te vertalen naar kwantitatieve regels voor landschapsbeheer. Ik concludeer dat de geschiktheid van landschappen voor de overleving van planten beoordeeld moet worden op basis van de ruimtelijke rangschikking en dynamiek van habitatplekken in relatie tot de kolonisatiestrategieën van de plantensoorten.