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Feasibility of target communities in a Dutch brook valley system

ADRIANA H. PRINS†, GERDIEN A. DIJKSTRA* and
RENÉE M. BEKKER‡

**DLO Institute for Forestry and Nature Research, PO Box 23, 6700 AA Wageningen; and*
‡Laboratory of Plant Ecology, University of Groningen, PO Box 14, 9750 AA Haren,
The Netherlands

SUMMARY

As a reaction to the ongoing deterioration of nature conservation interest in The Netherlands, an offensive nature strategy was formulated in the *1990 Nature Policy Plan.* In this Plan, target communities and target plant species are mentioned. For the 'Drentse A brook valley system', target communities were assessed by the Province of Drenthe. In the present study, a model is described that predicts the number of target plant species for four seminatural target communities, namely: *species-rich meadow, heathland, arable field* and *species-rich woodland.* Information is used on the present and past occurrence of target plant species in the study area. An estimate is made for the probability of germination from the seed bank and for the probability of seed dispersal for each of the four target communities. The model predicts a large deficit between the number of predicted plant species and a completely developed target community. Only half the target plant species can be expected at a maximum (for *species-rich meadow*). For *heathland,* 38% of the target plant species can be expected, while for *species-rich woodland* and *arable field* not more than 16% and, respectively, 8% of the target species are predicted to occur. Therefore, if nature policy in The Netherlands aims at completely developed target communities, there is an evident need for extra measures such as active introduction of species.

Key-words: arable field, heathland, model, Nature Policy Plan, species-rich meadow, species-rich woodland.

INTRODUCTION

Nature policy in The Netherlands

The decrease in diversity of plant species is a well-known phenomenon worldwide. In the last few years this has been reflected in several books dealing with biodiversity (e.g. Schulze & Mooney 1993; Boyle & Boyle 1994; Huston 1994; Krattiger *et al.* 1994; Hawksworth 1995; Gaston 1996). In The Netherlands it has been recognized since the beginning of this century, and it has become a topic of the public debate ever since

† Correspondence author.

(Van der Windt 1995). Eutrophication, acidification, desiccation, toxification and loss or fragmentation of habitat are the causes of this decreasing biodiversity. Nature conservation authorities tried to stop the decrease in nature reserves by careful management. Later, it was realized that the surroundings of nature areas should also be looked after: agricultural land use may have a great impact on nature reserves by means of eutrophication or desiccation. However, these strategies alone could not stop the ongoing deterioration of nature in The Netherlands. Therefore, an offensive nature strategy was formulated in the *1990 Nature Policy Plan* (Ministry of Agriculture, Nature Management & Fisheries 1990). The objectives of this plan are not only to restore nature reserves, but also to create new ones. These so-called 'nature development areas' are agricultural areas that have been designated to be developed into nature reserves. Ecological engineering and management are tools to achieve this aim. The concept of an 'Ecological Network' has been formulated, of which all existing nature reserves form the 'core areas'. For the existing nature reserves and the nature development areas, objectives and strategies have been formulated.

Target communities and target species

The Nature Policy Plan has two main principles: naturalness and biologicial diversity of species. Naturalness is defined in terms of degree of human interference. Four groups of target communities are distinguished. First, natural ecosystems are mentioned. Geomorphological and biological processes in this category are still relatively undisturbed by man. The second category includes ecosystems that are only rarely controlled by man. In these ecosystems, man manipulates natural processes such as erosion, sedimentation, seepage, inundation and grazing to only a limited extent. Since many species are confined to a more traditional agricultural landscape, a third category of semi-natural ecosystems is described. Management is aimed at maximizing biological diversity. Finally, in multifunctional ecosystems, species and plant communities coexist with different forms of land use. In the present study we focus on the third group of target communities: the semi-natural ecosystems. These systems are subdivided into nine groups according to their geographical range. We focus on the 'sand region': part of the area of The Netherlands that was formed mainly in the Pleistocene period.

The second principle of the Dutch nature policy is biological diversity, and is defined in terms of plant and animal species. We will concentrate on plant species. Species that are of national and international interest are called 'target species'. A target species has to meet at least two of the three following criteria:

I: The species is of international importance. A relatively large part of its biogeographical range is located in The Netherlands.
T: The distribution or the number of individuals of the species in The Netherlands exhibits a downward trend and has declined by at least 25% in the last 40 or 50 years.
R: The species is rare in The Netherlands.

This approach emphasizes the importance of species that are on the Red List of endangered species in The Netherlands. Using the above-mentioned criteria, 408 plant species (of a total of 1448 native species) have been selected as target species (Bal *et al.* 1995).

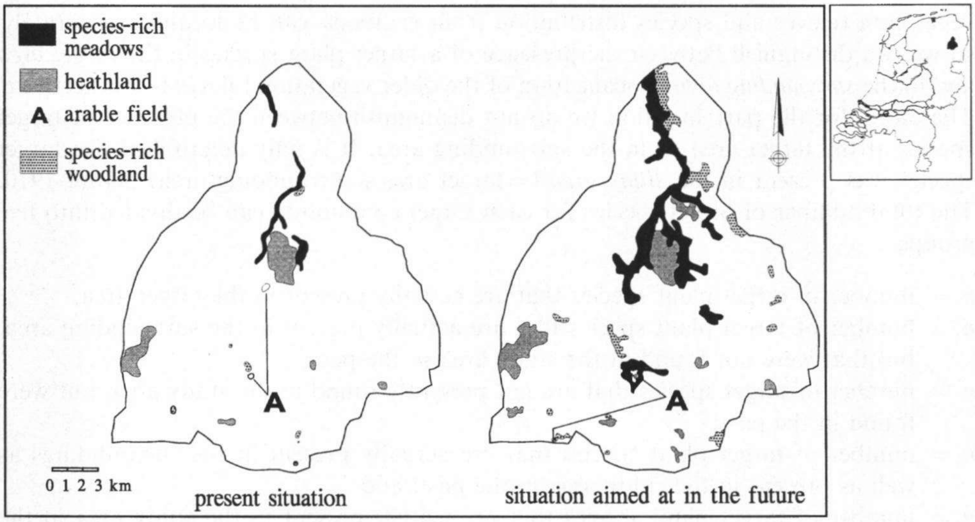

Fig. 1. Present situation with the spatial arrangements of the four target communities, and the situation aimed at in the future. Total surface area of the study area = 30 000 ha.

Aim of this study

The aim of the present study is to operationalize and evaluate the concept of target communities and target species. As a contribution to the debate on the feasibility of the Nature Policy Plan, we will try to acquire an insight into the feasibility of a few seminatural target communities in the catchment area of the 'Drentse A brook valley system' in the northern part of The Netherlands. The study will indicate whether extra measures such as deliberate introduction of plant species are needed to achieve a completely developed target community.

We will present a model for predicting the number of target plant species to be achieved. The model is fed with the present and past distribution of target plant species. For each target community, the probability of germination from a long-lived seed bank and the probability of seed dispersal are estimated.

STUDY AREA

The study area 'Drentse A' is situated in the northern part of The Netherlands (Fig. 1). The catchment area totals 30 000 ha. It contains a brook valley system and higher regions of the Drenthe plateau, and was previously formed by a characteristic combination of arable land, moist and dry grasslands, heathland, woodlands and hedges. Extensive heathland has decreased since 1800 and has partly become grassland. Woodland was reclaimed for grasslands until 1850 (Bakker 1989). In 1965, the nature reserve 'Drentsche A' was founded. Most of the study area is still in agricultural use.

MODEL

The distribution of the target plant species is available for the 'past' situation (c. 1930–70) and for the 'present' situation (1970–present). For the actual situation, vegetation relevés and species distribution from FLORBASE can be localized accurately, so we can distinguish between the presence of a target plant species in the *target area* and in the *surrounding area*. Localization of the older vegetation relevés is less accurate. Therefore, for the past situation we do not distinguish between the presence of target species at the target area or in the surrounding area. It is only determined if a target species was present in the *study area* (= target area + surrounding area) before 1970. The total number of target species for each target community can be divided into five groups:

n_1 = number of target plant species that are actually present in the target area;
n_2 = number of target plant species that are actually present in the surrounding area, but that were not found in the study area in the past;
n_3 = number of target species that are not presently found in the study area, but were found in the past;
n_4 = number of target plant species that are actually present in the surroundings as well as present in the study area in the past; and
n_5 = number of target plant species that are neither present in the study area in the actual situation nor in the past.

The number of target plant species that can be expected in the future situation is counted by:

$n_1 \times p_1 + n_2 \times p_2 + n_3 \times p_3 + n_4 \times p_4$, in which:

p_1 = 1 (it is assumed that plant species present at the target area will not disappear, because local management is aimed at preserving the species).
$p_2 = P_{\text{dispersal}} \times P_{\text{establishment}}$.
($P_{\text{establishment}}$ is distinguished because a seedling does not always grow to an adult plant, but is subject to herbivory, competition, fungal diseases or drought.)
$p_3 = P_{\text{germination from seed bank}} \times P_{\text{dispersal}} \times P_{\text{establishment}}$
$p_4 = (P_{\text{dispersal}} \times P_{\text{establishment}}) + (P_{\text{germination from seed bank}} \times P_{\text{dispersal}} \times P_{\text{establishment}}) - (P_{\text{dispersal}} \times P_{\text{establishment}}) (P_{\text{germination}} \times P_{\text{dispersal}} \times P_{\text{establishment}})$

For p_4, the duplicates must be subtracted from the sum of chances from dispersing out of the surrounding area into the target area or germinating out of the seed bank and then dispersing into the target area. When a seed is already dispersed from the surroundings into the target area, the chance of germination from the seed bank followed by dispersal into the target area no longer contributes to establishment in the target area.

As $P_{\text{establishment}}$ is assumed to be 1, this makes:

$$p_4 = P_{\text{dispersal}} \times (1 + P_{\text{germination from seed bank}} - P_{\text{dispersal}} \times P_{\text{germination from seed bank}})$$

A summary of the model is given in Fig. 2.

The variance can be calculated by:

$$n_2 \times p_2 \times (1\text{-}p_2) + n_3 \times p_3 \times (1\text{-}p_3) + n_4 \times p_4 \times (1\text{-}p_4)$$

(it is assumed that germination from the seed bank is independent of the germinating plant species).

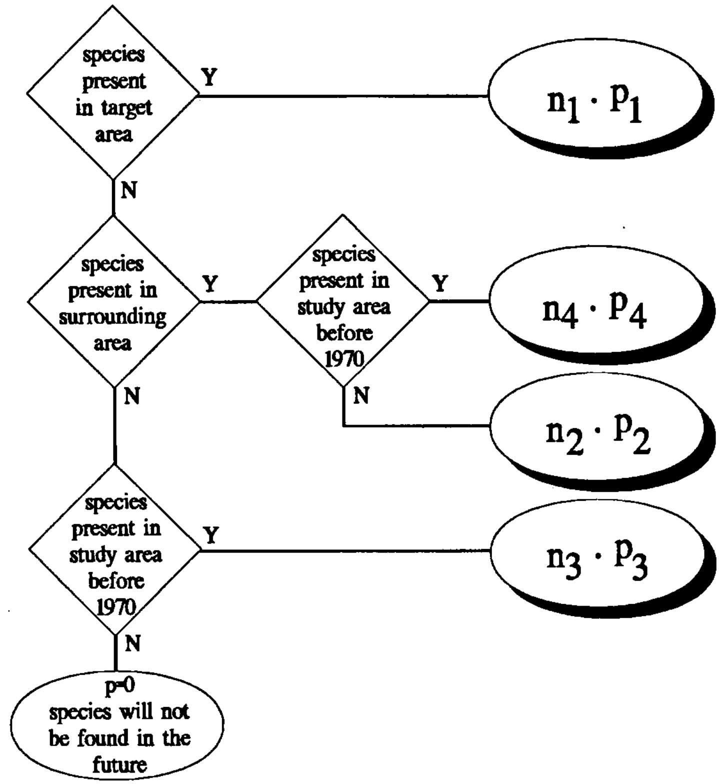

Fig. 2. A model for calculating the expected number of target plant species after 100 years. Target area = area where a target community is aimed at. Surrounding area = area within the study area where a target community is not aimed at. Study area = target area + surrounding area. For the actual presence of plant species we can distinguish between target area and surrounding area. For the presence of plant species in the past this distinction can not be made. Therefore, only the presence in the study area as a whole is used in the model.

MODEL PARAMETERS

Target communities and target species

For the study area 'Drentse A', the regional government has described target communities in terms of vegetation structure to be realized within 100 years. Four target communities have been selected, all of them representative of semi-natural ecosystems: *species-rich meadow, heathland, arable field* and *species-rich woodland.* For each of them, target plant species are derived from the Nature Policy Plan. For the 'sand region' we are left with 223 target plant species from a total of 408 for The Netherlands. For the four semi-natural target communities that are dealt with, 124 species were selected. Of these 124 species, 19 species are not characteristic of our study area, and were therefore omitted. Altogether, for the semi-natural ecosystems in this study, 105 target species were relevant. Some species can be target species for more than one target community. As the seed bank database by Thompson *et al.* (1997), which is used in this study, only includes higher vascular plants, spore-forming plants such as ferns and Orchids are excluded. Eleven spore-forming plants or Orchids are found. These species are excluded. Ninety-four target species, therefore, remain.

Actual presence of target plant species

The present vegetation map of the study area is based on vegetation relevés that have been made since the 1970s (Dijkstra *et al.* 1992). These vegetation relevés ($n=1654$ in our study area) are used to determine which plant species are found in the target areas, and which plant species are found in the surroundings (Fig. 1). A Geographical Information System (ARC-INFO; version 3.4.2) provides a useful tool for this analysis. Next to these vegetation relevés we made use of the national FLORBASE, which contains data on the presence of indigenous plant species in 1 km^2 plots. Data in FLORBASE originate from provinces, private people and nature conservation authorities.

Presence of target plant species in the past

To gain insight into the appearance of plant species from 1930 to 1970, we made use of vegetation relevés that are stored in a database at the DLO Institute for Forestry and Nature Research (Schaminée & Stortelder 1996); 434 vegetation relevés were available. Although the species list may not be complete, we assume most target plant species to be present in the relevés since the latter were usually made in areas with a high nature value. In these areas, rare plant species were most probably more frequent than in marginal areas.

Probability of germination from the seed bank

The established vegetation is often not similar to the viable seeds that are buried in the soil (e.g. Van Altena & Minderhoud 1972; Thompson & Grime 1979; Rice 1989; Lunt 1997). Some plant species have a persistent seed bank. Seeds may stay viable in the soil for many decades. *Juncus* species are renowned for developing large, persistent soil seed banks (Lunt 1997). Other plants are found without a persistent seed bank, e.g. long-lived ancient woodland species (Hodgson & Grime 1989; Hermy 1989). Plant species are usually divided into species having a transient seed bank (seeds persist in the soil for less than 1 year), and species with a short-term persistent seed bank (seeds persist in the soil for at least 1 year, but less than 5 years) and long-term persistent seed bank (seeds persist in the soil for at least 5 years) (Bakker 1989; Bakker *et al.* 1991; Thompson *et al.* 1997).

Data on the persistance of seeds in the soil is available for only a minority of species. Recently, Thompson *et al.* (1997) compiled a database of the available information on seed bank characteristics of North West European plant species ($n=2568$). For 1189 species, seed bank data are available. The quantity of data available for individual species varies: for 250 species only one record is available. Most information is available for common species from productive agricultural habitats, while less productive semi-natural habitats have received much less attention (Bakker *et al.* 1996a). Most of the target plant species defined in the Nature Policy Plan for The Netherlands are rare species. These species are, therefore, unfortunately under-representated or missing in the database. Of the 94 target plant species that we deal with in this study, 59 were mentioned in the seed bank database by Thompson *et al.* (1997). Of these 59 target species, 18 were mentioned at least once as having a long-term persistent seed bank (category 3 in Thompson *et al.* 1997). We assume, therefore, that on average 31% of the species (18 of 59) have a persistent seed bank. As data on most individual target plant species are lacking, we have to estimate the probability of having a persistent seed bank for the four target communities distinguished.

Species-rich meadow.. Grasslands can be classified as having a transient or short-term persistent seed bank (Bekker *et al.* 1997). For example, flood meadows (McDonald 1993; McDonald *et al.* 1996), dry alvar grasslands (Bakker *et al.* 1996b, 1997), chalk grasslands (Willems 1988), grassland in a woodland vegetation (Lunt 1997) or wet grasslands (Hofstede *et al.* 1991) were shown as having a transient or short-term persistent seed bank. For the species-rich communities, *Junco-Molinion* and *Meso-bromion* short-lived seed banks could be classified by Bekker *et al.* (1998, this issue). For *species-rich meadow* we therefore use the counted average proportion of 31% as an estimate of the probability of germinating seed from the seed bank. This probability is set at 0·31.

Heathland. Species of heathland communities are more likely to have a persistent seed bank. Species such as *Calluna vulgaris* tend to accumulate a large long-term persistent seed bank (Hodgson & Grime 1989; Willems 1988). Heathland species may survive in the soil of improved grassland on former heathland (Stieperaere & Timmerman 1983; Ter Heerdt *et al.* 1997). In general, we estimated the seed longevity of heathland communities as far larger than that of grassland communities. As an estimate of the probability of germination from the seed bank we multiplied the calculated average of 31% of the species having a seed bank by 1·5. For *heathland*, the probability of germination from the seed bank was therefore set on 0·47.

Arable field. Weed seed can remain in agricultural soil unsuitable for its development for a long time. It can germinate when conditions again become favourable, e.g. by ploughing old grasslands. Seed of arable plant species cannot germinate under dark conditions, as can seed of many grass species. When light conditions become favourable by disturbance, dormancy of seeds can be broken (Grime & Jarvis 1975). When former arable land that was under pasture for 6 years was disturbed, a large flush of germination was found during the subsequent 4 weeks (Wesson & Wareing 1969). For arable weed communities, high seed longevity was found by Bekker *et al.* (1998, this issue). We therefore doubled the percentage of species that were found to have a long-term persistent seed bank (31% for all target communities that are discussed in this paper). The probability of germination from the seed bank was thus 0·62.

Species-rich woodland. Forest species are rarely found in the seed bank and are mostly completely lacking (Brown & Oosterhuis 1981). Tree species that lack a persistent seed bank usually have alternative regeneration strategies: e.g. sprout (*Fagus*) or a seedling bank (*Prunus serotina*). Forest herbs possess alternative ways of propagation, such as bulbs or stolons. Species that do occur in the seed bank in deciduous forests can be characterized as shade-intolerant species, early successional species or colonizing species. These species dominate the ground layer after thinning (coppicing). The seed longevity of woodland communities can be illustrated by an example of deciduous woodland on limestone. This woodland was found to have a transient soil seed bank (Bekker *et al.* 1998, this issue). Since most woodland vegetation lacks a persistent seed bank for characteristic ancient wood species, we halved the average of 31% of the target plant species that were found to have a long-term persistent seed bank. Probability of germination from the seed bank was set at 0·16.

Table 1. Positive and negative effect of some characteristics on probability of dispersal for every target community

	Openness of the vegetation	Size and spatial arrangement	Management	Probability of dispersal
Species-rich meadow	+	+	+	0·50
Heathland	+	±	±	0·25
Arable field	+	−	−	0·13
Species-rich woodland	−	−	−	0·06

Probability of seed dispersal

Information on the method of dispersal of many plant species and on seed dispersal distance is even more rare than information on seed banks (Bakker *et al.* 1996a). For each target community, we therefore estimated the probability of effective seed dispersal into the target area. The average distance in the study area to be bridged was 15 km (Fig. 1). The target communities were aimed at being completely developed within 100 years. Therefore, we assumed that a distance of 150 m has to be bridged every year. The estimate of dispersal probability for each target community was based on openness of the vegetation, on the spatial arrangement of the target communities and on the expected impact of management on probability of dispersal.

Openness of the vegetation. Abiotic vectors for dispersal (wind, water) are particularly associated with open, disturbed and impermanent habitats. In more stable habitats (e.g. woodland), dispersal by animals may become more important (Hodgson & Grime 1989). Usually, wind dispersal is not far-reaching. Dispersal distances of less than 10 m are found for chalk grassland species (Verkaar *et al.* 1983), Asteraceae (Sheldon & Burrows 1973) and for four prairie grasses (Rabinowitz & Rapp 1981). In a model, Verkaar (1989) estimated that it could take more than a century to bridge only 500 m by wind dispersal. Patterns of seed rain follow a bell-shaped curve, with a small proportion dispersing over long distances and the majority falling close to the parent (Harper 1977; Strykstra & Bekker 1997; Strykstra *et al.* 1998, this issue). Sometimes long-distance transport is achieved by water or wind dispersal (Nip-Van der Voort *et al.* 1979; Marshall & Hopkins 1989). However, long-distance dispersal is often overemphasized, based on rare accidental dispersal (Stieperaere & Timmerman 1983).

Both ants and seed-collecting beetles do not usually disperse seeds for more than a few metres (Den Boer 1970; Beattie & Culver 1981). Grashof-Bokdam (1997a) found that in non-forest habitat only a limited distance was covered by forest birds and ants. *Anemone nemorosa* dispersed only 6–10 m or less during a century (Pigott 1982). The ant-dispersed plant species *Corydalis ambigua* is found to be spread $48{\cdot}3 \pm 34{\cdot}4$ cm per year (Ohkawara *et al.* 1997). For *Lonicera periclymenum* it was determined by genetic analysis that 80% of the seedlings can be found within a few metres from the parent plant, with a dispersal distance of 300 m (Grashof-Bokdam 1997b). For ancient woodland species, Hermy (1989, 1994) states that short-distance dispersal is the rule.

Regarding the openness of the vegetation, we assumed that probability of seed dispersal is higher in open areas with wind dispersal than in closed areas such as woodlands in which dispersal by animals is dominant (Table 1).

Size and spatial arrangement of the target communities. In the present situation, *species-rich meadows* are already partly connected (Fig. 1). This connection must be extended in the future. Some *heathland areas* are already large, but they are isolated (Fig. 1). *Arable field* is not only small at present, it is also isolated, and will be so in the future (Fig. 1). Only small, isolated patches of *species-rich woodland* are found presently. This target community is aimed at being developed in places where woodland is not always present currently. We expect that present and future size and spatial arrangement of the target communities have a positive effect on dispersal probability of *species-rich meadow* (Table 1). For *heathland,* we expect the probability of dispersal to be less positively influenced, since the areas are isolated. No positive effect on seed dispersal is expected for *arable field* and *species-rich woodland.* The latter target communities have a much smaller size and are isolated (Table 1).

Management. Seed dispersal can be influenced strongly by agricultural practices. In grassland plants, the mowing and hay-making process can result in dispersal over more than 10 m (Ter Borg 1985). Hay-making machinery is found to disperse seeds and may contribute to restoration of grasslands in nature reserves (Bakker 1989; Willems & Bobbink 1990; Bakker *et al.* 1996a; Strykstra *et al.* 1996). Due to active management, seeds can be exported from species-rich fields and imported into species-poor fields. In *heathland,* no such machinery is used. Dispersal of seeds may take place by sheep (Welch 1985). As grazing animals are not transported actively from one heathland area to another, management is expected to have a less positive impact on seed dispersal compared to *species-rich meadow* (Table 1). In historical times weeds were sown with uncleaned seeds. Because of the use today of cleaned seeds, weed species are found only rarely. As these species are not actively introduced, arable weed species have an extremely low dispersal capacity. We assume in this study that management has no positive effect on seed dispersal of *arable field.* Management in *species-rich woodland* is also not expected to contribute positively to seed dispersal (Table 1).

An estimate of the probability of seed dispersal for each target community. Combining the aforementioned impacts for the four target communities, we conclude that the highest probability of seed dispersal will be found for *species-rich meadow.* We estimate that probability of seed dispersal is 0·50, because of present management practices (moving mowing-machinery from species-rich to species-poor meadows) and because of favourably situated meadows at present and in the future (Table 1; Fig. 1). For *heathland,* we halve the probability of seed dispersal that is estimated for *species-rich meadow.* Probability of dispersal is set on 0·25 (Table 1). Again, probability of seed dispersal is halved for *arable field* ($P_{dispersal}=0{\cdot}13$), since only dispersal type has a positive impact. *Species-rich woodland* is estimated to have a probability of seed dispersal of half that of *arable field*: $P_{dispersal}=0{\cdot}06$. This last figure is supported by a dispersal distance of woodland species of maximally *c.* 10 m per year that is found by Grashof-Bokdam *et al.* (personal communication). This is *c.* 6% of the earlier-mentioned 150 m that has to be bridged each year.

RESULTS

Actual presence of plant species

Only 0–20% of the target species are already found in the target areas (Table 2). No target species are present at the moment in target areas for *arable field.* The present

Table 2. Target species for each target community. – not present in the database by Thompson *et al.* (1997); + – present in the database but not mentioned as having a long-term persistent seed bank; + + species that are mentioned at least once as having a long-term persistent seed bank (seed bank category 3 in Thompson *et al.* 1997)

Target community: species-rich meadow; number of target plant species = 46	
Already present in the target area ($n_1 = 9$)	
Carex aquatilis	+ +
Carex oederi subsp. *oederi*	–
Crepis paludosa	+ –
Cynosurus cristatus	+ +
Hieracium pilosella	–
Hierochloe odorata	–
Pedicularis palustris	+ –
Phytheuma spicatum subsp. *nigrum*	+ –
Danthonia decumbens	+ –
Not present in the target area, but in the surrounding area; not found in the past ($n_2 = 8$)	
Callitriche palustris	–
Carex pallescens	+ +
Euphorbia cyparissias	+ +
Narcissus pseudonarcissus subsp. pseudonarcissus	–
Taraxacum celticum	–
Vicia lathyroides	+ –
Alchemilla glabra	–
Festuca ovina subsp. *ovina*	+ +
Not presently found, but in the past ($n_3 = 4$)	
Briza media	+ –
Juncus tenageia	–
Parnassia palustris	–
Taraxacum palustre	–
Presently found in surroundings, as well as found in the past ($n_4 = 17$)	
Carex hostiana	+ –
Carex pulicaris	–
Cirsium dissectum	–
Corynephorus canescens	+ –
Filago minima	+ +
Genista anglica	+ –
Genista pilosa	+ –
Hypericum humifusum	+ +
Montia fontana subsp. *fontana*	+ +
Polygala serpyllifolia	+ –
Polygala vulgaris	+ –
Radiola linoides	–
Sagina nodosa	+ +
Scleranthus perennis	–
Scutellaria minor	+ –
Teesdalia nudicaulis	–
Bromus racemosus	–
Neither presently found, nor in the past ($n_5 = 8$)	
Artemisia absinthium	+ –
Carex dioica	+ –
Eleocharis quinqueflora	–
Genista tinctoria	+ –
Lathyrus linifolius	+ –
Pinguicula vulgaris	+ –

continued

Table 2—*continued*

Serratula tinctoria	+ −
Vulpia bromoides	+ −
Target community: heathland; number of target plant species = 35	
Already present in the target area ($n_1 = 7$)	
Arnica montana	+ −
Erica tetralix	+ +
Eriophorum vaginatum	+ +
Hieracium pilosella	−
Narthecium ossifragum	+ −
Rhynchospora fusca	+ −
Danthonia decumbens	+ −
Not present in the target area, but in the surrounding area; not found in the past ($n_2 = 0$)	
Not presently found, but in the past ($n_3 = 7$)	
Carex limosa	−
Anagallis minima	−
Cicendia filiformis	−
Eriophorum gracile	+ −
Juncus pygmaeus	−
Juncus tenageia	−
Scorzonera humilis	+ −
Presently found in surroundings, as well as found in the past ($n_4 = 16$)	
Antennaria dioica	+ −
Carex oederi subsp. *oederi*	−
Corrigiola litoralis	−
Cuscuta epithymum	−
Filago minima	+ −
Genista anglica	+ −
Genista pilosa	+ −
Hypericum humifusum	+ +
Hypericum pulchrum	+ +
Illecebrum verticillatum	−
Pedicularis sylvatica	−
Polygala serpyllifolia	+ −
Polygala vulgaris	+ −
Radiola linoides	−
Sagina nodosa	+ +
Thymus serpyllum	+ −
Neither presently found, nor in the past ($n_5 = 5$)	
Carex dioica	+ −
Carex trinervis	−
Drosera longifolia	−
Scheuchzeria palustris	−
Ulex europaeus	+ +
Target community: arable field; number of target plant species = 15	
Already present in the target area ($n_1 = 0$)	
Not present in the target area, but in the surrounding area; not found in the past ($n_2 = 1$)	
Aphanes inexpectata	+ −
Not presently found, but in the past ($n_3 = 4$)	
Agrostemma githago	+ −
Bromus secalinus	+ −

continued

Table 2—*continued*

Buglossoides arvensis	+ −
Veronica triphyllos	−
Presently found in surroundings, as well as found in the past ($n_4=4$)	
Anthemis arvensis	+ +
Aphanes arvensis	+ +
Arnoseris minima	+ −
Teesdalia nudicaulis	−
Neither presently found, nor in the past ($n_5=6$)	
Anthemis cotula	+ +
Fagopyrum tataricum	−
Hypochaeris glabra	+ −
Lilium bulbiferum subsp. *croceum*	−
Silene gallica	+ −
Vulpia bromoides	+ −
Target community: species-rich woodland; number of target plant species = 19	
Already present in the target area ($n_1=2$)	
Crepis paludosa	+ −
Solidago virgaurea	+ −
Not present in the target area, but in the surrounding area; not found in the past ($n_2=11$)	
Hieracium maculatum	−
Galeobdolon luteum	+ −
Luzula sylvatica	+ −
Mycelis muralis	+ −
Narcissus pseudonarcissus subsp. *pseudonarcissus*	−
Pyrola rotundifolia	+ −
Stellaria nemorum	+ −
Taxus baccata	−
Veronica montana	−
Vinca minor	−
Montia fontana subsp. *fontana*	+ +
Not presently found, but in the past ($n_3=0$)	
Presently found in surroundings, as well as found in the past ($n_4=5$)	
Hypericum pulchrum	+ +
Lysimachia nemorum	+ +
Phyteuma spicatum subsp. *nigrum*	+ −
Scutellaria minor	+ −
Viola reichenbachiana	+ +
Neither presently found, nor in the past ($n_5=1$)	
Pyrola minor	+ −

area where *arable field* is found is, however, very small (Fig. 1). In Fig. 1 it can be seen that not all present arable field is aimed at being the target community *arable field* in the future. The area in the middle of the study area is aimed at developing into woodland pasture (not studied in this paper). The same is found for *species-rich woodland.* A small area in the southern part of the study area, that was also not studied, is aimed at being a part of a greater woodland scenery. For *species-rich woodland* only two out of 19 target species (11%) are present. In areas where *species-rich meadow* or *heathland* has to be developed, 20% of the target species are already found (respectively,

Table 3. Number of species actually present and found in the past, and expected number of species after 100 years (% in parentheses; SD = standard deviation = square root of variance)

		Species-rich meadow (n=46)	Heathland (n=35)	Arable field (n=15)	Species-rich woodland (n=19)
Comparison of historical and actual data	n_1	9 (20%)	7 (20%)	0 (0%)	2 (11%)
	n_2	8 (17%)	0 (0%)	1 (7%)	11 (58%)
	n_3	4 (9%)	7 (20%)	4 (27%)	0 (0%)
	n_4	17 (37%)	16 (46%)	4 (27%)	5 (26%)
	n_5	8 (17%)	5 (14%)	6 (40%)	1 (5%)
Model parameters (see text)	$P_{germination}$	0·31	0·47	0·62	0·16
	$P_{dispersal}$	0·50	0·25	0·13	0·06
Calculated changes with the model	P_2	0·50	0·25	0·13	0·06
	P_3	0·16	0·12	0·08	0·01
	P_4	0·58	0·34	0·20	0·07
Outcome of the model	$n_{expected}$ ($\pm$SD)	23·5 (51%) $\pm$2·6	13·3 (38%) $\pm$2·1	1·3 (8%) $\pm$1·0	3·0 (16%) $\pm$1·0

nine of 46 and seven of 35; Tables 2 and 3). When looking at the surrounding area (n_2), up to 58% of the species are found for *species-rich woodland.* For the other target communities, the number of species found in the surrounding area is much smaller (Tables 2 and 3).

Presence of target plant species in the past

Fourteen species that are presently not found in the study area were found before 1970: no species for *species-rich woodland,* four species for *species-rich meadow,* four species for *arable field* and seven species for *heathland* (Tables 2 and 3; *Juncus tenageia* is a target species for *species-rich meadow* as well as for *heathland*). These species have to germinate from the seed bank and diaspores have to disperse into the target area before they can contribute to the realization of a target community.

Comparison of the four target communities

The number of target species that are calculated with our model to be found after 100 years varies from only 1·3 (8%) for *arable field* to 23·5 (51%) for *species-rich meadow* (Table 3). Comparing these figures with the number of target plant species that are already present, the highest increase is found for *heathland* and for *species-rich meadow.* For *species-rich meadow,* the number of plant species is found to be increasing from nine species already present to 23 species that are expected after 100 years, using our model. This is caused mainly by the large number of species (n = 17) that are present in the surrounding area and that were present in the past (n_4). For *heathland,* the increase from seven species in the actual situation to 13 species that are expected after 100 years is also due mainly to the presence of species currently in the surroundings and in the past. For *arable field,* only a small increase in number of species is found between the present situation and the situation after 100 years, due to the small number already present or found in the past, and a high percentage of species that are not presently found, but that were also not found in the past. According to the model, these species can never be found in the future. For *species-rich woodland*, a small increase in the number of species is also expected. Although a large number of species ($n = 11$; 58% of the target species) are already present in the surrounding area, the low probability of germination from the seed bank as well as the low probability of seed dispersal prevent a large increase in plant species during the next 100 years.

DISCUSSION

The model

In the present model several assumptions have been made. First, we assumed that seed that is present in the seed bank has a high probability to germinate. The probability of germination is supposed to be 1. Moreover, we assumed that once germination has taken place, establishment of a plant is always successful. However, seeds that are buried deep in the soil may not be able to germinate. Ploughing or vertical movement must bring the seed to the upper soil layer where germination can take place (Willems & Huijsmans 1994). Seed with a long-term persistent seed bank is known to need light to germinate (Wesson & Wareing 1969; Thompson & Grime 1979; Chancellor 1986; Thompson 1987). Once a seed has germinated the seedling may be prone to many threats (herbivory, competition, fungal diseases, drought). Only a few seedlings, or even no seedling at all, may be able to survive. Thus, the predicted number of species that will develop for each target community is probably much less than is predicted.

In the model we did not presume an interaction between seed bank and dispersal capacity of plants. For individual plant species, generalizations were made regarding dispersal strategy and environmental characteristics (Bakker *et al.* 1996a). In environments that are unpredictable in space, species used to rely on long-distance dispersal. Environments predictable in space may maintain species with a long-term persistent seed bank. Plant species are often found having either a well-developed dispersal capacity or a long-term persistent seed bank. However, on one hand some species are found having both a long-distance dispersal and a long-term persistent seed bank (e.g. species colonizing gaps in forests) (Thompson 1992). On the other hand, species without a well-developed dispersal capacity and a long-term persistent seed bank are found in environments with predictable circumstances for establishment in space and in time (Bakker *et al.* 1996a). These species rely on clonal recolonization. At the level of target communities, these general characteristics can also be recognized. *Species-rich meadow* was expected in our model to have an average seed bank probability. Dispersal capacity was intermediate when it was not helped by management. The dispersal capacity is upgraded in our model because of the active dispersion by haymaking machinery (Strykstra *et al.* 1996; Bakker *et al.* 1996a). *Heathland* has a higher seed bank probability compared to *species-rich meadow*. Probability of dispersal is artificially raised, as in *species-rich meadow*, because of seed dispersal by sheep (Willems 1988; Fischer *et al.* 1996). *Arable field* has a high probability of containing a seed bank, but has a low dispersal capacity. This target community meets the description of an environment predictable in space. It did not achieve upgrading of dispersal capacity by active management. Finally, *species-rich woodland* does not have a high probability of seed bank nor a high probability of seed dispersal in our model. This target community meets the description of environments with predictable circumstances for establishment in space and in time. Woodland species tend to have a long life span and to disperse by means of clonal recolonization. In fact, woodland species are considered extremely sensitive to extinction because of their limited colonization capacities and their absence of persistent seed banks (Hermy 1994). The estimates used in our model for seed bank and dispersal probability thus meet the general findings of dispersal strategy in relation to environment (Bakker *et al.* 1996a).

The present model could be improved by taking into account seed bank characteristics and dispersal capacity for *each individual target species*. This is not possible at the moment, because information on seed bank is available mainly for common species in productive environments (Bakker *et al.* 1996a). Much less information is available about rare species. Burial experiments, both in fertilized and unfertilized both in wet and dry conditions in various environments, on the survival in a seed bank are necessary (Albrecht & Forster 1996; Knevel, personal communication). However, it may take years to be certain if a species has a long-term persistent seed bank. Moreover, it will be difficult to perform such experiments as the species we deal with are only rarely found. Information on seed dispersal for each individual target species is even more difficult to obtain. Experiments may give information about the mean distance that can be travelled by a seed, but as patterns of seed rain are likely to follow a bell-shaped curve (Harper 1977) the small proportion of seed that disperses over large distances may have an important impact on the results of our model (Strykstra *et al.* 1996; Strykstra & Bekker 1997; Strykstra *et al.* 1998, this issue). Genetic analysis and studies on spatial arrangement on plant species may also be helpful in determining dispersal distance of plants (Grashof-Bokdam 1997b).

The model could be extended with a historical component if more information could be made available on spatial arrangement of the vegetation in the past and on management in former days. Albrecht & Forster (1996) found that former land use and soil humidity have a high impact on the number of seed in arable soil seed bank. Also, we did not take into account that in the absence of input of seed from seed production, the seed bank declines more readily with cultivation than without cultivation. The total loss of viable seed in the soil seed bank increases with the number of cultivations (Grime & Jarvis 1975; Chancellor 1986). Therefore, if cultivation has taken place frequently since the input of seed had stopped, the seed bank may be overemphasized. This would imply an even lower number of plant species in the future.

Evaluation of nature policy for the 'Drentse A brook valley system'

Although we have used optimistic assumptions in the model, 50% or even more of the target plant species will *not* appear in the target areas in a period of 100 years. The maximum number of species that can ever be found are the total number of target species for each target community minus the number of species that are neither found in the present situation nor in the past (Table 3; n_5). In *arable field* it is found that as many as 40% of the target species can never reappear (Table 3). For *species-rich woodland* a maximum of 92% of the target species may be found in future ($n_5 = 8\%$), but even by using an optimistic scenario, not 92% but only 18% of the target plant species of *species-rich woodland* may (re)appear in the target areas. This is due mainly to the low probability of having a long-term persistent seed bank combined with a low dispersal capacity. This is in agreement with the expectation that if ancient woodland species are not present, one should not expect them to be imminent. It may take centuries for a species to reach a new site (Hermy 1992). Peterken (1997) even suggests that it may take more than 800 years if the present agricultural land is considered as a starting point for restoration of woodlands. Particularly on nutrient-rich soils, the feasibility reduces even further because abandonment is often followed by an enormous expansion of competitive species. *Species-rich meadow* and *heathland* are expected to develop into more complete target communities because of the relatively high dispersal capacity. In these target communities a large deficit also exists between the number of predicted plant species and a completely developed target community. If nature policy in The Netherlands aims at completely developed target communities, there is an evident need for extra measures such as active introduction of species.

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