Evaluation of vegetation changes in Midden Groningen using plant and environmental traits

Photo by Bart Slot

Masterproject by Bram Verheijen, S1467689

Supervisors: Rudy van Diggelen and Jelte Pieter Dijkstra

September 2007 - April 2008

university of groningen

Introduction

Connecting fragmented areas

Nowadays, one of the major problems restoration ecology has to deal with are the negative consequences caused by fragmentation, which leads to large decline in number of species and plant population size and in general to a loss of biodiversity. Due to fragmentation it becomes more difficult for plant species to disperse their seeds and exchange genes between populations with the ultimate consequence: the risk of extinction.
The dispersal capacity of plant species depends on their dispersal factor. For example: water, wind or animal dispersal or combinations of these (Mouissie et al., 2005;Ozinga et al., 2004). Ozinga et al. (2004) showed that for the Netherlands (were fragmentation is severe), in particular, the species depending on water and animal dispersal had the largest decline.

One important solution to counteract negative results of fragmentation is that small fragmented nature areas should be connected into larger nature areas, so that plant species can disperse more easily. If plant species are able to exchange genes again and are therefore no longer subject to inbreeding and genetic erosion, the plant populations, but also individuals, will have a better chance to survive in the long run (Ozinga et al., 2004).
In the Netherlands small fragmented nature areas will be connected in to larger natures areas with realization of the National Ecological Network (Minestry of LNV, 1990) (In Dutch called the Ecologische Hoofdstructuur, EHS). In this project existing nature areas will be enlarged and connected, so that one large network of 728.500 ha. is created, which is 17.5% of the total land surface of the Netherlands. In addition, this national governmental project has started in 1990 and should be finished in 2018. However realization can only be accomplished by the restoration of 151.500 ha. of former agricultural fields and restoration of 27.000 ha. to form corridors between the areas and form a solid nature network. (Minestry of LNV, 1990)

Constraints in restoration

To restore nature to its original natural state or to a certain target state, (which first needs to be defined before restoration will actually take place) many bottlenecks need to be overcome. This is even more true for former agricultural fields that require total re-colonization of (target-)species (Verhagen et al., 2001;Bakker et al., 2002). Besides, most of the time little or no seeds are left in the seed bank if agricultural practices have been applied for several decennia (Bakker et al., 1996;Middleton, 2003). So, restoration often takes a very long time. To speed up colonization it is thought that creating the right abiotic conditions are very important. For example groundwater levels, pH, nutrient content, soil type and other abiotic factors should first be restored before establishment of target species or target vegetation types can take place.
An important biotic factor that constrains restoration is limitation in seed dispersal, as most of the source populations are too far away from restoration sites. Therefore it still takes a long time for species to establish, even if an area is completely suited for it regarding the abiotics conditions (Verhagen et al., 2001). There is a call in restoration to help plant dispersal by active transport of seeds, however, this is beyond the focus of this master research.
Once species have established, their competition capacity for light also seems very important (Schmitt and Wulff, 1993). Only restoring abiotic factors is not enough to ensure success, also biotic factors should be favorable for the target species of that area.

Vegetation shifts

In general, changes in vegetation composition over time can be very variable. However, when the environmental conditions are more or less stable, only some random changes can be expected: some species drop out and some enter the area, or some increase and some decline in their abundance. However, restoration measures are meant to change abiotic conditions in a directional way. For example, when the area becomes wetter due to a rise in the water table this will increase the selection for species that are more adapted to wet conditions and which will lead on its turn into a directional change in the vegetation composition.

Traits

Plant species can have many different characteristics or traits, (like: leaf morphology, canopy height, seed weight and many others) which differ a lot between species. Traits 'assist' species to cope with environmental conditions. The last decades, plant functional traits have been used more and more in ecological studies (Violle et al., 2007;Violle et al., 2006) as traits make it more easier to scale up from individuals to levels of communities or even ecosystems. In restoration plant functional traits (together with abiotic indicator values (Ellenberg values) which also can be characterized as traits) could be useful in order to evaluate restoration measures. If an area has been restored, new selection pressures will have an impact on traits and this will determine which species are able to colonize and survive after restoration measures have taken place. Which traits are good predictors for surviving and colonizing is off course the question.

Research questions

In this master research effects of restoration measures and changes in management on the vegetation composition will be analysed. This will be done for existing small nature areas, but also for former agricultural fields. Possible changes will be explained with use of plant functional traits and abiotic indicator values. The next three questions are addressed:

1) Are there changes in vegetation composition of the restored nature area Midden Groningen over the period 1999-2007?
2) If there is a directional shift in vegetation, which (combination of) plant traits and abiotic indicator values will best explain this change?
3) What is the ecological meaning of changes in vegetation composition and its impact on traits and abiotic indicator values?

Material and Methods

Study area and sites

The study area is Midden-Groningen (1850 hectares, province of Groningen, The Netherlands) which is part of the Dutch National Ecological Network, but not connected to it yet. There are small fragments of nature left (29% of the whole area), but the main part of the area consists of former agricultural fields. In the south and in the middle former agricultural fields were abandoned since 2000. In the north agricultural fields will be abandoned in 2010. Subsequently, new management was introduced: rising water tables, mowing less frequently and in the south whole-year-round cow grazing. In several places in the area, restoration measures like top soil removal were carried out in order to create nutrient poor conditions and open germination sites for species to establish (Van Diggelen et al., 2000-2007).

Possible effects of taken measures were analysed in four sites in Midden Groningen, located in the south (sand), the middle (peat), the north-west (peat) and the north-east (clay). Characteristics of the four sites can be found in Table 1.
In every site permanent quadrates (2m x 2m) were established, for a total of 57. Figure 1 points out the positions of these quadrates. Each year the species composition and cover of the permanent quadrates were recorded using the scale of Londo (Londo, 1976). In this way detailed information could be obtained about changes in species composition over time. Establishment of permanent quadrates and subsequently recordings did not start in the same year for all the four sites.

Table 1: The four study sites and their characteristics.
**At Woudbloem the numbers between the brackets are of the later added permanent quadrates.*

Site	*Soil Type*	*In management since (year)*	*Monitored since (year)*	*Number of permanent quadrates*	*New Management Type*
Dannemeer	Clay	1982	1999	12	Fertilisation on some spots, Mowing
Woudbloem	Peat	1978	1999 *(2005)	15 (6)	Mowing (removing hay)
Kolham	Sand	2000	2003	24	Mowing, grazing, some top-soil removal
Berkenbosje	Peat	1983	1999	6	First mowing, now no management

Change in management

It is expected that introduction of new management will lead to several main changes in study area Midden Groningen. For example as agricultural practices like adding artificial fertilizer and liming has been stopped, it is expected that the area will become more acid and nutrient poor. Productivity will decrease and therefore competition for light will not be as harsh. Besides the whole study area will be wetter as a consequence of water table rise, so that now locally upwelling groundwater might become to play a role. Salt in the upwelling groundwater in the north could put pressure on the salt tolerance of plants. Mowing regimes are now less frequent and later in the year, where the more late flowering plant species can benefit from. At last, the parts where top soil has been removed will become poorer in nutrients and also, due to bare soil, germination of many less competitive species will be favored. To look at the sod-cutting effect, sod-cutted permanent quadrates were compared with non sod-cutted quadrates of the same site. If no sod-cutting effect was found, no difference was made between those quadrates for the rest of the analysis.

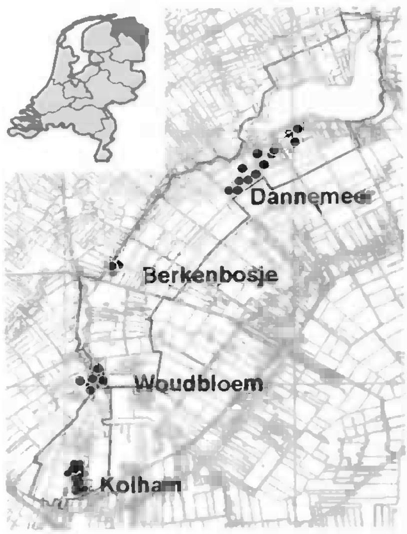

Figure 1: The 57 permanent quadrants that were selected for yearly vegetation recording in the four sites.

Selection of plant functional traits and abiotic indictor values

Traits we used in this research were derived from several European databases: German database BiolFlor (Kühn, I. & Klotz, S., 2002), Dutch Botanisch Basisregister from the Central Office of Statistics (CBS) (1991) and British Comparative Plant Ecology Database (Grime, J.P. et al. 2007). These databases included almost all our plant species and the few species that were not in these databases had a very low abundance in the study area.

To look indirectly at environmental changes in our study area, abiotic indicator values were selected. These are shown in Table 2 together with effecting restoration measures and expectations. We also selected plant traits that were important for plant survival and plant dispersal or which could be related to expected environmental changes. Selected plant traits are shown in Table 3, together with effecting restoration measures and expectations.

Table 2: the 8 selected abiotic indicator values with corresponding environmental expectations. BB = Botanisch Basisregister and CPE = Comparative Plant Ecology database.

Abiotic indicator values	Database	Type	Restoration measure	Expected environmental change
Humidity Dependence	BB	Quantitative	Filling up ditches	Increase wetness
Flood Indicator	BB	Binomial	Filling up ditches	Increase wetness
Watertable Fluctuation Indicator	BB	Binomial	Filling up ditches	Less fluctuations in watertable
Light Dependence	BB	Quantitative	Fertilisation stopped	Productivity will drop
Nitrogen Dependence	BB	Quantitative	Fertilisation stopped	Nitrogen level will decrease
pH	BB	Quantitative	Liming stopped	Decrease of pH
Soil pH	CPE	Quantitative	Liming stopped	Decrease of pH
Temperature Dependence	BB	Quantitative	-	-

Data preparation

In order to compare the traits between the different permanent quadrates, selected traits were linked to recorded plant species in each quadrate. Plant traits and abiotic indicator values were transformed into quantitative or binomial values and categorical traits were subdivided into binomial categories. In this way traits had a value so that they could be multiplied with the species abundance to create weighted averages for each permanent quadrate.

Table 3: The 33 selected plant traits. BB = Botanisch Basisregister, BF = BiolFlor Database and CPE = Comparative Plant Ecology Database.

Trait	Database	Type	Categories	Restoration measure	Expected change
Canopy Height	CPE	Quantitative	-	Lower productivity	Smaller plants
Canopy Structure	CPE	Categorial	5	Lower productivity	Smaller plants
CSR Strategy	BF	Categorial	3	Lower productivity	Decrease C, R strategy
CSR Strategy	CPE	Categorial	3	Lower productivity	Decrease C, R strategy
Dispersal Form	CPE	Categorial	3	Dispersal	Change
Dispersal Method	CPE	Categorial	4	Dispersal	Increase water and animal dispersal
Dispersule Shape	CPE	Quantitative	-	Dispersal	Change
Dispersule Weight	CPE	Quantitative	-	Dispersal	Change
Fertilisation Method	BB	Categorial	5	Dispersal	Change
Flowering Begin	BF	Quantitative	-	Later mowing	Starts later
Flowering Begin	BB	Quantitative	-	Later mowing	Starts later
Flowering Begin	CPE	Quantitative	-	Later mowing	Starts later
Flowering Duration	BF	Quantitative	-	Later mowing	Shorter
Flowering Duration	BB	Quantitative	-	Later mowing	Shorter
Flowering Duration	CPE	Quantitative	-	Later mowing	Shorter
Flowering End	BF	Quantitative	-	Later mowing	Ends earlier
Flowering End	BB	Quantitative	-	Later mowing	Ends earlier
Flowering End	CPE	Quantitative	-	Later mowing	Ends earlier
Lateral spread	CPE	Quantitative	-	Lower productivity	Increase
Leaf Anatomy	BF	Categorial	5	Increase wetness	More adapted to wet conditions
Leaf Persistence	BF	Categorial	4	Mowing decreased	Increases
Leaf Phenology	CPE	Categorial	4	Mowing decreased	Increases
Life Form	BF	Categorial	7	Increase wetness	More adapted to wet conditions
Life Form	CPE	Categorial	7	Increase wetness	More adapted to wet conditions
Life Span	BF	Categorial	4	Mowing decreased	Increase
Regenerative Strategy	CPE	Categorial	4	Dispersal	Increase seed dispersal
Rosettes	BF	Categorial	3	Lower productivity	Increase
SeedHeightMean (mm)	BF	Quantitative	-	Dispersal	Change
SeedLengthMean (mm)	BF	Quantitative	-	Dispersal	Change
SeedWeightMean (mg)	BF	Quantitative	-	Dispersal	Change
SeedWidthMean (mm)	BF	Quantitative	-	Dispersal	Change
Self Fertilisation	BB	Binomial	-	Dispersal	Change
Type of Reproduction	BF	Categorial	2	Dispersal	Increase seed dispersal

Statistical analysis

Ordinations

Ordinations of permanent quadrates were done to look whether there was a random or a directional shift over the years in the vegetation composition in each site. For the ordinations we used the PC-ORD 4.0 software package (McCune, B. & M. J. Mefford. 1999). Ordinations were done with a Nonmetric Multidimensional Scaling (NMS) method, which corrects for the overload of zero's in the data and avoids linear relationship among variables (McCune B. & Grace J.B., 2002). This was done to detect directional changes in vegetation composition over the years, which would indicate a directional pressure on the vegetation in that site.

After ordinations of vegetation composition in the sites were done, an ordination of the traits was done in the same way as described above. Traits or abiotic indicator values that showed the same direction as the year trend are positively correlated with it and could therefore be related to changes in vegetation composition, as could traits that are clearly negatively related to the year trend.

Scatterplots

To measure which traits and abiotic indicator values have changed over the years, we used scatterplots. With these scatterplots we could see which variables had significantly increased or decreased over the years by adding trendlines to simple xy plots of the data. Also was checked if these changes were linear, exponential or showed other patterns. Scatterplots were made with the Statistica 7.0 software package. (StatSoft, Inc., 2007)

Factor analysis

It is very likely that traits and abiotic indicator values are not independent of each other. This because all used traits were linked to each other via the species and some used traits are only categories of original traits. Also, traits that are highly correlated with each other often explain the same variance in the model. Therefore we used factor analysis for further analysis of the data which grouped the variables in different factors. Each variable had a certain correlation with each factor and the factors were chosen so that all the factors were independent of each other. The minimal correlation with a factor was 0.7 as a correlation of 0.7 or higher is rather strong and the variable could only be correlated with other factors by 0.3 or less. So each independent factor would explain a part of the variance in data and correlates with a group of traits or abiotic factors. The factors were varimax rotated to maximize the variance explained by the different axis. Factor analysis is also available in the Statistica software package (StatSoft, Inc., 2007).

Repeated measures

After changing dependent traits and abiotic factors into independent factors, the data was further analysed with a repeated measures Friedman-ANOVA. This is a non-parametric ANOVA, which compares multiple dependent samples with each other. So values of the independent factors of the different years could be compared per plot and statistical increase or decrease of each factor was calculated. Significantly changing factors were pairwise compared between years.

Results

Vegetation composition

Ordinations

Shifts in vegetation composition of all four sites are shown in the Figures 2a-c and Figure 2d. As you can see there is only a directional shift in Kolham, while other ordinations show a general random pattern. Therefore we will only further analyse Kolham, as it is the only site that shows a directional change in vegetation composition.

Figure 2a-c: The NMS ordinations of three sites: Berkenbosje (top left), Woudbloem (top right), and Dannemeer (bottom left). The years are displayed in different colors as is specified in the legenda of the figures.

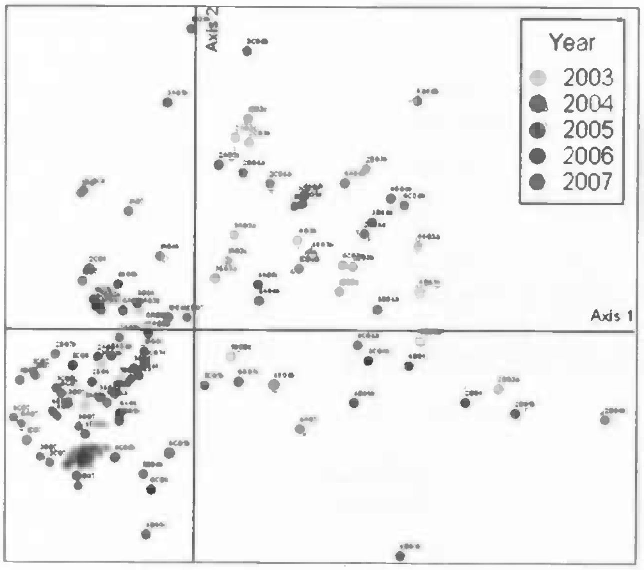

Figure 2d: The NMS ordination of the Kolham site. The years are displayed in different colors as is specified in the legenda of the figure.

There was no effect of sod-cutting (comparison of sod-cutted plots versus non sod-cutted permanent quadrates) as the sod-cutted permanent quadrates were not significantly different from the non sod-cutted ones (results not shown, $P > 0,05$).
Wet quadrates were significantly different from dry quadrates, but the wet group did not show a clear pattern presumably due to the small number of permanent quadrates (results not shown).

Abiotic indicator values

Scatterplots

Results of the scatterplots are shown in Table 4. Light Dependence, Soil pH and Nitrogen Dependence are significantly decreasing over the years. The other abiotic indicator values are not significant.

Table 4: Scatterplot results of the 8 abiotic indicator values. Significance levels * = 0.05 – 0.01, ** = 0.01 – 0.001, *** ≤ 0.001.

Abiotic Indicator Value	Significant	Direction of change (2003-2006)
Humidity Dependence	-	-
Flood Indicator	-	-
Water Table Fluctuation Indicator	-	-
Light Dependence	*	Decreasing
Nitrogen Dependence	***	Decreasing
Temperature Dependence	-	-
pH	-	-
Soil pH	***	Decreasing

Factor analysis

Factor analysis resulted in a model where all the abiotic indicator values were selected. This resulted in three independent factors with an eigenvalue that was higher than one. Table 5 shows the different selected factors (1,2 and 3) and explained variance.

Table 5: The three selected factors. Per factor and in total are listed: correlating abiotic indicator values, eigenvalues and variance explained.

	Variance Explained	Eigenvalue	Abiotic Indicator Values	Correlation with Factor
Factor 1	34,37%	2,75	Soil pH	0,89
			Nitrogen Dependence	0,85
			pH	0,76
Factor 2	17,40%	1,39	Humidity Dependence	0,86
			Flood Indicator Species	0,81
Factor 3	16,33%	1,31	Water Table Fluctuation Indicator Species	0,84
			Light Dependence	0,64
			Temperature Dependence	-0,49
Total	68,10%	5,45		

The first independent factor consists of the pH ranges and the nitrogen dependency of the plant species. Factor 2 consists of humidity dependence and flooding indicator values. The third factor consists mainly of water table fluctuation indication and to some extends of light dependence. Temperature dependence is also added to Factor 3, although it only correlates for ca. fifty percent with it.

Repeated measures

The different factor scores from the factor analysis were then analysed with a Friedman non-parametric test to determine significant differences between years, with the following H_0: Variable is the same in each year

Table 6: Results of Repeated measures analysis for abiotic indicator factor 1 to 3.

Factor	ANOVA Chi Sqr. value	*P*-value
Factor 1	21.25	0.00009
Factor 2	6.85	0.07675
Factor 3	4.45	0.21656

As you can see in Table 6, there is a significant change of Factor 1 over the years, while Factor 2 is showing a trend and Factor 3 has not changed significantly.

Pairwise comparison

In Figure 3a, Factor 1 is clearly decreasing over the years, with 2003 being higher than 2006. This means that soil pH and nitrogen dependence are decreasing as well. This is because they are positively correlated with Factor 1.
Factor 2 is not significantly changing, but when analysed for separate years, a significant difference between the years 2003, 2004 and 2006 can be found, with 2006 being higher than 2003 and 2004. So there seems to be a trend that Factor 2 is increasing over the years, which can be seen in Figure 3b. This would mean that the humidity dependence and the flood indication of the species is increasing over the years as they are positively correlating with Factor 2, indicating wetter circumstances.

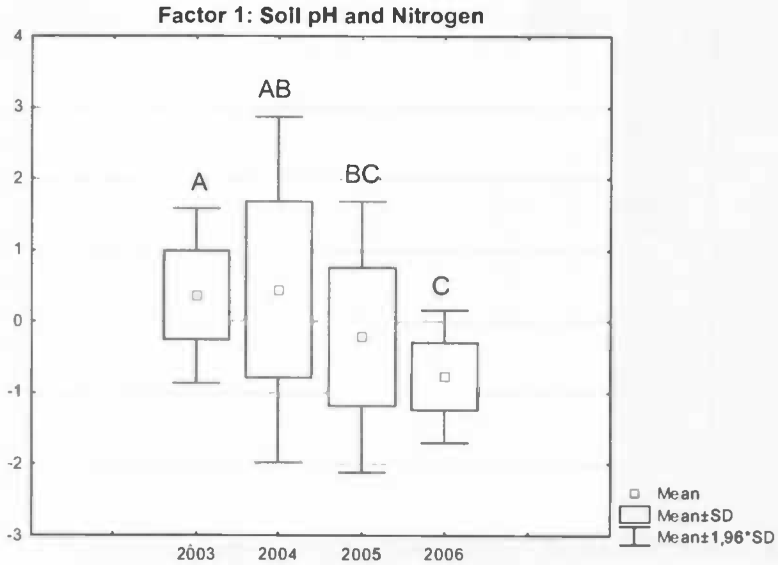

Figure 3a: The factor scores are decreasing over the years. Boxes with different letters are significantly different ($P < 0.05$).

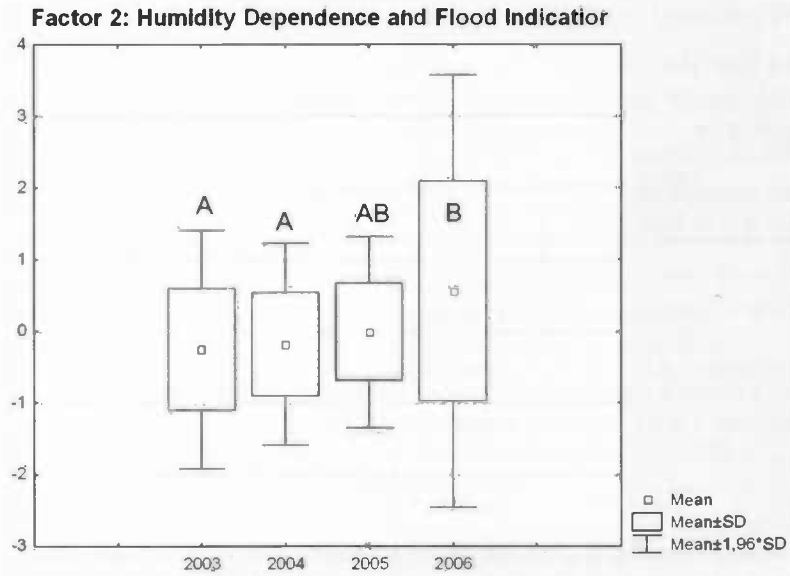

Figure 3b: The factor scores are increasing over the years. Boxes with different letters are significantly different ($P < 0.05$).

Plant functional traits

Scatterplots

Results of scatterplots of the plant traits are shown in Table 7. Only significant results are shown as well as significance levels of traits.

Table 7: Scatterplot results of the 36 significant plant traits. Significance levels: * = 0.05 – 0.01, ** = 0.01 – 0.001, *** ≤ 0.001. BB = Botanisch Basisregister, BF = BiolFlor Database and CPE = Comparative Plant Ecology Database.

Plant traits	Subtrait	Database	Significant	Direction of change (2003-2006)
Reproduction	Seeds	BF	**	Decreasing
Reproduction	Vegetatively	BF	**	Increasing
Flower duration		BF	***	Decreasing
Flower ending		BF	***	Decreasing
Leaf persistence	Overwintering green	BF	**	Decreasing
Leaf persistence	Summer green	BF	*	Increasing
Life form	Chamaephyte	BF	*	Increasing
Life form	Hemicryptophyte	BF	*	Increasing
Life form	Therophyte	BF	**	Decreasing
Life span	Annual	BF	**	Decreasing
Life span	Biennial	BF	**	Decreasing
Life span	Perrenial	BF	***	Increasing
Rosettes		BF	*	Decreasing
CSR strategy	Competitors	BF	**	Decreasing
CSR stratgey	Stresstolerators	BF	***	Increasing
Seed length		BF	**	Decreasing
Seed weight		BF	*	Decreasing
Seed width		BF	***	Decreasing
Fertilisation method	Insects	BB	**	Decreasing
Fertilisation method	Wind	BB	***	Increasing
Self fertilisation		BB	*	Decreasing
CSR strategy	Stresstolerators	CPE	***	Increasing
CSR strategy	Ruderals	CPE	**	Decreasing
Life form	Hemicryptophyte	CPE	*	Increasing
Life form	Therophyte	CPE	***	Decreasing
Canopy structure	Floating	CPE	*	Increasing
Canopy height		CPE	*	Decreasing
Lateral spread		CPE	***	Increasing
Leaf persistence	Always evergreen	CPE	***	Increasing
Leaf persistence	Partially evergreen	CPE	**	Decreasing
Flower ending		CPE	*	Decreasing
Reproduction	Seeds	CPE	***	Decreasing
Reproduction	Vegetatively lateral	CPE	**	Increasing
Dispersal method	Unspecialized	CPE	***	Increasing
Dispersal method	Wind	CPE	***	Decreasing
Dispersule weight		CPE	**	Decreasing

Factor analysis

Factor analysis selected a model where most of the plant traits were selected in the model. The model consists of ten independent factors with an eigenvalue that was higher than one. Table 8 shows which different factors were selected and explained variance.

Table 8: Ten selected factor. Per factor and in total are listed: correlating plant traits, eigenvalues and variance explained.

	Variance Explained	Eigenvalue	Plant Traits	Correlation with Factor
Factor 1	20.26%	16.41	Life Span Annual (BF)	0,92
			Life Span Pluriennial-pollakanthic (BF)	-0,92
			Life Form Therophyte (CPE)	0,92
			Life Form Therophyte (BF)	0,88
			Lateral Spread (CPE)	-0,82
			End of Flowering (BF)	0,81
			End of Flowering (BB)	0,81
			Reproduction via Seeds (BF)	0,79
			Vegetative Reproduction (BF)	-0,79
			Overwintering Green Leaf Persistence (BF)	0,77
			Flower Duration (BB)	0,77
			Vegetative Reproduction (CPE)	-0,74
Factor 2	15,88%	12,86	Fertilisation via Water (BB)	-0,99
			Underwater Canopy Structure (CPE)	-0,98
			No Dispersal Form (CPE)	-0,98
			Life Form Hydrophyte (CPE)	-0,93
			Life Form Hydrophyte (BF)	-0,91
			Leaf Anatomy Hydromorphic (BF)	-0,88
			Seed Height (BF)	-0,75
Factor 3	11,25%	9,12	Dispersal Form Seed (CPE)	0,92
			Dispersal Form Fruit (CPE)	-0,90
			Dispersal Method via Animals (CPE)	0,87
			Leaf Anatomy Scleromorphic (BF)	0,84
			Canopy Height (CPE)	0,84
			Erosulate Plant (BF)	0,80
			Hemirosette Plant (BF)	-0,77
			Leaf Anatomy Mesomorphic (BF)	-0,73
			Competitor Strategy (CPE)	0,70
Factor 4	8,88%	7,19	Leaf Anatomy Hygromorphic (BF)	-0,84
Factor 5	5,91%	4,79		
Factor 6	4,66%	3,78	Begin of Flowering (BF)	-0,93
			Begin of Flowering (CPE)	-0,89
Factor 7	4,21%	3,41	Life Form Geophyte (BF)	0,83
			Dispersule Weight (CPE)	0,76
			Seed Width (BF)	0,73
Factor 8	3,97%	3,22	Life Form Phanerophyte (CPE)	-0,96
			Life Form Macrophanerophyte (BF)	-0,94
			Life Form Nanophanerophyte (BF)	-0,93
			Seed Weight (BF)	-0,87
Factor 9	3,42%	2,77	Canopy Structure Basal (CPE)	0,81
			Rosette plant (BF)	0,71
Factor 10	2,74%	2,22	Canopy Structure Floating (CPE)	-0,83
			Life Form Helophyte (CPE)	-0,76
Total	60,92%	49,36		

Factor 1 consists mainly of traits that are related to the reproductive strategy of the plant like reproduction method and flower duration. It explains about twenty percent of variance. Factor 2 consists of water related traits, water related sub-traits of the life form, canopy structure, leaf anatomy and other traits. Factor 3 includes a lot of traits that are related to morphology of plant species, like canopy height, canopy structure and leaf morphology. Factor 4 explains quite a lot of variance although it only consists of the trait hygromorphic leafanatomy. This is also the case for the fifth factor, which explains six percent of variance, but does not have any traits included at all. Five remaining factors explain less variance, but had an eigenvalue higher than one. Included traits can be found in Table 8.

Repeated measures

Factor scores from the factor analysis were then analysed with a Friedman non parametric test to determine significant differences between years, with the following H_0:Variable is the same in each year

Table 9: Results of Repeated measures analysis for plant trait factors 1 to 10.

Factor	**ANOVA Chi Sqr. value**	***P*-value**
Factor 1	**16.73**	**0.0008**
Factor 2	0.47	0.93
Factor 3	**12.87**	**0.005**
Factor 4	0.53	0.91
Factor 5	4.80	0.19
Factor 6	1.67	0.64
Factor 7	**13.27**	**0.004**
Factor 8	6.13	0.11
Factor 9	**11.13**	**0.01**
Factor 10	1.13	0.77

As you can see in Table 9, there are significant changes over years in factors 1, 3, 7 and 9, while all the other factors did not change significantly over the years.

Pairwise comparison

Figure 4a shows that Factor 1 decreased over the years, with 2003 being higher than 2006. Positively correlated reproductive plant traits like life span, flowering time and therophytic life form also decreased over years, while negatively correlated traits like vegetative reproduction increased.
Factor 3 (figure 4b) also decreased over years, which means that traits positively related to Factor 3, like canopy height and leaf adaptations to drier conditions, also decreased and traits like lateral spread and mesomorphic leaf anatomy actually increased due to negative correlation with factor 3.

Factor 7, displayed in figure 4c, also decreased over years, as are positively correlated traits: seed width, seed weight and geophytic lifeform. While there are significant differences in the factor scores of Factor 9, there is no clear decrease or increase, but instead a fluctuation over years (figure 4d).

The stress tolerator trait also increased over years, although it did not fall in any of the ten factors.

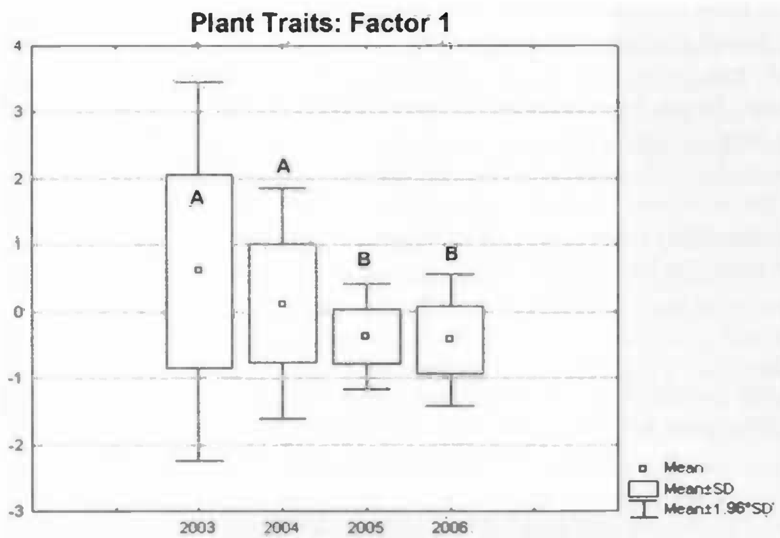

Figure 4a: Displayed are factor scores of Factor 1. Boxes with different letters are significantly different ($P < 0.05$).

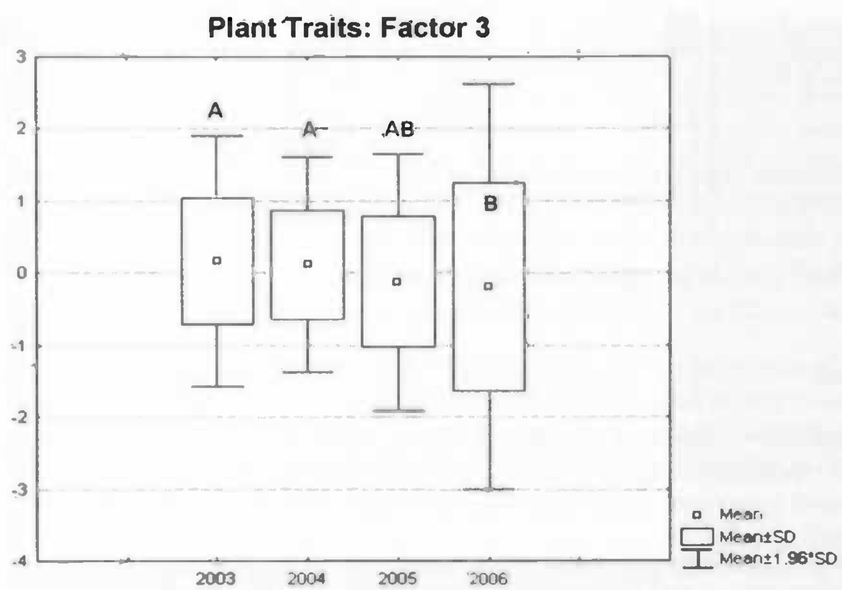

Figure 4b: Displayed are the factor scores of factor 3. Boxes with different letters are significantly different ($P < 0.05$).

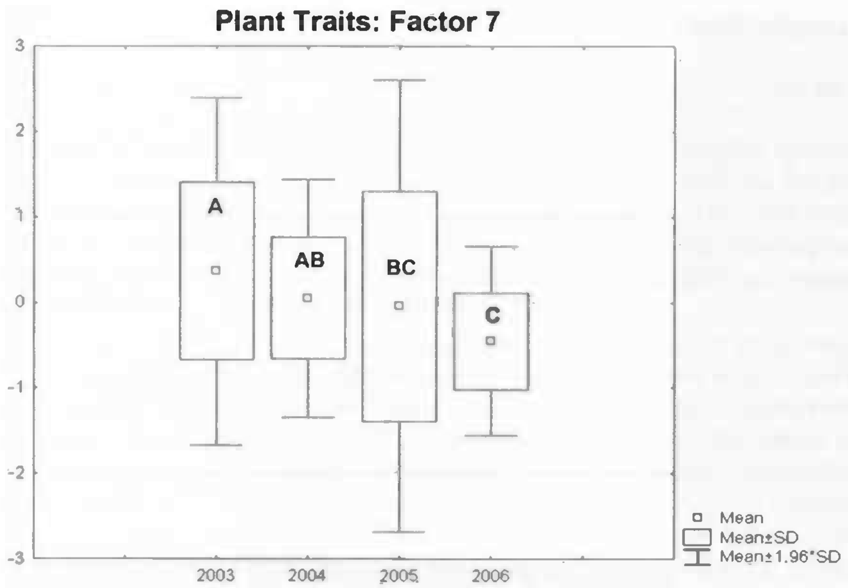

Figure 4c: Displayed are the factor scores of factor 7. Boxes with different letters are significantly different ($P < 0.05$).

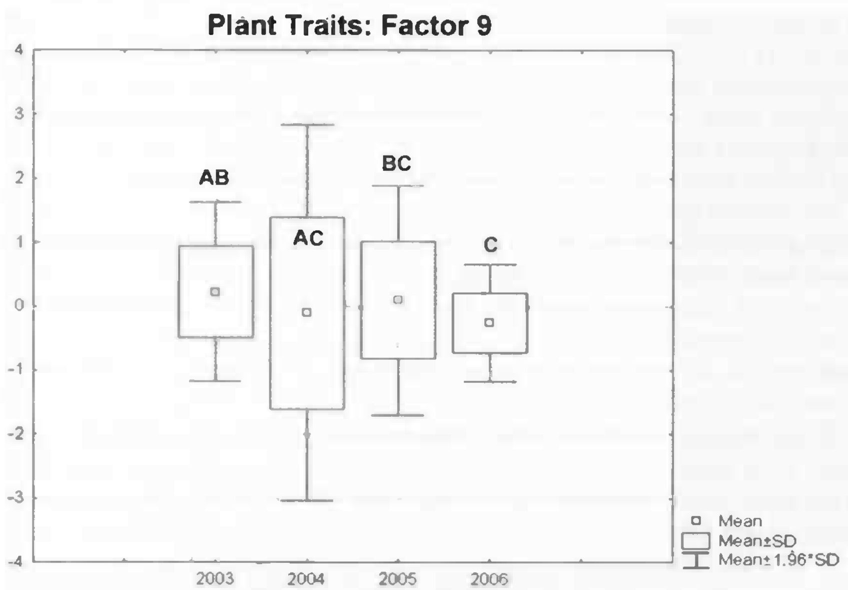

Figure 4d: Displayed are the factor scores of factor 9. Boxes with different letters are significantly different ($P < 0.05$).

Discussion and conclusions

Vegetation composition

From ordinations random movements in vegetation composition were observed in the sites of Dannemeer, Woudbloem and Berkenbosje. However, a directional shift in vegetation composition was only observed in Kolham This was probably due to that Kolham has be taken out of use quite recently reflecting a change on management regime (see Table 1). As in other sites this is not the case, because they are out of agricultural use for a far longer period.

Changing management might have quiet a big impact just after restoration due to its abrupt nature. After that it would have a more steady but smaller impact on the area due to its continues nature. Also with a relatively short observation and recording period (six years for Kolham, eight years for the other areas) it is possible and likely that we were able to detect the early changes of Kolham, but were not able to see changes in vegetation composition that occurred in the other sites.

Second difference is that the management changes in the sites were most pronounced in Kolham, even with "the sod-cutting effect" being neglected (as the sod-cutted plots, about one third, failed to be different from the plots that were non sod-cutted). We expected that more drastic changes in management (like sod-cutting) would lead to bigger shifts in vegetation composition. There could be multiple reasons that the effect of sod-cutting was not found. First of all, it could be that the number of permanent squares was too small.
Secondly (and more likely) it could be that although a lot of soil has been removed from those sites, the sod-cutted permanent quadrates did not change much in their abiotic parameters. No information was available about how deep the sod-cutting was done. Also, as the Kolham site has been in agricultural use for quite some time it is likely that the soil is still very rich in nutrients even if you remove the top layer.

Another reason could be that although the abiotic parameters were drastically changed, the plant species that were more suitable to establish in those plots were restricted by dispersal and therefore could not reach these sites. Here, also no data was available of target species in the neighboring areas. A combination of dispersal problems and unsufficient nutrient removal is also a good possibility.

So, both difference in year since agricultural use and difference in scale of management impact could be a very good explanation of detection of a shift in vegetation composition in Kolham, but not in the other sites. Longer periods of vegetation recording could probably detect vegetation shifts caused by the management type or the change in management in the other sites.

Abiotic indicator values

Regarding change in abiotic indicator values over years, several things can be concluded. As Factor 1 is decreasing (and soil pH as well as the nitrogen dependence is positively correlated with Factor 1), soil pH and nitrogen dependence are also decreasing over years. This would mean that plant composition in Kolham is adapting to more acid and less nitrogen rich conditions, which is in line with our expectations since agricultural use has stopped (Bakker, J.P. et al., 2002)(Smits, N.A.C. et al., 2008). Smits et al. (2008) found that after fertilization stopped, plant species adapted to nutrient-rich conditions gradually disappeared from the sites, especially species with a high nitrogen demand.

Factor 2, which is positively correlated with humidity dependence, is showing an increasing trend. This would mean that Kolham is getting wetter, which is in line with our expectations, as ditches were filled up to raise the watertable. Another hydrology study in the same area by Van Diggelen et al. (2000-2007) shows that the area has indeed become wetter. However, it could be that plant species composition needs more time to adapt to wetter conditions.
The plant species with high Ellenberg values for humidity dependence could be present in the area, but are not yet able to dominate those sites. It also could be that dispersal problems restrict the dispersal of plant species that are adapted to wet conditions. In other words, plant species that dominate in more wet circumstances in Kolham are not automatically the plant species which are best adapted to wet conditions, but are just the best to wetness adapted species actually able to reach the site. Therefore the change in Ellenberg values is far less than expected.

Plant traits

Factor 1 is decreasing over years and so are plant traits that are positively correlated with Factor 1. Traits that are negatively correlated to Factor 1 are increasing over years. Regarding these relations there is a shift towards longer living species with higher lateral spread and ones that reproduce vegetatively. While short living species that survive and reproduce via seeds are disappearing in Kolham. Flowering time also gets shorter, with both the ending as the duration decreasing over the years.

When abiotic factors like soil pH and nitrogen contents change, the area becomes more suitable for plants with adaptations for these conditions. Plants could already be there, or be absent from the site. When absent, they can still regenerate from the seedbank or disperse from outside the area via seeds.
Factor 1 shows that especially plant species that do not reproduce or survive via seeds increase in Kolham. This would imply that plants that are better adapted to the new conditions already were in the area and are now increasing their abundance. On the other hand this result implies limitation in seed dispersal (factors).

The first suggestion could be the case for nitrogen dependence and soil pH as the vegetation composition adapted quite well to a decrease in these parameters, but it is another story for the changes in the humidity. The vegetation composition is not adapting well, with Ellenberg values for humidity only showing a slight trend. Also factor 2, consisting of mainly adaptation traits for wet conditions, is not increasing at all. Nevertheless, wetness of the site is found to be increasing (Van Diggelen et al. 2000-2007). As plants with adaptations for wetter conditions stay absent from the analysed sites, while abiotic site conditions are more favorable for them, dispersal probably still limits presence of those plant species.

Factor 3, consisting of plant morphology related traits like canopy height, canopy structure and leaf morphology, is also decreasing over the years. This means that there is a shift towards species that are less adapted to dry conditions and smaller plants that also tend to have more lateral spread. Also is the proportion of plants with a competitor related strategy (Grime strategy) decreasing over years, while leaf adaptations for non-extreme conditions tend to increase. It could be said that dry conditions disappear (so the area becomes wetter) as the adaptations to dry conditions decline, but at the same time there is no increase of adaptations to wet conditions (see Factor 2). This also points towards dispersal problems, with plants adapted to wet conditions unable to colonize the area.
Plant species also tend to be less high and have more lateral spread, which could be due to less nutrients, less productivity and therefore less competition for light, which agrees with the decline in nitrogen (and probably other nutrients) that was found when analysing abiotic indicator values. Also decrease of competitor strategies and increase of stress tolerator strategies points towards this conclusion. Other studies that analyzed traits after abondonment showed similar results. Eler et al (2005) shows that fertilization promotes the abundance of therophytes (survivors via seeds). Eler et al (2005) also shows that traits that lead to small species and species using a stress-tolerator strategy are very important for vegetation similar to the vegetation type targeted for this study.
The seventh factor, traits related to seed characteristics, is also decreasing over the years and with decreases in seed width, seed weight and geophytic life form strengthens the conclusions made after analyzing Factor 1.
Factor 9 is again morphology related, like Factor 3, but shows no clear increase or decrease. It shows that there are big differences between years and that vegetation composition can change a lot in a year.

Overall conclusions

Due to management changes we expected that a noticeable change in vegetation composition would take place as plant species adapt to the new abiotic conditions. This only occurred in Kolham. In this site a recent change in management took place, while for the other sites duration of vegetation recordings was presumably not long enough, as here change in management was longer ago. Therefore we perhaps missed the most pronounced changes in these sites.

For Kolham counts that the site becomes wetter, more acid and nitrogen poorer, by means of analysing abiotic indicator values. When analysing plant traits however, we found that humidity related traits did not respond at all, which is most likely caused by dispersal problems as traits correlated with reproduction from seed were declining much. This also suggests that no seed source population is available or efficient dispersal vectors are lacking. Large herbivores, like cattle, can act as seed dispersers (Mouissie M. et al., 2004), however, seeds still can not colonize the site if target species are not within the grazing area of the herbivores. Besides Mouissie et al. (2004) also states that large herbivores will bring seeds and nutrients from nutrient-rich soils to nutrient-poor soils, which can enrich just created poor systems.
Although abiotic parameters of Kolham have clearly changed in the expected and desired direction, vegetation composition can only partly follow the process. This process could be caused by limitation in dispersal and therefore limiting the success of the management changes in Kolham. To overcome this, management implication should focus on introduction of more efficient dispersers or active introduction of seeds from source populations.

Reference List

1. Bakker,J.P., J.A.Elzinga, and Y.de Vries. 2002. Effects of long-term cutting in a grassland system: perspectives for restoration of plant communities on nutrient-poor soils. Applied Vegetation Science 5:107-120.

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

3. CBS. 1991. Botanisch Basisregister.

4. Eler,K., M.Vidrih, and F.Batic. 2005. Vegetation characteristics in relation to different management regimes of calcareous grassland: A functional analysis using plant traits. Phyton-Annales Rei Botanicae 45:417-426.

5. Grime, J.P. et al. 2007. Comparative Plant Ecology.

6. Kühn, I. and Klotz, S. 2002. Biolflor database.

7. Londo,G. 1976. Decimal Scale for Releves of Permanent Quadrats. Vegetatio 33:61-64.

8. McCune, B. and M. J. Mefford. 1999. Multivariate Analysis of Ecological Data,Version 4.25. MjM Software, Gleneden Beach, Oregon, U.S.A.

9. McCune, B. and Grace, J.B. 2002. Analysis of Ecological Communities

10. Middleton,B.A. 2003. Soil seed banks and the potential restoration of forested wetlands after farming. Journal of Applied Ecology 40:1025-1034.

11. Mouissie, A.M. et al. 2004. Seed dispersal by large herbivores: Implications for the restoration of plant biodiversity. Thesis: 1-120

12. Mouissie,A.M., P.Vos, H.M.C.Verhagen, and J.P.Bakker. 2005. Endozoochory by free-ranging, large herbivores: Ecological correlates and perspectives for restoration. Basic and Applied Ecology 6:547-558.

13. Ozinga,W.A., R.M.Bekker, J.H.J.Schaminee, and J.M.van Groenendael. 2004. Dispersal potential in plant communities depends on environmental conditions. Journal of Ecology 92:767-777.

14. Schmitt,J., andR.D.Wulff. 1993. Light Spectral Quality, Phytochrome and Plant Competition. Trends in Ecology & Evolution 8:47-51.

15. Smits,N.A.C., J.H.Willems, and R.Bobbink. 2008. Long-term after-effects of fertilisation on the restoration of calcareous grasslands. Applied Vegetation Science 11:279-U92.

16. StatSoft, Inc. (2007). STATISTICA (data analysis software system), version 8.0. www.statsoft.com.

17. Verhagen,R., J.Klooker, J.P.Bakker, and R.van Diggelen. 2001. Restoration success of low-production plant communities on former agricultural soils after top-soil removal. Applied Vegetation Science 4:75-82.

18. Van Diggelen, R., et al. 2000-2007. Laagland Bekenproject: Natuurontwikkeling in Midden Groningen.

19. Violle,C., M.L.Navas, D.Vile, E.Kazakou, C.Fortunel, I.Hummel, and E.Garnier. 2007. Let the concept of trait be functional! Oikos 116:882-892.

20. Violle,C., J.Richarte, and M.L.Navas. 2006. Effects of litter and standing biomass on growth and reproduction of two annual species in a Mediterranean old-field. Journal of Ecology 94:196-205.