

Simulation of vegetation dynamics as affected by nitrogen deposition

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Simulation of vegetation dynamics as affected by nitrogen deposition

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To boldly go where no one has gone before

Jean Luc Picard
Star Trek Next Generation

Effect of nitrogen deposition reduction on biodiversity and carbon sequestration

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Abstract

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The first two chapters of this thesis deal with indicator values for plant species. Ellenberg's widely used, expert-based system was validated. There appeared to be a community dependent bias in the indicator values. An alternative indicator system was developed, based on vegetation relevés combined with measured abiotic conditions (in this example soil pH). Response curves per species were estimated, and used to back-predict the pH of independent relevés. Several procedures were tested, but the simplest one yielded the best results: the indicator value of a species is the mean pH of the relevés containing that species, and the back-predicted pH of a new relevé is the mean of the indicator values of its constituent species. A validation on independent Dutch and European data showed that this method performed better than the Ellenberg method.

In the next two chapters two models are described that simulate the response of vegetation to nitrogen (deposition) and management. A dynamic model (SUMO) was developed that simulates vegetation succession in relation to the nitrogen and carbon cycle. The model predicted that a decrease of nitrogen deposition increases biodiversity in heathland but probably not in forest. As a follow-up the static NTM3 model was developed, that links plant biodiversity to abiotic variables. This model was parameterized using over 33,000 vegetation relevés in which abiotics were estimated from Ellenberg indicator values and linked to a biodiversity indicator based on the red list for plant species. This model showed that in the Netherlands plant biodiversity had a tendency to increase in the next 20 years, especially when atmospheric deposition of nitrogen and acidifying compounds decreases.

In the last two chapters the models were used to estimate the amount of money that can be saved on vegetation management when nitrogen deposition drops, and to investigate the possible conflict between biodiversity goals and targets resulting from the Kyoto protocol. The model showed that when nitrogen deposition decreases, up to 42 m€/y can be saved on the national level. However, a decrease in nitrogen deposition from 40 to 10 kg/ha/y will cause a drop in the net carbon sequestration of forests in The Netherlands down to 27% of the present amount. This decrease in carbon sequestration may jeopardise the goals set by the Kyoto protocol.

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Introduction



1 Introduction

The change in human evolution from hunter and collector to farmer marks the start of intensive human effect on the environment. With the domestication of cattle and the breeding of crops, the area of cultivated land grew rapidly together with the human population. Over the millennia, this led to large areas of natural land being turned into extensively and later intensely managed agricultural areas, but also into infrastructure and settlements. Natural areas dramatically declined and their remains were often fragmented (Eriksson et al., 2002). These changes caused a major loss of biodiversity, which continues until present day on a global scale (Sala et al., 2000; Loreau et al., 2003; Foley et al., 2005). But not only land use itself threatened the existence of many species, also the intensive exploitation of other natural resources became a threat. The large-scale use of fossil fuel changed the chemical composition of the atmosphere, causing e.g. land and surface water acidification, eutrophication and climate change (Sala et al., 2000; Root et al., 2003; Thomas et al., 2004).

On a local scale industrial activities, intense farming and a growing mobility led to increasing concentrations of sulphur dioxide, nitrogen oxides and ammonia in the air (Pearson & Stewart, 1993; Fowler et al., 2005; Erisman et al., 2005). These forms of air pollution are widespread in Europe, North America and Asia. Acidification and nutrient enrichment of the remaining natural areas in these regions caused a further decline of biodiversity (Bobbink et al., 1998; Cairney & Meharg, 1999; Roem et al., 2002; Stevens et al., 2004; Gilliam, 2006). With the decline of biodiversity, the willingness to take countermeasures and to preserve the remaining biodiversity increased. Witnesses of this are the efforts of governmental and non-governmental organisations to protect nature, either directly or through political pressure. Large conferences dedicated to the protection of biodiversity were held in Rio de Janeiro and Johannesburg. Moreover, the Kyoto protocol to reduce carbon dioxide concentration was ratified.

It is still highly uncertain how the proposed or implemented countermeasures will influence biodiversity. The effects of the raised carbon dioxide concentrations are only just becoming significant. The effect of atmospheric pollution by sulphur and nitrogen are better known and countermeasures already have a noticeable effect on the amount of pollution (Kelly et al., 2000; Wright et al., 2001). However, the effect on the biodiversity of a lowering of the nitrogen deposition after years of high deposition still remains uncertain. Evaluation of such effects in the field may take a long time and in the end, measures may prove to be ineffective. Therefore, tools are needed to evaluate different scenarios of measures beforehand, and models might provide such a tool. When correctly parameterised and after proper validation they may be used to compare different scenarios regarding environmental policy with respect to air pollution and ecosystem management. The outcome of such analysis can

then be used to decide which measures are the most effective or the most cost effective. Moreover, when nitrogen deposition drops, money may be saved on the mitigating measures the nature manager has to take to preserve biodiversity.

The modelling approach

Ecological models have become a powerful tool and they appear in many forms, e.g. static (data-driven) or dynamic (process-driven). However, in the absence of sufficient data or knowledge, expert opinion may also be considered to be a shortcut method to evaluate scenarios. Scenarios may be based on policy options, i.e. legislation to reduce sulphur or nitrogen deposition by power plants or farmers, respectively. They may also take into account the different vegetation management intensities to reduce the effects of deposition on the vegetation, i.e. increasing the sod cutting frequency heathlands.

Various types of ecological models will be explained below.

1. **Formalised expert knowledge.** A perfect example of a formalised expert system is the Ellenberg indicator system (Ellenberg, 1979; Ellenberg et al., 1991). Expert knowledge about the occurrence of plant species under various environmental conditions of e.g. temperature, moisture or nutrient availability was formalised in an indicator system. In this expert system each species' optimum relative to several environmental variables is expressed in an arbitrary, nine- or twelve-point scale. This is probably the simplest model possible, and it has the advantage that it is reproducible and can be validated. A disadvantage is that it is still based on expert knowledge and not on measured data. Translation of the arbitrary scale units in physically measurable values (e.g. pH or nutrient concentration) is often necessary, for instance to establish the management intensity needed to compensate for nitrogen deposition. This translation introduces additional uncertainty (Ertsen et al., 1998; Wamelink et al., 2003; Schaffers & Sýkora, 2000).
2. **Data-driven models.** The simplest form of models is a linear regression equation. More complicated models are multivariate or nonlinear. Linear regression was used by Ertsen et al., (1998) and Schaffers & Sýkora (2002) to translate the arbitrary Ellenberg units into physical units. An advantage is that these kinds of models are easy to parameterise when sufficient data are available and they do not require knowledge about the processes behind it. A disadvantage is that the results of regression are limited to the range covered by the collected data. Unprecedented changes cannot be evaluated without extrapolation. This may be the case when pollution drops to historically low levels for which no data are available, or when climate changes. Another problem is that changes often take time to become effective on the plant species level. The apparent relation between the measurements and the present plant species may not reflect the actual relation. Moreover, huge amounts of data may be needed to make predictions within

acceptable uncertainty ranges, and for proper validation still more data are required.

3. Process-driven models. Process models need to be fed with information about fundamental processes, and numerical values for parameters that characterise these processes. This information has either to be derived from field measurements or from experimental research. A major advantage of this type of models over the previous type is that it should be able to evaluate unprecedented situations. A disadvantage is that unravelling processes may be a complicated task. It may even be unknown beforehand what the key processes are for new unprecedented changes in the environment.

Models do not only have to include the most essential processes to be able to evaluate government policies, they also have to provide results in a simple and comprehensible way. This is particularly true for more complex models such as process models. Although interesting for scientists, the outcome of simulated processes in terms of ammonium content of the soil, nitrogen content of the aboveground biomass or the biomass change in the vegetation will often not be of real interest to a broader audience of nature managers, policy makers or the general public. A more straightforward approach is necessary. But also for scientists a well defined end result of a complicated model will provide more insight into the overall effect of different scenarios. In this study, the output of a process model is used as input for a simple regression model to predict potential plant biodiversity using a relative scale.

The processes described operate on different spatial and time scales. Climate change and land use change operate on a global scale during many years, nitrogen and sulphur deposition mostly on a continental scale, and vegetation management on a local scale. Up to now measures to counteract biodiversity loss are mostly taken on a national scale. Models to evaluate these measures have to be able to work on the smallest scale, say a management unit (a meadow or a heathland), but to be useful for national policy they should also be able to evaluate effects on national regional and local scales. This brings limitations in terms of e.g. data availability and computation time, and in practice only key processes can be simulated in a model that has to run simulations on a national or supra national scale. To keep computation time and data requirements within acceptable limits I chose to develop point models without any spatial interaction and with a time step of one year. Simulations are carried out on 250*250m grids assuming homogeneity within each grid cell. I applied all three types of models described above to assess the effects of a changing environment on the biodiversity.

Aim

The general aim of this study is to develop a tool to evaluate the effects of policy and management scenarios on biodiversity. The tool should be able to evaluate the

combined effects of deposition and vegetation management on plant diversity. Our focus was on the effects of nitrogen cycling as influenced by nitrogen and sulphur deposition and removal of nitrogen. The tool should facilitate the choice of solutions to restore biodiversity in natural areas now suffering from nitrogen deposition. Using a model approach I tested the hypothesis that a reduction in nitrogen deposition does not automatically lead to a decrease of the amount of nitrogen in the system and thereby to an increase in plant diversity. I investigated how much nature managers spend to counteract the effects of nitrogen deposition, and consequently how much money could be saved when nitrogen deposition drops. Finally, I tested the hypothesis that a reduction of nitrogen deposition hampers the targets for C-sequestration set by the Kyoto protocol in areas where nitrogen deposition is high.

Outline of the thesis

Ellenberg indicator values (Ellenberg et al., 1991) are used in many disciplines of vegetation research. I validated the Ellenberg expert model for soil pH and groundwater level, and investigated how the indicator values can be used in vegetation modelling (Chapter 2).

In the next Chapter (3), I developed an alternative indicator system based on field measurements of soil pH and species composition.

Natural vegetation has been largely influenced by men, through management as well as through the effects of industrialization and the intensification of agriculture. The latter two have resulted in an increase in nitrogen deposition and a decline in plant species richness. To be able to simulate the effects of natural and anthropogenic changes of the vegetation, and to evaluate countermeasures, the vegetation succession model (SUMO) was developed as an extension to the soil model SMART2. This model is described in Chapter 4.

The model SUMO simulates the development of vegetation structure as influenced by management and nitrogen deposition (Chapter 4). Although this model yields basic information on plant diversity, it does produce information on changes in the occurrence of plant species. In Chapter 5, a regression model (NTM3) is described that predicts the potential plant biodiversity based on the simulations by the models SMART2 and SUMO.

Nature managers spend a lot of money to mitigate the negative effects of nitrogen deposition on nature. The models SMART2, SUMO and MOVE3 were used to estimate the cost that may be saved on nature management when the nitrogen deposition drops, where the MOVE3 model predicts the change of occurrence of plant species based on soil parameters (Chapter 6).

Finally in Chapter 7 the application of the models SMART2, SUMO and NTM3 is used to analyse the apparently contradicting targets agreed in the Kyoto protocol to

reduce carbon dioxide in earth's atmosphere and on the other hand the wish to enhance biodiversity.

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Validity of Ellenberg indicator values judged from physico-chemical field measurements



2 Validity of Ellenberg indicator values judged from physico-chemical field measurements

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Abstract

The relationship between average Ellenberg's indicator scores per vegetation relevés and environmental parameters measured in the field usually shows a large variation. We tested the hypothesis that this variation is caused by a vegetation-class dependent bias. For this purpose we collected data containing vegetation relevés and measured soil pH (3631 records) or mean spring groundwater level (MSL, 1600 records). The relevés were assigned to vegetation types by an automated procedure. Regression of the Ellenberg indicator scores for acidity on soil pH and the Ellenberg indicator scores for moisture on MSL gave percentages explained variance similar to values that were earlier reported in literature. When the phytosociological class was added as an explanatory factor the explained variance increased dramatically. Regression lines per vegetation type were estimated, many of which were significantly different from each other. In most cases the intercepts were different, but in some cases their slopes differed as well. The results show that Ellenberg indicator values for acidity and moisture appear to be biased towards the values that experts expect for the various phytosociological classes. On the basis of the results, we advise to use Ellenberg indicator values only for comparison within the same vegetation type.

Introduction

Ellenberg indicator values (IV) are widely used in vegetation assessment, both to estimate soil variables from vegetation relevés as well as to predict vegetation composition from given soil variables. Calibration of IVs on measured environmental parameters plays an important role in connecting ecological models with each other and with field data. If the relationship between vegetation and environment is satisfactorily quantified, information on abiotic factors can be derived simply and cheaply by the description of vegetation, instead of by time-consuming, and hence expensive, soil and groundwater measurements (e.g. Kruijne et al., 1967; Ellenberg et al., 1991; Grime et al., 1988; Diekmann & Dupré, 1997; Hawkes et al., 1997). Thus, vegetation can provide information on e.g. grazing (Briemle & Ellenberg, 1994),

management (Bakker, 1989), temperature (Ellenberg et al., 1991), availability of nutrients (Kruijne et al., 1967; Ellenberg et al., 1991), moisture (Ellenberg, 1991), and acidity (Kruijne et al., 1967; Ellenberg et al., 1991).

With a reliable set of indicator values the vegetation can thus be used as an estimator for environmental characteristics, but, *vice versa*, the environment can also be used as a predictor for vegetation composition. Therefore, Ellenberg indicator values are also applied in vegetation models, such as MOVE (Latour et al., 1993), NTM (Wamelink et al., 1998) and NUCOM (van Oene et al., 2000). These models estimate the probability of occurrence of plant species or species diversity on the basis of simulated soil variables. The factors moisture and soil acidity are the subject of this study.

To gain information about abiotic factors on the basis of vegetation data, a consistent system of indicator values is needed. As early as 1967, Kruijne et al., developed such a system for The Netherlands based on field measurements. They used the species present in vegetation samples as indicators for acidity and moisture content of the soil, and scored their response on a five-point scale.

Ellenberg (1979) and Ellenberg et al. (1991) developed their well-known indicator system for Central Europe. A 9-point scale for acidity ('Reaktionzahl', R) and a 12-point scale for water availability ('Feuchtzahl', F). Ellenberg's system is a typical expert system, because the indicator values were only for a small part based on measured data and mostly on Ellenberg's and others' knowledge of the environmental conditions that plant species prefer. Many authors have estimated similar indicator values (or adapted Ellenberg values) for their own countries (Wiertz et al., 1992 and ter Braak & Gremmen, 1987 for the Netherlands; Diekmann, 1995 and Diekmann & Falkengren-Grerup, 1998 for Sweden; Grime et al., 1988 and Hill et al., 1999 for Great Britain; Landolt, 1977 for Switzerland, Zółomi et al., 1967 for Hungary; Frank & Klotz, 1990 for eastern Germany), but IVs have been most widely used in various disciplines.

For both the assessment of the environmental conditions from vegetation relevés, and for the prediction of the vegetation from known or simulated abiotic values, it is necessary to translate indicator values into abiotic parameters, or *vice versa*. Several efforts have been made to calibrate Ellenberg indicator values with the aid of vegetation relevés for which abiotic variables have been measured (Thompson et al., 1993; Seidling & Rohner, 1993; Diekmann 1995; Wamelink et al., 1996; Hill & Cary 1997; Ertsen et al., 1998; Schaffers & Sýkora, 2000; Dzwonko, 2001). Although statistically significant relations were found between measured soil pH and groundwater level on the one hand, and Ellenberg R and F on the other hand, the percentages explained variance were never very high and the regressions always showed a large spread. This introduces a large uncertainty in the translated data, which in turn strongly contributes to the uncertainty in model output. Narrowing the spread in the calibration equations would strongly benefit the final result of ecological models

that make predictions on the species level, as shown by Jansen et al. (1999) and Schouwenberg et al. (1999).

The present study focuses on the validity of IVs by comparing averages over the species per relevé (average Ellenberg indicator scores) with actually measured values. We hypothesized that the large spread that is observed when relating Ellenberg indicator values to measured data is at least partly due to the use of widely different vegetation types. Although Ellenberg (1979) already warned against comparing average Ellenberg indicator values between different vegetation types, little attention has been paid to this warning, partly due to the lack of data needed for its verification. If our hypothesis is true, different vegetation types would require different calibration lines.

To test our hypothesis a large set of vegetation relevés with accompanying abiotic data was used to calibrate the Ellenberg's R and F on measured pH and spring groundwater level, respectively. Although we consider nutrient availability as an equally important ecological factor, we did not include this factor in our study because insufficient data were available. We used the syntaxonomic class as an indicator for the vegetation type of each relevé, and included this as an additional explanatory variable in our regression equations.

Material and Methods

We composed a large dataset of vegetation relevés from The Netherlands on sites where one or more soil variables were also measured. The data were mostly collected from literature, but unpublished data were also included (see Sanders et al., 2000 for an overview). The soil variables used in this study were either pH (H₂O) or groundwater level. When the pH was measured in more than one soil layer the measurement in the upper layer was used. When more than one pH measurement was available per relevé (for the same soil layer) the average was used. The pH was always measured in water extract, field measurements with pH indicator paper or -fluid were not included in the dataset. The pH was measured between 2 and 24 hours after the extraction using different types of pH meters. Because our data were taken from various sources, their uncertainty cannot be quantified.

The groundwater level is expressed as mean phreatic level in spring (MSL), in cm below soil surface. The MSL was calculated as the average groundwater level over 3 to 5 yr in the months March and April (the beginning of the growing season in The Netherlands), or estimated from the soil profile. The use of the soil profile can give rise to unwanted variation, because the MSL estimated by this method reflects the long-term MSL. After a rapid change in MSL the estimated value will only apply to the stable situation before this change, and rapidly reacting species may be misclassified. However, we estimated that this will be the case for only an insignificant part of the

data. For both methods the uncertainty of the measurements is within a few centimetres, which is well within the yearly fluctuation in MSL.

The ranges of pH and MSL values in the dataset were 3.0 to 8.5 and -48 to 212 cm, respectively (for MSL, negative numbers denote water level above soil surface). The corresponding ranges for average Ellenberg indicator values for R and F were 1.0 to 8.5 and 3.9 to 10.0, respectively. For each relevé the mean Ellenberg F and R values were calculated as the unweighted arithmetic mean indicator values over all species.

Each relevé was assigned to a syntaxonomic class using the computer program ASSOCIA (van Tongeren, 2000). ASSOCIA identifies vegetation relevés by comparing them with a training set that consists of relevés that have been classified beforehand. The training set used in our case was taken from Schaminée et al. (1995, 1996 & 1998) and Stortelder et al. (1999). ASSOCIA calculates the similarity of a given relevé with all relevés in the training set. The identification is based on both quantitative and qualitative data, i.e. presence-absence and abundance per plant species. A vegetation type is assigned to a relevé on the basis of the calculated maximum likelihood using the dissimilarity between the relevé and the pre-classified relevés. The maximum likelihood combines the quantitative and the qualitative data into one index. ASSOCIA also calculates the ‘completeness’ and the ‘weirdness’ of the relevé from the pre-classified relevés. The completeness of the relevé gives information on the number of species that are expected to be present (according to the training set). The weirdness gives information on the number of ‘unexpected’ species in the relevé. The final assignment of a relevé to an association is based on the three above-mentioned characteristics, where the weirdness and incompleteness function as controllers. We only used this information on the class level (with the exception of a few classes, where relevés were classified on the association level for further analysis). The phytosociological class with the highest similarity was assigned to the relevé. Since the phytosociological classification is hierarchical, misclassifications are more likely when using associations instead of phytosociological classes (misclassification in ASSOCIA is less than 10% for associations, pers. comm. S. Hennekens). We had data for 36 phytosociological classes for pH and for 33 classes regarding groundwater level, which means that most of the 38 terrestrial classes in The Netherlands were represented.

The dataset contained 1600 combinations of F with MSL and 3631 of R with pH. The fit of each regression model (see Table 1 and 2) was expressed as the percentage explained variance (R^2_{adj}). By adding interaction terms between the abiotic variable (pH or MSL) and the phytosociological class to the regression model, we also allowed the intercepts and slopes of the regression lines to be different for each phytosociological class.

This resulted in three nested models that were fitted:

- (1) $y = \alpha + \beta x$ (common intercept α and common effect β of abiotic variable),
- (2) $y = \alpha_i + \beta x$ (different intercept α_i for each class and common effect β of abiotic variable),
- (3) $y = \alpha_i + \beta_i x$ (different intercept α_i and effect β_i of abiotic variable for each phytosociological class),

in which: y = MIV (mean Ellenberg IV), x = measured abiotic value, β = slope of regression line, α = intercept of regression line, the index i denotes the different phytosociological classes. Model (1) is the straightforward general relationship between the Ellenberg indicator score and the abiotic variable. Model (3) is essentially a different linear relationship for each phytosociological class, while model (2) is an intermediate model with parallel lines fitted to the data. To obtain stable estimates for the parameters β_i and α_i , only phytosociological classes with more than 20 occurrences were used. This resulted in regressions for 25 classes for pH and 19 classes for MSL. The fitting of the models (2) and (3) is fully described in Montgomery and Peck (1992, Ch. 6). The statistical package Genstat (Payne et al., 1993) was used to fit the models.

Results

Table 1 shows the results of the regression analysis of Ellenberg R on measured pH using the three models. The simple regression model (1) explains 44.3% of the variance. However, when allowing different intercepts for each phytosociological class (model (2)) the percentage explained variance increases to 73.9%. When different regression coefficients per phytosociological class are also allowed (model (3)), the percentage explained variance increases just slightly to 75.1% (Table 1).

Table 1. Regression analyses of the mean Ellenberg indicator score for acidity (R) on soil pH. The 3 models are: $y = \alpha + \beta x$ where R is regressed on pH, $y = \alpha_i + \beta x$ where R is regressed on pH with separate intercepts α_i for each phytosociological class, $y = \alpha_i + \beta_i x$ where R is regressed on pH with class dependent intercepts α_i and slopes β_i . The accumulated analysis of variance is shown, with degrees of freedom (d.f.), sum of squares (s.s.), mean of squares (m.s.), variance ratio (v.r.), F probability (F pr.) and percentage explained variance (R^2_{adj}).

no	Model	d.f.	s.s.	m.s.	v.r.	F pr.	R^2_{adj}
1	$y = \alpha + \beta x$	1	3043.8	3043.8	6311.1	<.001	44.3
2	$y = \alpha_i + \beta x$	24	2039.4	85.0	176.2	<.001	73.9
3	$y = \alpha_i + \beta_i x$	24	95.6	4.0	8.3	<.001	75.1
	Residual	3488	1682.2	0.4			

Similarly, for the regression of F on MSL the percentage explained variance is 26.3% for the simple model (1) and 74.0% for model (2). When different regression coefficients per phytosociological class are also included (model (3)) the percentage explained variance increases to 75.0% (Table 2).

The regression lines are shown in Figure 1 and 2 for R on pH and F on MSL, respectively (the relationship between F and MSL is negative because high F values correspond with wet situations and thus low MSL values).

Table 2. Regression analyses of the mean Ellenberg indicator values for moisture (F) on mean spring groundwater level (MSL). The 3 models are: $y=\alpha+\beta x$ where F is regressed on MSL, $y=\alpha_i+\beta x$ where F is regressed on MSL with class dependent intercepts α_i , $y=\alpha_i+\beta_i x$ where F is regressed on MSL with class dependent intercepts α_i and slope β_i . The accumulated analysis of variance is shown, with degrees of freedom (d.f.), sum of squares (s.s.), mean of squares (m.s.), variance ratio (v.r.), F probability (F pr.) and percentage of explained variance (R^2_{adj}).

no	Model	d.f.	s.s.	m.s.	v.r.	F pr.	R^2_{adj}
1	$y=\alpha+\beta x$	1	512.4	512.4	1568.7	<.001	26.3
2	$y=\alpha_i+\beta x$	18	931.4	51.7	158.4	<.001	74.0
3	$y=\alpha_i+\beta_i x$	18	26	1.4	4.4	<.001	75.0
	Residual	1448	472.9	0.3			

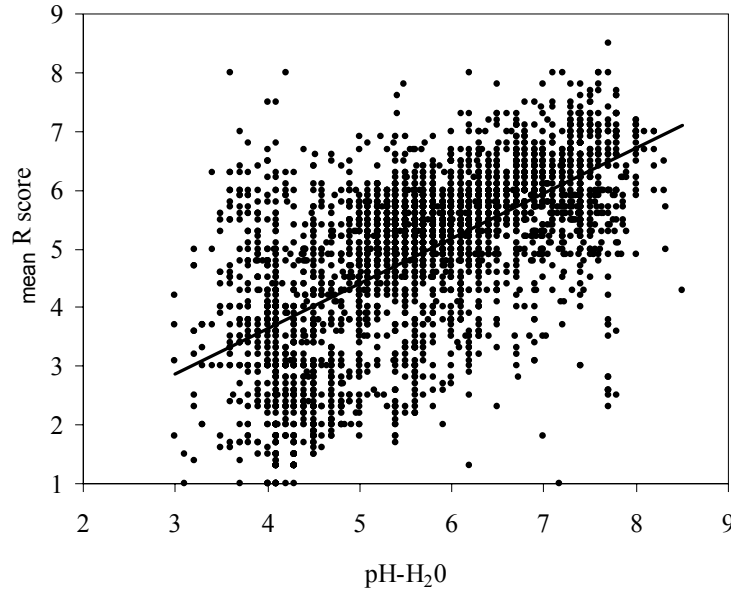


Figure 1. Regression of mean Ellenberg indicator scores for acidity (R) on soil pH-H₂O for the total dataset ($n=3631$, $R^2_{adj} = 44.3\%$).

For the 25 classes with ≥ 20 observations, 18 classes showed a significant relationship between R and pH ($p < 0.05$, Table 3), for 7 classes this relationship was not significant. For the *Vaccinio-Piceetea* we even found a significant negative relationship. The statistically significant relationships per class are shown in Figure 3. For the other

classes, mean Ellenberg indicator scores for acidity apparently do not provide information on pH within each class (Table 3).

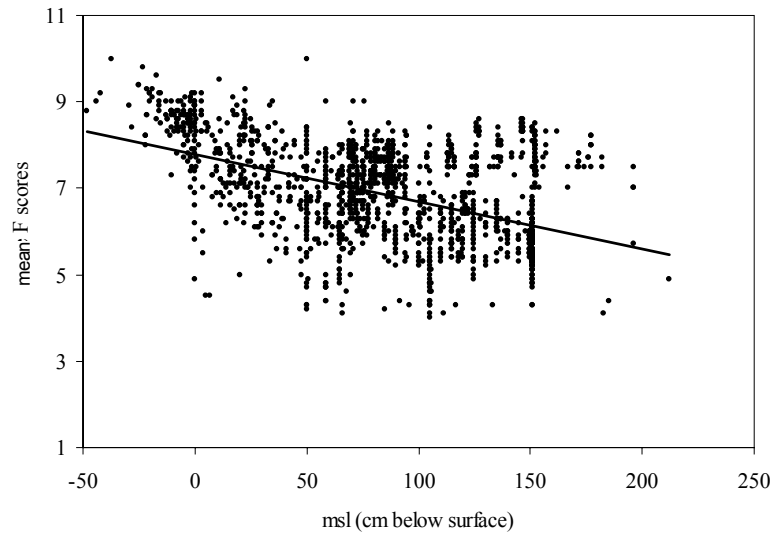


Figure 2. Regression of mean Ellenberg indicator scores for moisture (F) on MSL for the total dataset ($n=1600$, $R^2_{adj} = 26.3\%$).

The regression equations of the classes were compared with each other. Many of the intercepts of the regression equations are significantly different from each other (as can be deduced from Table 3). Differences between slopes of the regression lines are smaller. The differences in intercepts and slopes cause large differences in the predicted Ellenberg scores for the various phytosociological classes at a given pH value. For example, there is a difference in predicted R of 3.8 units at pH 5.0 between *Calluno-Ulicetea* and *Galio-Urticetea*. For each phytosociological class we calculated the predicted R value at pH 5.0 (for the classes with a nonsignificant response we used the overall mean R value). We plotted these values versus the mean R over all relevés in that class (Figure 4, the mean R values can be found in Table 3). If the Ellenberg indicator values were not biased we would expect no significant relationship between the predicted and the mean R scores; for each class we would expect the same predicted R. However, Figure 4 shows that there is a significant positive relationship ($p < .0001$) between predicted and mean R score, so Ellenberg indicator values are apparently biased. These differences are mainly caused by the difference in the intercepts.

Table 3. Estimates of the parameters (with the standard error s.e., t probability and p values for the regression coefficient) for the regression analyses of R on pH, per phytosociological class for model 2 and 3 (classes with less than 20 observations were excluded). For model 1 ($y=\alpha+\beta x$) $\alpha=0.14$, $s.e.=0.09$, $t_{3631}=1.49$, $\beta=0.84$, $s.e.=0.02$, $t_{3631}=53.10$ ($p<.001$). For model 2 ($y=\alpha_i+\beta x$) $\beta=0.50$, $s.e.=0.02$, $t=34.04$ ($p<.001$), the values for α_i are given in the table per phytosociological class. The statistical significance of the regression coefficients for model 3 are given in the table (n.s. = not significant, * $p<0.05$, ** $p<0.01$, *** $p<0.001$).

vegetation type	n	class mean ($y=\alpha_i$)	intercept model 2	intercept model 3	regression coefficient model 3
			estimate (s.e.)	estimate (s.e.)	estimate (s.e.)
<i>Saginetea maritima</i>	35	5.76	2.07 (0.16)	-2.06 (3.45)	1.07* (0.47)
<i>Littorelletea</i>	61	3.89	1.36 (0.12)	-1.44 (0.61)	1.07*** (0.12)
<i>Oxycocco-Sphagneteta</i>	195	2.27	0.03 (0.08)	-0.26 (0.31)	0.57*** (0.07)
<i>Scheuchzerietea</i>	24	2.30	0.21 (0.16)	-0.18 (1.52)	0.60 n.s. (0.37)
<i>Calluno-Ulicetea</i>	100	2.50	0.11 (0.10)	-0.15 (0.52)	0.56*** (0.11)
<i>Koelerio-Corynephoretea</i>	357	4.54	1.41 (0.10)	0.06 (0.20)	0.72*** (0.03)
<i>Phragmitetea</i>	30	5.29	2.28 (0.16)	0.77 (0.89)	0.76*** (0.15)
<i>Nardetea</i>	76	2.90	0.59 (0.11)	0.87 (0.47)	0.44*** (0.10)
<i>Franguletea</i>	37	4.32	2.07 (0.13)	1.87 (0.69)	0.55** (0.15)
<i>Parvocaricetea</i>	90	4.33	1.69 (0.11)	1.92 (0.40)	0.46*** (0.08)
<i>Alnetea glutinosae</i>	26	5.41	2.63 (0.16)	1.97 (0.85)	0.62*** (0.15)
<i>Molinio-Arrhenatheretea</i>	1643	5.45	2.48 (0.09)	2.22 (0.15)	0.55*** (0.03)
<i>Epilobietea angustifolii</i>	21	4.15	1.90 (0.17)	2.48 (0.69)	0.37* (0.15)
<i>Vaccinio-Betuletea pubescentis</i>	66	3.40	1.28 (0.11)	2.89 (1.01)	0.12 n.s. (0.24)
<i>Isoeto-Nanojuncetea</i>	130	4.44	1.65 (0.10)	3.04 (0.41)	0.25*** (0.07)
<i>Artemisietea vulgaris</i>	20	6.03	2.60 (0.19)	3.35 (1.05)	0.39* (0.15)
<i>Galio-Urticetea</i>	79	6.80	3.50 (0.13)	3.53 (0.48)	0.50*** (0.07)
<i>Asteretea tripolii</i>	60	6.46	2.83 (0.14)	3.92 (0.98)	0.35* (0.14)
<i>Trifolio-Geranietea sanguinei</i>	35	6.94	3.11 (0.17)	4.20 (2.40)	0.36 n.s. (0.32)
<i>Quercetea robori-petraeae</i>	105	4.00	1.97 (0.09)	4.21 (0.47)	-0.06 n.s. (0.12)
<i>Quercu-Fageteta</i>	175	5.77	2.98 (0.10)	4.25 (0.22)	0.27*** (0.04)
<i>Bidentetea tripartitae</i>	21	6.30	2.87 (0.19)	4.62 (1.22)	0.25 n.s. (0.18)
<i>Vaccinio-Piceetea</i>	41	3.22	0.97 (0.13)	4.76 (0.68)	-0.34* (0.15)
<i>Plantaginetea majoris</i>	81	6.10	2.80 (0.13)	4.87 (0.71)	0.19 n.s. (0.10)
<i>Festuco-Brometea</i>	30	7.03	3.30 (0.17)	6.24 (3.57)	0.11 n.s. (0.48)

Validity of Ellenberg indicator values judged from physico-chemical field measurements

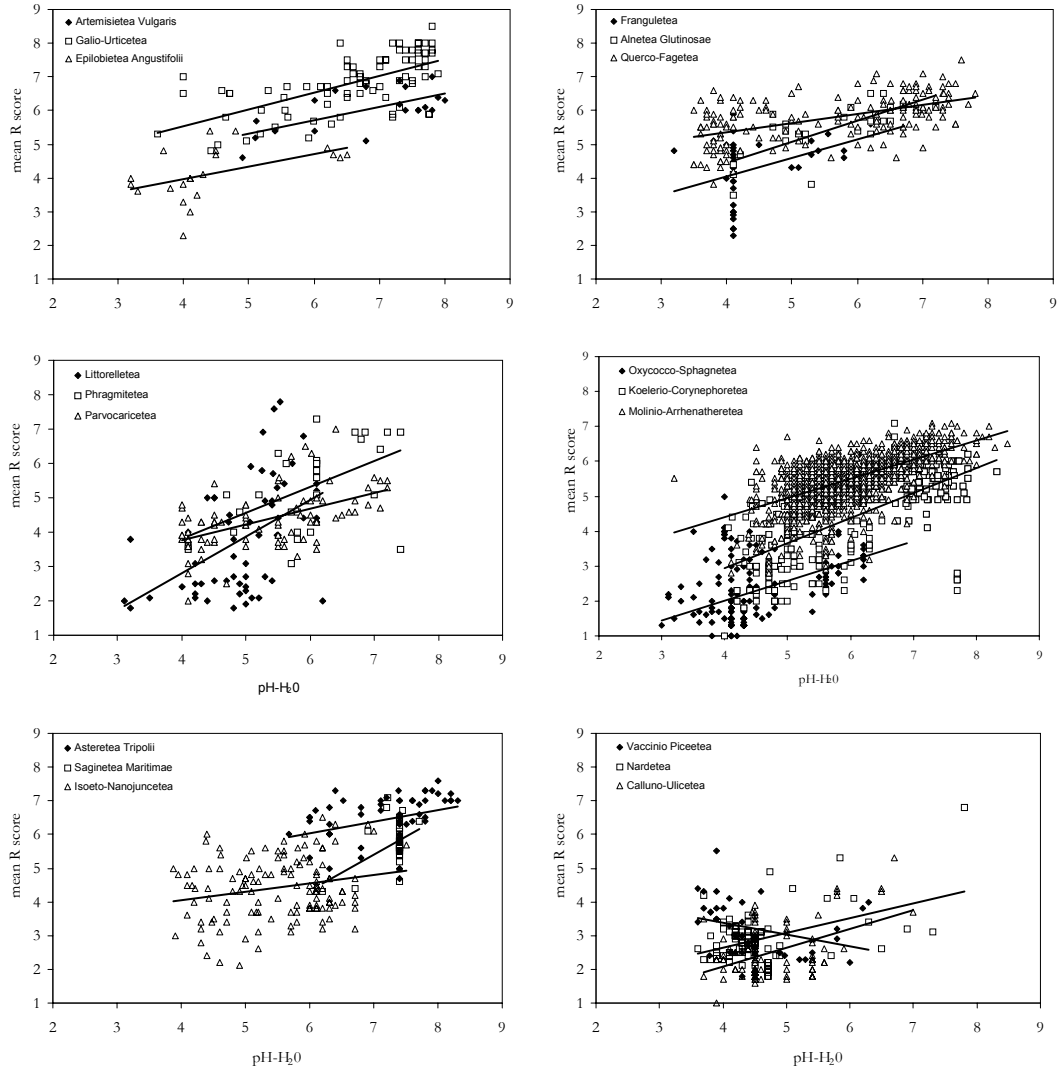


Figure 3. Regression of mean Ellenberg indicator values for acidity on pH per phytosociological class. Only the phytosociological classes with more than 20 observations and a statistically significant relationship are shown. The phytosociological classification is after Schaminée et al. (1995, 1996 and 1998) and Stortelder et al. (1999).

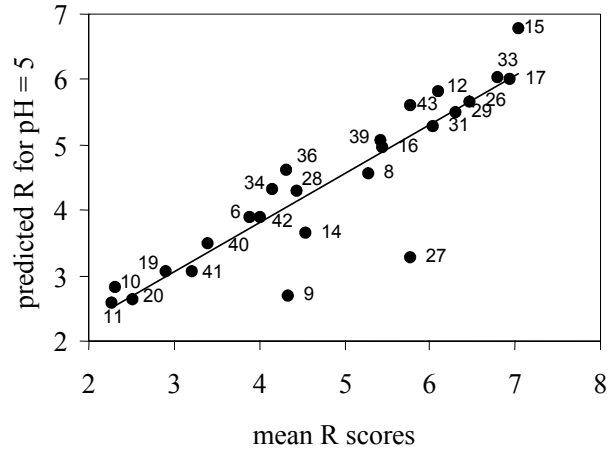


Figure 4. Mean Ellenberg indicator value for acidity per phytosociological class against the predicted Ellenberg indicator for acidity at pH = 5.0; significant relationship ($p < .0001$, $R^2_{adj} = 81\%$). Class numbers (after Schaminée et al. 1995, 1996, 1997 and Stortelder et al. 1999): 6: *Litorelletea*, 8: *Phragmitetea*, 9: *Parvocaricetea*, 10: *Scheuchzerietea*, 11: *Oxycocco-Sphagnetes*, 12: *Plantaginetea majoris*, 14: *Koelerio-Corynephoretea*, 15: *Festuco-Brometea*, 16: *Molinio-Arrhenatheretea*, 17: *Trifolio-Geranietea sanguinei*, 19: *Nardetea*, 20: *Calluno-Ulicetea*, 26: *Asteretea tripolii*, 27: *Saginetes maritimae*, 28: *Isoeto-Nanojuncetea*, 29: *Bidentetea tripartitae*, 31: *Artemisietea vulgaris*, 33: *Galio-Urticetea*, 34: *Epilobietea angustifolii*, 36: *Franguletea*, 39: *Alnetea glutinosae*, 40: *Vaccinio-Betuletea pubescentis*, 42: *Quercetea robore-petraeae*, 43: *Querceto-Fagetea*.

For 9 classes with ≥ 20 observations there was a significant negative relationship ($p < 0.05$) between F and MSL, for 10 classes this relationship was not significant (Figure 5 and Table 4). For the latter mean Ellenberg indicator value for moisture per relevé do not provide information on spring groundwater level. There is a significant positive relationship present between F and MSL for *Calluno-Ulicetea*.

As for pH, the intercepts and slopes differ widely (and in many cases, significantly) between the phytosociological classes. For example a MSL of 20 cm below surface gives a 2.4 F units higher value for *Scheuchzerietea* than for *Rhamno-Prunetea*. The main part of the variation is caused by the difference in intercepts. As for R we related the predicted F at MSL = 20 cm below soil surface to the mean F per phytosociological class. Also in this case there appeared to be a statistically significant relationship between the predicted F at MSL = 20 cm and the mean F score per phytosociological class ($p < .0001$, Figure 6, the mean F values can be found in Table 4). Apparently the MIV for moisture is also biased.

Table 4. Estimates of the parameters (with the standard error s.e. *t* probability and *p* values for the regression coefficient) for the regression analyses of *F* on *MSL*, per phytosociological class for model 2 and 3 (classes with less than 20 observations were excluded). For model 1 ($y=\alpha+\beta x$) $\alpha=7.83$, $s.e.=0.05$, $t_{1484}=155.71$, $\beta=-0.0111$, $s.e.=0.0005$, $t_{1484}=-23.06$ ($p<.001$). For model 2 ($y=\alpha_i+\beta x$) $\beta=-0.0037$, $s.e.=0.0004$, $t=-9.77$ ($p<.001$), the values for α_i are given in the table per phytosociological class. The statistical significance of the regression coefficients for model 3 are given in the table (n.s. = not significant, * $p<0.05$, ** $p<0.01$, *** $p<0.001$).

Phytosociological class	n	Class mean ($y=\alpha_i$)	Intercept model 2	Intercept model 3	Regression coefficient model 3	
			estimate (s.e.)	estimate (s.e.)	estimate	(s.e.)
<i>Koelerio-Corynephoraceae</i>	43	4.71	5.03 (0.10)	5.12 (0.25)	-0.0047 ^{n.s.}	(0.0025)
<i>Calluno-Ulicetea</i>	21	6.00	6.24 (0.13)	5.12 (0.37)	0.0138*	(0.0054)
<i>Galio-Urticetea</i>	35	5.99	6.44 (0.11)	6.21 (0.37)	-0.0019 ^{n.s.}	(0.0028)
<i>Quercetea roboret-petraeae</i>	21	5.90	6.36 (0.14)	6.25 (0.39)	-0.0028 ^{n.s.}	(0.0030)
<i>Rhamno-Prunetea</i>	37	5.57	6.03 (0.11)	6.33 (0.35)	-0.0062*	(0.0027)
<i>Nardetea</i>	34	6.68	7.02 (0.11)	6.73 (0.21)	-0.0005 ^{n.s.}	(0.0019)
<i>Saginetea maritima</i>	32	6.51	6.79 (0.11)	6.78 (0.37)	-0.0035 ^{n.s.}	(0.0047)
<i>Quercu-Fagetea</i>	384	5.79	6.28 (0.06)	6.79 (0.13)	-0.0076***	(0.0009)
<i>Plantaginietalia majoris</i>	60	7.00	7.18 (0.08)	7.42 (0.16)	-0.0087**	(0.0030)
<i>Vaccinio-Betuletea pubescentis</i>	63	7.80	8.25 (0.09)	7.49 (0.21)	0.0025 ^{n.s.}	(0.0016)
<i>Molinio-Arrhenatheretea</i>	318	7.15	7.41 (0.04)	7.52 (0.07)	-0.0054***	(0.0010)
<i>Oxycocco-Sphagnetetea</i>	186	7.56	7.88 (0.05)	7.71 (0.08)	-0.0017*	(0.0008)
<i>Isoeto-Nanojuncetea</i>	52	7.38	7.58 (0.08)	7.77 (0.17)	-0.0073*	(0.0027)
<i>Asteretea tripolii</i>	28	7.06	7.33 (0.11)	8.17 (0.29)	-0.0152***	(0.0037)
<i>Parvocaricetea</i>	49	8.16	8.40 (0.09)	8.19 (0.13)	-0.0006 ^{n.s.}	(0.0014)
<i>Franguletea</i>	36	8.01	8.35 (0.10)	8.25 (0.15)	-0.0026 ^{n.s.}	(0.0013)
<i>Scheuchzerietea</i>	26	8.39	8.54 (0.12)	8.65 (0.13)	-0.0063***	(0.0014)
<i>Phragmitetea</i>	20	8.83	8.89 (0.13)	8.87 (0.14)	-0.0025 ^{n.s.}	(0.0028)
<i>Littorelletea</i>	41	9.00	8.93 (0.09)	8.91 (0.10)	-0.0079 ^{n.s.}	(0.0065)

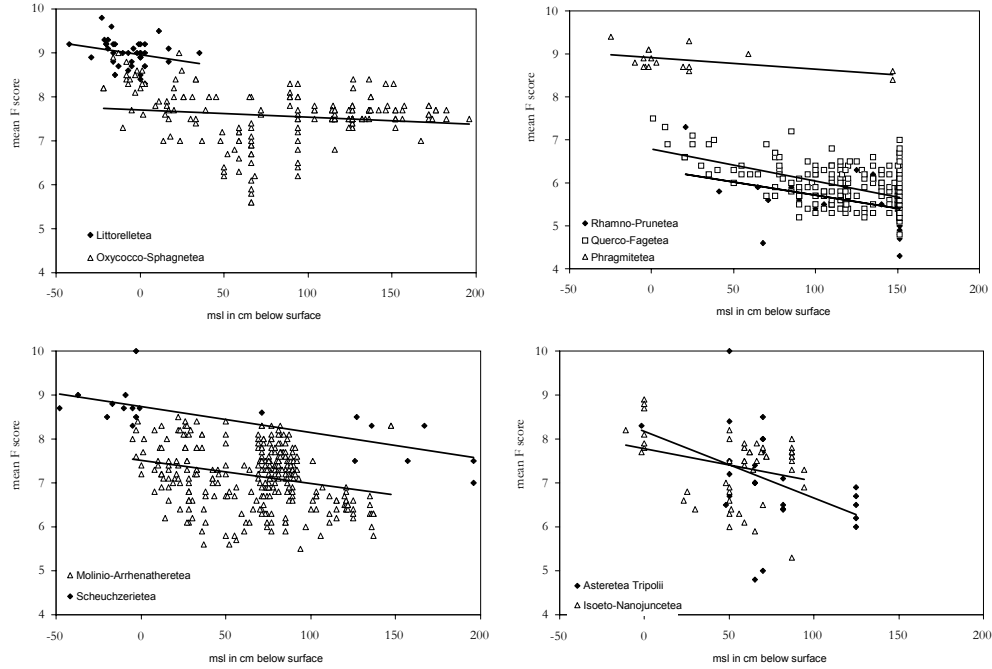


Figure 5. Regression of mean Ellenberg indicator values for moisture on MSL per phytosociological class. Only the phytosociological classes with more than 20 observations and a statistically significant relationship are shown. The phytosociological classification is after Schaminée et al. (1995, 1996 and 1998) and Stortelder et al. (1999).

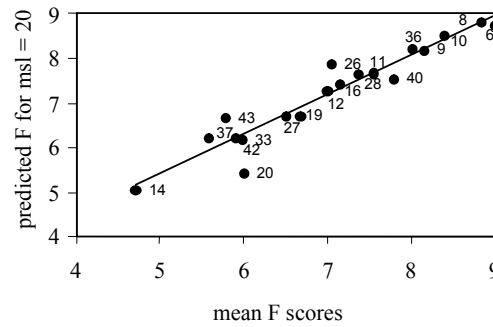


Figure 6. Mean Ellenberg indicator value for moisture per phytosociological class against the predicted Ellenberg indicator for moisture at MSL = 20 cm; significant relationship ($p < .0001$, $R^2_{adj} = 91\%$). Class numbers (after Schaminée et al. 1995, 1996, 1997 and Stortelder et al. 1999): 6: Littorelletea, 8: Phragmitetea, 9: Parvocaricetea, 10: Scheuchzerietea, 11: Oxycocco-Sphagnetum, 12: Plantaginetea majoris, 14: Koelerio-Corynephoretea, 16: Molinio-Arrhenatheretea, 19: Nardetea, 20: Calluno-Ulicetea, 26: Asteretea tripolii, 27: Saginetea maritimae, 28: Isoeto-Nanojuncetea, 33: Galio-Urticetea, 36: Franguletea, 37: Rhamno-Prunetea, 40: Vaccinio-Betuletea pubescentis, 42: Quercetea roburi-petraeae, 43: Quercus-Fagetea.

Discussion

In our dataset the variance explained by the regression of mean R values on measured soil pH, or mean F values on measured spring ground water level, strongly increases when the phytosociological classes are added to the regression model. The hypothesis that differences in phytosociological class cause the large spreads around the calibration lines is strongly confirmed by the results of our analysis, although a part of the variance remains unexplained even when taking the phytosociological classes into account.

Figure 4 and 6 show that for each class, the mean Ellenberg indicator value predicted per relevé at given abiotic circumstances is strongly and positively related to the MIV of that class, i.e. the abiotic circumstances where phytosociologists expect that class to occur. Or, in other words, the IVS, which for the greater part are a reflection of the phytosociological experience, tend to be biased towards the values expected for the phytosociological classes. Strictly speaking, we have only proven that MIVs for relevés are biased, but as these are made up of individual species, we assume that this is also the case for IVs.

Relatively low R values at pH 5.0 are found for *Oxycocco-Sphagnetum* and *Littorelletea*. *Oxycocco-Sphagnetum* communities (peat bogs and wet heathland) are dominated by *Erica tetralix* (Schaminée et al., 1995), commonly occurring on very nutrient-poor substrates with a very low pH. *Littorelletea* communities (shore vegetation), commonly occurring at modestly acid soils, but suffering from acidification, are dominated by *Juncus bulbosus* (Schaminée et al., 1995). High means for pH are found for *Galio-Urticetea* and *Quercu-Fagetea*. *Galio-Urticetea* are tall forb communities, dominated by *Urtica dioica* and *Galium aparine*, commonly occurring on rich soil, e.g. roadsides and forest edges (Stortelder et al., 1999). *Quercu-Fagetea* are forest communities, dominated by species like *Quercus robur*, *Fagus sylvatica* and *Fraxinus excelsior* (Stortelder et al., 1999). Both classes occur on rich and wet soils (clay and loam), with a relatively high pH.

The results for groundwater levels show a similar pattern. Here our data suggest that at a given MSL phytosociological classes which are expected at high MSL (the higher the MSL the deeper the groundwater table) have relative low mean F values, while phytosociological classes that are expected at low MSL have relatively high F values.

The results presented here have important implications for the practical application of Ellenberg indicator values. It is clear from our analyses that Ellenberg values cannot be compared between phytosociological classes. This strongly limits the application range of these IVs. We recommend therefore that in ecological models, where pH and MSL are translated into R and F respectively, calibration equations per phytosociological class are used, rather than general equations. This narrows the spread in the estimated values and therefore the uncertainty in the final results of the model.

The results raise the question whether the same pattern will be found when the dataset is split up further, down to the level of association. However, a far larger

dataset would then be required. A preliminary analysis for just a fraction of the relevés in our dataset (for pH, for the phytosociological classes *Oxycocco-Sphagneteta*, *Koelerio-Corynephorsetea*, *Molinio-Arrhenatheretea*, *Calluno-Ulicetea*, *Quercetea roburi-petreaea* and *Querceto-Fagetea*) indicated that within an association there is no relationship between R and pH. The ranges for both R and pH appeared to be too narrow to reveal any relationship (data not shown).

The regression of mean Ellenberg R and F scores with the total data set gives similar results as found by Ertsen et al. (1998), Schaffers & Sikora (2000) and Dzwonko (2001), although in our case the percentage explained variance is lower. This is probably due to the composition of our database, which contains a wider range of vegetation types and environmental conditions. Ertsen et al. (1998) found that for pH, a non-linear fit gave the highest explained variance. We tested both quadratic and log transformations, but no evidence for non-linearity was found in our study.

For many phytosociological classes there was no significant relationship between R and pH (7, Table 3) and between F and MSL (10, Table 4). Apparently, in many habitats mean Ellenberg indicator values are no predictor for environmental conditions, at least not soil pH and MSL, which strongly limits their use. For the phytosociological class *Vaccinio-Piceetea* a significant negative relationship was found between R and pH, while a positive relationship was expected. For *Calluno-Ulicetea* a significant positive relationship between F and MSL was found, while a negative relationship was expected. There is no apparent explanation for these unexpected relationships.

Part of the large variation in the data for soil pH is probably caused by the variation in the methods that have been applied. Soil pH has been measured at different depths and with different techniques (although they were all taken from the upper layer and measured in water extract). The seasonal variation of the pH is also influencing the spread; measurements have been taken from spring till (late) summer. Also for MSL differences in measurement technique may partly explain the spread. Although the measurement technique is well described and there is almost no seasonal influence (because either it covers a well-defined short period in the growing season or it refers to a long-term mean), differences in method (either piezometers or soil profile description) and years of measurements give rise to spread.

Regarding the disadvantages of the use of mean Ellenberg indicator values shown here, and those recently shown by Schaffers et al. (2000), we recommend the development of an indicator system based on vegetation relevés combined with measurements of abiotic factor using a standardised method (e.g. pH always at the same depth). Until such a system is available, Ellenberg indicator values can still be used for comparison within phytosociological classes, and between phytosociological classes by using the regression lines given in this paper. But whenever possible the use of data based on measurement (i.e., not biased by expert judgement, Verboom & Wamelink, 1999) should be preferred.

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**Plant species as predictors of soil pH: replacing
expert judgment with measurements**



3 Plant species as predictors of soil pH: replacing expert judgment with measurements

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Abstract

Question: The use of expert-based indicator values to estimate abiotic conditions from vegetation is widespread. However, recent research has shown that expert judgement may contain considerable bias and thereby introduces a large amount of uncertainty. Could expert based indicator values be replaced by indicator values based on field measurements?

Location: Europe.

Methods: We developed a method to estimate species response based on measured physical data, and a method to predict abiotic conditions from the vegetation composition using these responses. This method was tested for soil pH.

Results: We were able to estimate the pH response of 556 species of the Dutch flora. Circa 20% of the responses were at least, bimodal and responses had a very wide range. For both the ecological consequences are discussed. The simplest method ("raw mean") yielded the best prediction of pH; the indicator value of a species is the mean of the soil pH-values of the sites where it was observed. A list of all raw mean estimates per species is given. The predicted pH of a new site is the mean of the indicator values of the present species. The estimated species responses were validated on independent Dutch and European data sets. Older successional stages seem to be predicted better than younger stages.

Conclusions: Our method performed better than the popular Ellenberg indicator system for the Dutch data set, while being just as easy to use, because it only needs a single value per species. We foresee that, when more data become available, our method will have the potential to replace the Ellenberg system.

Introduction

Although, in isolation, most plant species are able to grow under widely varying circumstances, in natural communities they do so within a limited range of abiotic conditions. Their occurrence is influenced by many variables, both abiotic and biotic. The question why plant species only occur under certain environmental conditions and what these conditions are, have been the subject of many studies (e.g. Campbell & Grime, 1992; Loreau, 2001; Bobbink et al., 1998; Pugnaire & Luque, 2001; Maestre et

al., 2003; Endels et al., 2004). This paper aims to answer the second question. Information on the abiotic requirements of plant species enables us to estimate their response to human activities such as management, air pollution, climate change or urbanisation. However, direct measurement of the variables of interest is usually time consuming and costly, and therefore expert knowledge is often used instead. The reliability of such expert judgement appears to be questionable (Schaffers & Sýkora, 2000; Wamelink et al., 2002). Here, we aim to characterise the response of a large set of plant species to a single environmental factor (pH) on the basis of field measurements.

In vegetation assessments the use of expert-based indicator values is widespread (e.g. Diekmann, 1995; Wohlgemuth et al., 1999; Smart et al., 2003; Bouriaud et al., 2003; Korvenpää et al., 2003; Diekmann, 2003; Gegout et al., 2003). Indicator values can be used to provide information about the abiotic environment of a certain plant species assemblage. They are derived from the relation between the presence of species and a characterisation of its environment. Following this approach the species can provide information on the environmental conditions without measuring these. Moreover, if the abiotic conditions are known, the probability of occurrence per species can be predicted on the basis of these conditions (Latour et al., 1994). Usually, many species occur together and we would expect that combinations of their indicator values would allow more reliable estimates of the abiotic conditions.

Although many indicator systems work well in certain areas and vegetation types (Kruijne et al., 1967; Zólyomi et al., 1967; Landolt, 1977; Ellenberg, 1979; Ellenberg et al., 1991; Grime et al., 1988; Diekmann & Falkengren-Grerup, 1998), there are several disadvantages:

1. Indicator systems do not provide information on ecological amplitudes. Species occur over a range of abiotic values, and the width of this range may vary per species. The indicator value per species is just a single value, which can be considered as the hypothetical optimum of the species.
2. Most systems are based on expert knowledge while only a minor part is based on field measurements. Wamelink et al. (2002) showed that expert systems can be biased, which restricts their application.
3. Often a transformation of the indicator values into abiotic values is necessary, for instance in the calculation of critical loads (Van Hinsberg & Kros, 2001; Wamelink & Van Dobben, 2003). The indicator values have an arbitrary scale, while the results of actual measurements are in abiotic units. The transformation of indicator values into variables with abiotic dimensions often introduces a large amount of uncertainty (Ertsen et al., 1998; Schaffers & Sýkora, 2000; Wamelink et al., 2002; Wamelink & Van Dobben, 2003). It would be a significant improvement if this transformation could be omitted, basing indicator values directly on actual measurements.

Therefore, we tried to develop an indicator system directly based on abiotic characteristics measured in the field. Such a system is easier to validate than expert estimates (Verboom and Wamelink, 2005). Furthermore, it can be directly used in the field without the difficult step of transformation of indicator values into abiotic characteristics.

The aim of this study is to investigate the feasibility of an indicator system based on abiotic measurements. We do this by (1) developing a method to derive response curves for individual plant species to soil pH and (2) using these response curves to predict soil pH on the basis of the species composition alone. We attempted to develop a method that is sufficiently general, so that it can be applied to other abiotic values as well. We aimed to get the best balance between reliability and simplicity. We tested several related methods to estimate response curves. Our training set for the estimation of species responses consisted of a large data set of vegetation relevés and measured soil pH from the Netherlands. We then tested a number of methods to obtain predictions based on the response curves for vegetation relevés. These predictions were validated for independent data sets, containing relevés with measured pH, from The Netherlands and from several other European countries.

Material and Methods

Training set

Vegetation relevés that include data on abiotic variables were collected from published and unpublished sources and stored in a database. The collected relevés had to match the following criteria:

- 1 At least one of the following soil characteristics had to be measured: pH-H₂O, pH-KCl, or pH-CaCl₂.
2. The relevés had to be made in The Netherlands or directly adjacent areas.
3. From a time series only one relevé was used.

A total of 5428 relevés were established in The Netherlands and a site near Antwerp in Belgium. The relevés are, geographically, well distributed over The Netherlands; only areas with intensive agricultural use (grasslands and arable land) were excluded. Normally, soil samples are not taken in the plot but in its direct proximity, and therefore the soil samples had to be assigned to the relevés. When more than one relevé was in the proximity of a soil sample, a maximum of two, randomly chosen, relevés was included in the database. If soil variables were measured in more than one soil layer, the measurements in the upper layer were entered in the database. Conditions of the litter layer were not included. When more than one soil sample was taken, the mean of the upper layer was used. The range of pH-H₂O values and the number of observations per pH unit are given in Figure 1.

The number of available pH-H₂O values was extended by estimating pH-H₂O on the basis of pH-KCl values. For this purpose a regression equation was derived from the available data, i.e. soil samples where both were measured. The relation is highly significant ($p < 0.001$; $R^2_{\text{adj}} = 0.94$: $\text{pH-H}_2\text{O} = 1.53 + 0.82 \cdot \text{pH-KCl} \pm 0.26$). For the relevés where only pH-KCl was available, pH-H₂O was calculated using this relation. In this way the number of relevés with an ‘observed’ value of pH-H₂O increased to 5428.

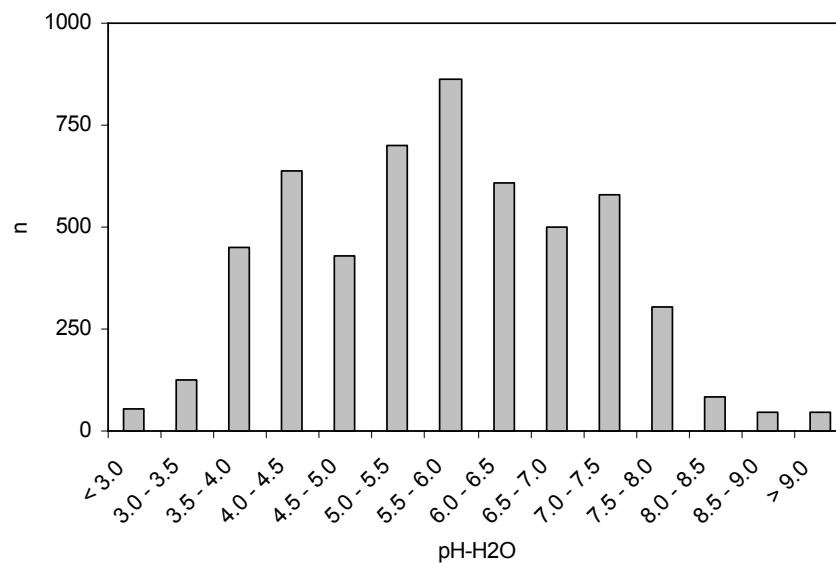


Figure 1. Number of occurrences for pH-H₂O per 0.5 pH unit. The total number of occurrences is 5428; this includes the values that are calculated from the measured pH-KCl.

Species response curves

For relevés with a known abiotic variable such as pH, the presence-absence data of a species can be used to relate the probability of occurrence (p) of that species to pH. We applied logistic regression (Jongman et al., 1995) and a generalised additive model, also called smoothing spline, to model the relationships (Hastie & Tibshirani, 1990; Green & Silverman, 1994). The flexibility of a smoothing spline can be expressed by the number of degrees of freedom (df) of the spline, with flexible curves having more degrees of freedom (App. 1). Figure 2 gives examples of estimated response curves for varying degrees of freedom. The degrees of freedom of the smoothing spline were determined by backward deviance testing (Van Dobben & Ter Braak, 1999): the number of degrees of freedom was decreased one at a time, starting at 5 and was stopped when the resulting decrease in fit was significant at the 1% level as judged on the basis of a deviance test (Hastie & Tibshirani, 1990). This was indicated here as the

‘automatic method’. Some response curves did not fit well at the extremes of the pH range. Therefore, we also used a fixed number of degrees of freedom for each species, and a manual selection of the best response curve by eye (see App. 2). The smoothing splines were fitted using the statistical program GenStat (Payne & Ainsly, 2000). Since smoothing splines are not explicitly parameterized, the response curves were saved on an equidistant grid of 500 pH values. This is sufficiently dense compared to the rounding of the pH values to 0.1.

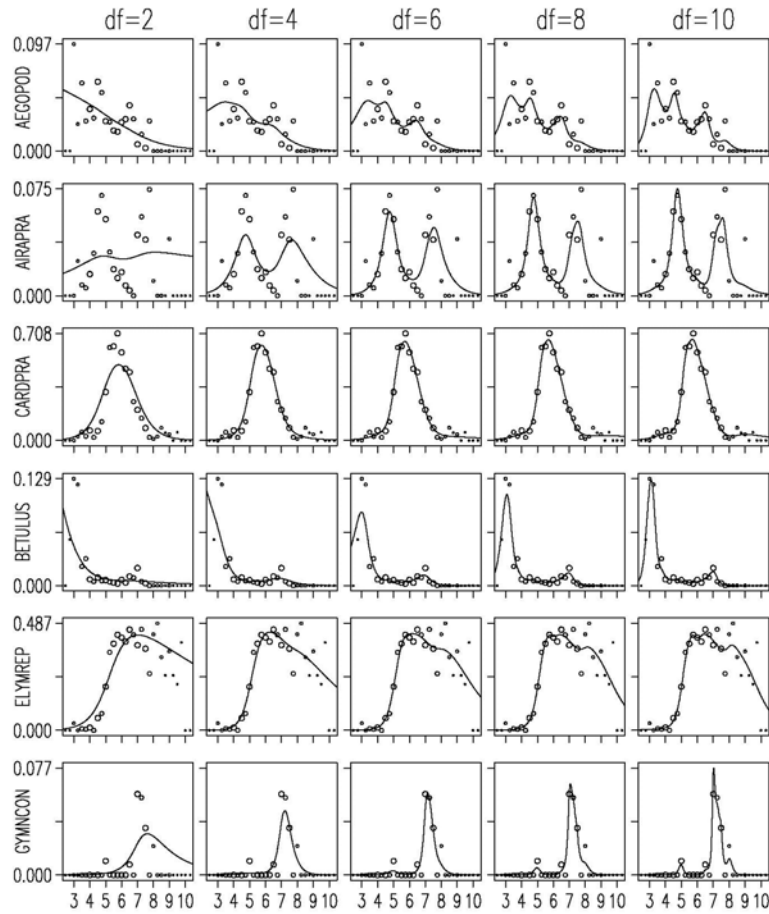


Figure 2. Estimated response for the species *Aegopodium podagraria* (AEGOPOD), *Aira praecox* (AIRAPRA), *Cardamine pratensis* (CARDPRA), *Carpinus betulus* (BETULUS), *Elymus repens* (ELYMREP) and *Gymnadenia conopsea* (GYMNCON). The estimation of the optimum degrees of freedom gave $df = 2, 5, 5, 2, 5, 5$ for the ‘automatic’ method, the visual method resulted in $df = 6$ for all species, except for *Cardamine pratensis* with $df = 8$. On the y axis the chance of occurrence in the data set is given, the axis size is adjusted to the maximum chance of occurrence per species for soil pH. The centre of the dot gives the mean response for a pH-interval. There are four sizes of dots indicating the number of occurrences per pH class (respectively 1-20, 21-100, 101-250 and > 250 occurrences).

The width of a species response curve was defined by the standard deviation of the curve, after scaling the curve to have an area of unit one. Moreover, the number of modes of every curve was counted. Small bumps, i.e. smaller than 1/10 of the maximum of the curve, were not counted as modes. The response curves (Fig. 2) for $df=4$, top to bottom, have a width of 1.60, 1.86, 0.93, 1.52, 1.56 and 0.71, respectively. The number of modes for the curves with $df=4$ is 1, except for AIRAPRA which has 2 modes. For the curves with $df=10$ the number of modes is 3, 2, 1, 2, 1 and 1 respectively. This shows that small bumps are not counted as modes.

Validation sets

Four validation sets from The Netherlands were used:

- 1) A dune area on the island of Ameland. It contains relevés of several successional stages: young dunes bordering a salt marsh, grasslands which are flooded occasionally and old dunes (Eysink et al., 1995).
- 2) A dune area with only old dunes in the province of North Holland (pers. comm. P. Hommel).
- 3) A wet grassland and freshwater reed marsh area (pers. comm. R. van 't Veer).
- 4) A forest data set that is part of the forest vitality monitoring program in The Netherlands (Van Dobben et al., 1997). This last set contains data from both coniferous and deciduous forest on various soil types. Three validation sets from other European countries were used.
- 5) A data set from 20 countries in Europe that are part of a European forest monitoring project conducted by UN-ECE (De Vries et al., 2001). This data set contains relevés from all climatic zones (Boreal, Atlantic, Central and Mediterranean), many soil types and different altitudes.
- 6) Relevés made for the 'countryside survey' of the vegetation of the UK in 2000 (Smart et al., 2003), which contains relevés made in many vegetation types and soils.
- 7) A set of relevés made in experimental fields in Bierbza in Poland (Okruszko 1989). These relevés were made in 1996 in a grassland fertilisation and management experiment; only the control plots were used. The predicted pH values are compared with the observed pH values.

For the Ameland and Bierbza data sets the pH-KCl was measured, which was transformed to pH-H₂O using the method mentioned earlier. The pH-CaCl₂ was measured for all relevés of the UN-ECE data set. They were converted to pH-KCl using a transfer function estimated by Fotyma & Jadczyzyn (1998) and then into pH-H₂O using our relation. The transfer function increases the uncertainty in the measured data, but since the transformation functions do have high correlations ($r=0.99$ and $r=0.97$ respectively), the introduced uncertainty was expected to be acceptable.

Prediction methods

The fitted splines were used to estimate the pH of a relevé based on its species composition alone. We explored four different methods to predict the pH. Three further methods are presented in App. 3.

1. The first method, called ‘full’, uses the presence as well as the absence of species in a relevé. Consider, for instance, a hypothetical situation with only three species (A, B and C) for which spline response curves $p_A(\text{pH})$, $p_B(\text{pH})$ and $p_C(\text{pH})$, all functions of pH, are available. The probability of occurrence of a relevé with abiotic value pH, species A and B present and C absent, is given by $p_A(\text{pH}) \times p_B(\text{pH}) \times [1 - p_C(\text{pH})]$, assuming that species A, B and C occur independently of each other. The pH value at which this probability is maximal is then an estimate for the pH of that relevé, and this is the usual maximum likelihood estimation method (Jongman et al., 1995). It is clear that for every species composition a product of probabilities similar to the one above can be maximised to give an estimate of pH. This method is called the ‘full’ method since both present and absent species is used in the calculation of the probability product (for further explanation see Gegout et al., 2003).
2. The ‘present’ method only uses species that are present in the relevé, yielding the pH value at which the function $p_A(\text{pH}) \times p_B(\text{pH})$ is maximal in the hypothetical situation. Two further methods, called ‘mean spline’ and ‘raw mean’, were tested. These methods first estimate an indicator value for the pH of single species. The predicted pH for a new relevé is then the mean of the indicator values of the species present in that relevé. These methods can be seen as an indicator value for a species based on data rather than on expert judgement.
3. The ‘mean spline’ method first scales the response curve of a single species to have an area of unit one, i.e. a density function, and then calculates the mean of this density. So the indicator represents the mean of the response curve.
4. Finally, the ‘raw mean’ method does not use the spline approach, but simply takes, as the indicator, the mean of all pH values of relevés where that species is observed.

Response curves were estimated from the training set. The four prediction methods were tested on the training set and subsequently on the seven validation sets. The methods are compared by means of the root mean squared error of prediction (RMSEP), which is the square root of the mean of all squared differences between observed and predicted pH. The RMSEP is similar to a standard error, and smaller RMSEP values indicate better predictions. The RMSEP for the seven validation data sets can be used for proper validation of the methods, as these data were independently collected.

Results

Species responses

The training set contained data about 1363 species. Initially, response curves were fitted for 402 species for which at least 50 data points were available. By lowering the minimum number of data points to 25, we were able to estimate response curves for 556 species. From Table 1 it can be seen that a minimum number of observations of 25 reduced the RMSEP of the ‘full’ method, while for the ‘present’, the ‘mean spline’ and the ‘raw mean’ methods the differences are minor. Since a minimum of 25 occurrences more or less improved almost all prediction methods (they have a lower RMSEP), further results are presented for species with at least 25 data points. Basically, there are three types of response curves (Fig. 2), one that has an optimum for pH at the lower end of the pH-scale, one that has an optimum somewhere along the pH scale and one that has an optimum at the higher end of the scale. It is clear that more degrees of freedom gives a closer fit to the data. This may also introduce multiple optima which is exemplified by *Aegopodium podagraria* and *Aira praecox*. The location of the optimum is relatively independent of the number of degrees of freedom when the location is not too close to either end of the pH scale. In contrast the optimum for *Carpinus betulus* which is near the lower end is shifted when adding more degrees of freedom. Too many degrees of freedom may result in a fit which is too close to the data as is shown for *Gymnadenia conopsea*. Here, four degrees of freedom give a reasonable curve, adding more degrees of freedom results in extra optima and a less smooth curve.

Table 1. Root Mean Squared Error of Prediction (RMSEP) for the training set using the ‘automatic’ method for selecting the degrees of freedom of the spline curves. For ‘RMSEP 50’ the predictions were based on 402 species with a minimum of 50 occurrences, for ‘RMSEP 25’ the predictions were based on 556 species with a minimum of 25 occurrences.

Method	RMSEP 50	RMSEP 25	Description, see text for further details
pH-H ₂ O	1.344	1.344	Standard deviation of all observed pH
Full	1.207	1.128	Prediction based on present and absent species
Present	1.340	1.327	Prediction based on present species
Meanspline	0.986	0.973	Prediction based on the mean of the spline curve
Rawmean	0.887	0.857	Prediction based on the raw averages

The number of estimated curves which are unimodal, including curves with a single optimum at either end of the pH range, is 442, while 114 species are bimodal. There are no curves with more than 2 modes (App. 4). There are 22 species response curves with a SD < 0.5, which is quite narrow. However for 18 of these 22 species, there are less than 50 relevés where that species is present. There are 158 species with a SD between 0.5 and 1, which is moderately narrow. Wider curves, with SD > 1.5, occur for 180 species, and 55 curves have a SD > 2.0.

Table 2. Root mean squared error of prediction (RMSEP) for the validation sets for the four prediction methods of the pH. The degrees of freedom for the estimation of the species response are according the automatic method, except for the ‘raw mean’ method which does not employ spline curves. The best method per set is highlighted in grey (the results for three more methods are given in App. 3). The number of relevés (n_{rel}), the number of species in the dataset (n_{spec}) and the number of species common between the training set and the validation sets (common) are given as well.

Set	n_{rel}	n_{spec}	Communal species	Full	Present	Mean spline	Raw mean
Training set	5428	556	556	1.13	1.33	0.97	0.86
Ameland	66	211	145	1.19	1.05	0.84	0.80
Dunes	48	166	119	1.29	1.16	0.56	0.65
Grassland	84	166	115	1.43	1.23	0.97	0.93
Forest NL	395	339	214	1.15	1.55	0.60	0.68
Forest EU	589	806	299	1.31	1.87	0.74	0.66
Grassland Poland	144	137	93	1.75	1.20	1.64	0.99
UK	1648	426	246	1.72	2.03	1.00	0.95

Validation

The test using independent validation sets produced results similar to the test on the training data set (Table 2). In general the ‘raw mean’ method gives the lowest RMSEP, although the ‘mean spline’ method performed slightly better in two cases (dunes and forest NL). We judge that the raw mean method is the best method for predicting soil pH; in most cases it gives the best result or is second best, and it is by far the simplest method (the values per species are given in Appendix 6). The predictions are best for the dune and forest NL data sets (in both cases with the ‘mean spline’ method) and worst for the grassland and UK data sets. The ‘full’ method performs worst for all data sets.

The differences between measured and predicted pH for the European forest data set are visualised in Figure 3 for the ‘raw mean’ method. The differences are smoothed using the Arc Info kriging algorithm (ESRI, Redlands CA, USA), so they represent a regional difference rather than a difference per relevé. To achieve a smoother map, four very deviant points located in Mallorca (2), Portugal (1) and Denmark (1) were omitted (marked yellow in Figure 3). The smaller variations can be found in the north of Europe and some parts of western and central Europe. Large variations occur in Spain and Italy. The mean absolute difference between predicted and measured pH, including the above mentioned outliers, is 0.5 units. To explore whether the difference between measured and predicted pH systematically depends on the pH itself, the mean absolute differences were calculated per 0.5 pH unit (Figure 4). The differences, and thus the uncertainty of the predictions are larger at extreme values, both at the high and at the low end of the pH scale. The very low number of observations for the extreme values may partly be responsible for this.

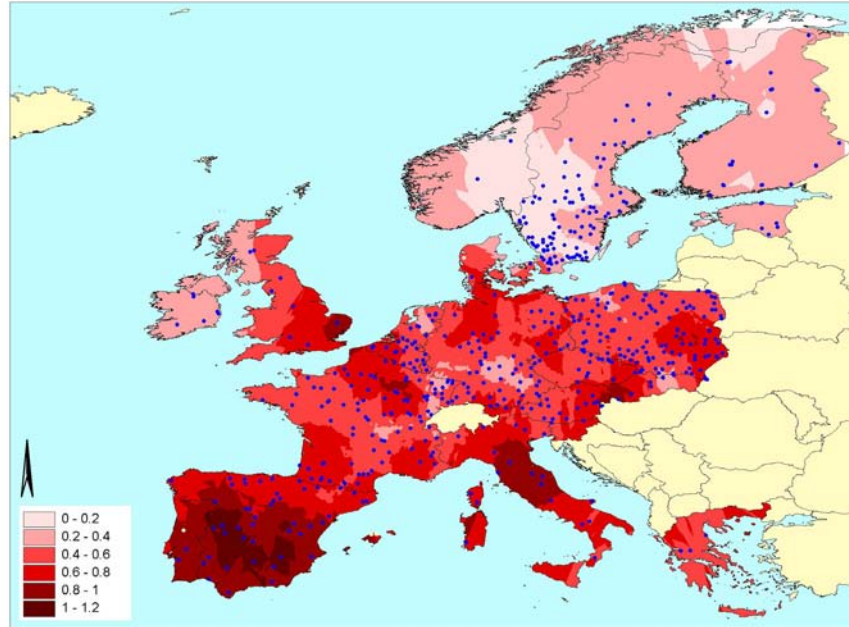


Figure 3. Overview of the smoothed difference between estimated and measured pH in European forest; the darker the colour, the higher the difference. The blue dots indicate the measured sites, the yellow dots the four outliers that were left out in the kriging process to smoothen the mean absolute difference between predicted and measured pH.

Discussion

The validation showed that our method is able to predict the soil pH of a relevé with a RMSEP of c. 0.81 pH unit (the mean RMSEP over all validation data sets for the raw mean method). The easiest method, the raw mean method, seems to be the best. Calculating the mean of the species response for pH and then using the single values per species to calculate the pH of a plot based on the constituting species provides the best results. From our earlier work (Wamelink et al., 2002, Table 1) it can be calculated that the RMSEP of pH values predicted from the mean Ellenberg indicator value for acidity (R), without taking account of the phytosociological classes, is 1.04 in pH units (App. 5) for the same training data set. As the mean RMSEP over all validation sets using the ‘raw mean’ method is smaller, we conclude that not only it is possible to develop an indicator system that is based on the measured pH values, but also it performs better. Moreover, predictions for Europe are as good as predictions for the Netherlands, which is promising for a Europe-wide application of our method. In the present study all prediction methods result in a single prediction value without a standard error. We believe that in the raw mean method we found a good balance between accuracy and simplicity. Bootstrap methods (Efron & Tibshirani, 1993) can

be employed to estimate a standard error of prediction. We assume that a similar approach can be used to estimate the response of plant species to other environmental variables, such as groundwater level or soil nitrogen content.

There are three major sources of uncertainty in the training data set we used:

1. Data were collected from over 50 authors, who used different methods, with respect to both the vegetation relevés and the pH measurement. The depth at which the pH is measured ranges between the upper 5 cm and the upper 100 cm of the soil. Moreover, often there is a (horizontal) spatial heterogeneity present in soil pH.
2. Soil samples were almost always taken at a single point in time. During the season pH may change, even after a heavy rain pH may be altered.
3. Many response curves are fairly ragged with multiple modes and sometimes awkward edge effects. This might be due to (non random) selection of relevés that constitute the training set. For instance relevés with a very low pH value or relevés with unusual species composition might be over- or under-represented in the database.

The used data set consists of all relevés with measured pH that were available to us. There is an urgent need to narrow down the uncertainty by collecting new data following a standardized protocol.

Several types of responses of plant species for soil pH were found, including responses with optima outside the pH-range, responses with a clear single mode and responses with two modes. The number of species that show two modes is significant (ca. 20%). This indicates that using a unimodal response curve, as a Gaussian curve, may lead to wrong conclusions for quite a number of species. A bimodal response may be simply an effect of lack of data (some pH-ranges are under-represented in the data), but may also be the effect of another factor that is correlated with pH, or be the effect of competition with other species. All three causes could lead to an under-representation of species at certain pH values, resulting in a bimodal response. The width of the response curves varies from very narrow to very wide. In fact some of the species with a very wide response may be considered pH-independent. Many species with a narrow response have a low number of occurrences (χ^2 test, $p < 0.001$, based on App. 4). The narrow amplitude of these species may be an artefact caused by a lack of data. However, it may also be real, because rare species may have a narrow niche for an environmental factor, in this case pH.

The large variation in width, height and shape of the response curves suggests that the whole curve is necessary to characterise a species' response, rather than a single value. This is in strong contrast with our results for the prediction of the soil pH from the species, where a single (mean) value gives the best result. We do not have a straightforward explanation for this phenomenon. It is generally believed that a response curve, whether Gaussian or spline, will give a better estimation of the species response to an abiotic variable (e.g. Ter Braak & Gremmen, 1987; Austin et al., 1994;

Wamelink et al., 1998; Van Dobben et al., 2001; Lawesson, 2003; Rydgren et al., 2003; Thuiler et al., 2004; Godefroid & Koedam, 2004). Overall, it seems to be wise to take the whole response curve into account when a single species is the focus of interest; but when the whole species assemblage is taken as an indicator for soil pH, single values seem to be appropriate. The advantage of the latter is that it is easy to handle; it can be calculated in the field with a simple calculator. This contradicts the results found by Gegout et al. (2003). Their maximum likelihood method (our 'full' method) performed better than their 'classical indicator values approach' (our 'raw mean' method). This may be caused by the data set they used; unlike our data set, theirs was based on data collected following a standardised protocol in a limited number of vegetation types.

The wide amplitude of the responses of many species may indicate that these species are able to grow on a wide range of pH values. However it may also indicate a strong local variation within the measured plot, causing the measured pH to be different from the pH at the exact spot where a species is growing. In that case a species with an apparently wide amplitude could still have a narrow one, and only occur in microsites where a suitable pH occurs. In theory this could even be the case for all species with a wide range. Only direct measurements near the roots of the individual plants can reveal to what extent this explanation is true.

The validation results show that the prediction error is smaller in forests. At least part of these forests will be in final stages of succession, where the occurrence of species and soil variables can be assumed to be more or less stable. Younger (i.e., non-forest) successional stages show a higher prediction error. It seems that later successional stages can be predicted better, which is also supported by the difference between the Ameland data set and the Dune data set. The first set contains relevés of several successional stages, whether the latter only consists of relevés of an older, more stable successional stage, and has the smaller RMSEP of the two. Dzwonko et al. (2001) also reported that ancient forest could be predicted better than younger forests using indicator values.

Although the system is calibrated with relevés from The Netherlands, the results are equally good or sometimes even better for other countries. The sample for which we were able to estimate a response is apparently large enough to be applicable to large parts of Europe, at least in forests. Figure 3 suggests that predictions are better in the North. The pH gradient over Europe (with low values in the North and high values in the South) might be responsible for this. The data summarised in Figure 4 support this hypothesis. But the larger prediction error towards the South may also be caused by the low number of observations for higher pH values. Another explanation might be that at high pH values, calcium may be a better predictor for the occurrence of species than pH itself, as suggested by Schaffers & Sýkora (2000).

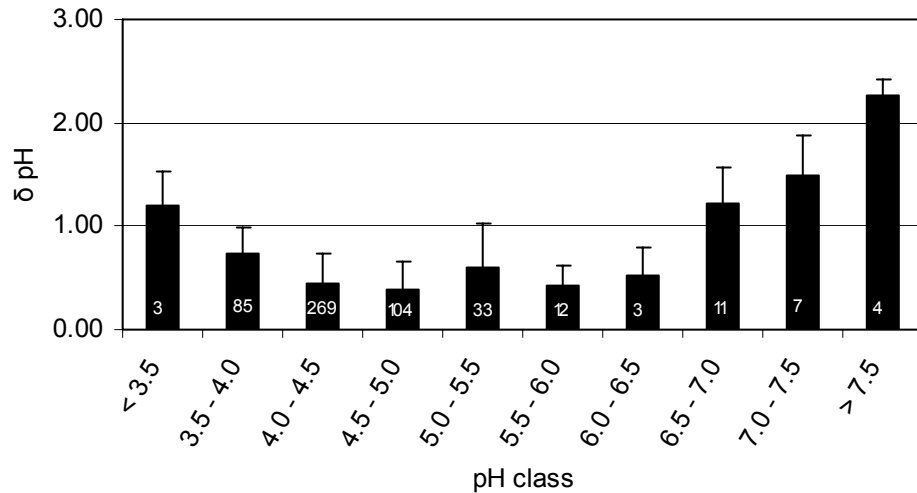


Figure 4. The mean absolute difference between measured and predicted pH (with SD) for the European forest data set. The numbers in the bars denote the number of observations in the category.

We believe that the indicator system proposed here has several advantages compared to the Ellenberg indicator system. The first is that it is expressed in physically measurable units (i.e. soil pH) instead of being based on an arbitrary scale. This makes it possible to estimate the soil pH in a field situation, which allows an absolute instead of a relative comparison with other situations in the field, without being restricted to the same vegetation type (cf. Wamelink et al., 2002 and the discussion that followed it: Witte & Von Asmuth, 2003; Wamelink et al., 2003; Smart & Scott, 2004; Wamelink et al., 2004). The use of indicator values on an arbitrary scale often creates the necessity to translate these values into physical values, which comes with unnecessary extra uncertainties (Ertsen et al., 1998; Schaffers et al., 2000; Wamelink et al., 2002; Wamelink & van Dobben, 2003). For instance, in vegetation management, biotic goals such as higher species diversity may be translated into (abiotic) target conditions which have to be in measurable units, i.e. soil pH. Second, the uncertainty in the Ellenberg indicator value for acidity itself is larger than for our system for pH (as is shown by the larger RMSEP). Although the differences are small for some validation sets, even this difference may already have a large impact, especially since the pH is on a log-scale. Improvement of the system is still possible, as shown by Gegout et al. (2003), who found a much smaller RMSEP for a more homogenous data set. A third advantage of our system (which is so far theoretical) is that it is possible to investigate interactions between measured (abiotic) factors. In order to do this, however, sufficient vegetation data should be available with measurements of more than one abiotic factor, which is not the case at present. Finally, expert-based systems (including Ellenberg's) consist of single values. At least on the species level, response curves

seem to be more appropriate in view of the wide variety of shapes of the response curves found in our data.

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Appendix 1. Extra information about the spline method

Linear logistic regression employs the model $\text{Logit}(p) = \beta_0 + \beta_1 \text{pH}$, which represents a S-shaped curve for the probability of occurrence, while the Gaussian logit curve $\text{Logit}(p) = \beta_0 + \beta_1 \text{pH} + \beta_2 \text{pH}^2$ represents a unimodal (single-peaked) symmetric response curve. Further polynomial terms can be added to increase the flexibility of the response curve. However, polynomials have certain drawbacks such as the implicit symmetry of the quadratic model and undesirable edge effects. For this reason we used a generalised additive model, also called smoothing spline, to model the relationships. The flexibility of a smoothing spline can be expressed by the number of degrees of freedom (*df*) of the spline, with flexible curves having more degrees of freedom. The degrees of freedom of a spline can be regarded as the number of parameters associated with it. A spline with one degree of freedom is equivalent to the linear logit model, while a spline with two degrees of freedom is already capable of fitting a bimodal response when the two modes are well separated.

Appendix 2. Effect of the degrees of freedom for the spline on the pH prediction

We applied three methods for the determination of the degrees of freedom of the spline. The first method is the backward deviance testing method which is described in the main text. This method is further called the ‘automatic’ method. The ‘automatic’ degrees of freedom differs from species to species. Some response curves did not fit well at the extremes of the pH range. To correct for these deviations, graphs of response curves with 2, 4, 6, 8 and 10 degrees of freedom, were examined manually and compared with the raw data for each species, and the ‘best’ response curve was selected by eye (‘manual’ method, method two). This method uses expert-judgement. Although we wanted to minimise the expert-judgement in the estimation of indicator values, we thought it was worthwhile to explore this as one of the possible methods. Furthermore, to evaluate whether the spline degrees of freedom were critical, the response curves were also estimated with a fixed number of degrees of freedom (2, 4, 6 and 8) for each species (‘fixed’ method, method three).

Table 1. *Root mean squared error of prediction (RMSEP) for seven pH prediction methods using estimated species response curves with various methods for selecting degrees of freedom: ‘Fixed’ uses a fixed degrees of freedom for every species, ‘Automatic’ uses backward deviance testing, and ‘Manual’ employs a adjustment of the ‘Automatic’ degrees of freedom by visual inspection of response curves. The prediction methods are explained in the main text and in Appendix 3.*

df	Method of pH prediction						
	Full	Present	Mean spline	Raw mean	Full kernel	Present kernel	Max spline
Fixed 2	1.21	1.59	0.94	0.86	1.14	1.25	1.32
Fixed 4	1.67	1.27	0.97	0.86	1.53	1.00	1.18
Fixed 6	1.19	1.12	0.97	0.86	1.12	0.95	1.05
Fixed 8	1.44	1.07	0.96	0.86	1.33	0.95	1.03
Automatic	1.13	1.33	0.97	0.86	1.08	1.04	1.18
Manual	1.20	1.12	0.96	0.86	1.12	0.97	1.07

Table 1 shows the RMSEP (root mean squared error of prediction) for the seven prediction methods when applied to the training set and the validation sets, based on the same data sets used in the main text. The RMSEPs are given for response curves with varying degrees of freedom. The impact of the number of degrees of freedom is generally small, although splines with 4 degrees of freedom have a higher RMSEP for the ‘full’ methods, and splines with 2 degrees of freedom give poorer results for the other prediction methods. Note that the number of degrees of freedom does not affect the RMSEP values calculated for the ‘raw mean’ method. The ‘raw mean’ method results in the best prediction, the ‘mean spline’ method and the ‘present kernel’ methods sometimes come close to the ‘raw mean’ method. The ‘full’ method gives the highest RMSEPs and thus the worst predictions.

Appendix 3. Three extra methods of prediction of the pH

The three further prediction methods are as follows:

5. and 6. The ‘full kernel’ and ‘present kernel’ methods are variants of the ‘full’ and ‘present’ methods: a kernel density estimate of the pH in all relevés is added to the probability product. The kernel method (Silverman, 1986) constructs an estimate of the true density function by replacing each observed pH by a normal probability density function with a small variance. The variance was estimated by the method of Sheather & Jones (1991). In the hypothetical situation the ‘presentkernel’ method estimates the pH by maximising $p_A(\text{pH}) \times p_B(\text{pH}) \times \text{Kernel}(\text{pH})$. This additional factor will make a small difference when there are many species present. However for small numbers of species, and thus possibly unreliable predictions, this will push the maximum of the probability product towards the optimum of the kernel density.

7. The ‘maxspline’ method is similar in spirit to the ‘mean spline’ method. For every single species it first takes, as an indicator value, the pH value for which the spline response curve is maximal. That is the location of the optimum of the estimated curve of each species. The predicted pH for a new relevé is then the mean of the indicator values of the species present in that relevé. Note that the ‘max spline’ and ‘mean spline’ indicator values are identical for symmetric response curves.

Note that the ‘raw mean’ method is the only method that does not employ the spline response curve. The RMSEP for all prediction methods and validation data sets is given in Table 1

Table 1. Root mean squared error of prediction (RMSEP) for the training set and validation sets for all prediction methods of the pH. The degrees of freedom for the estimation of the species response is according the automatic method, except for the ‘raw mean’ method which does not employ spline curves. The best method per set is highlighted in grey (this table is an extension of Table 2 in the manuscript).

Set	Full	Present	Mean spline	Raw mean	Fullkernel	Presentkernel	Maxspline
Training set	1.13	1.33	0.97	0.86	1.08	1.04	1.18
Ameland	1.19	1.05	0.84	0.80	1.17	0.91	0.87
Dunes	1.29	1.16	0.56	0.65	1.29	1.14	0.68
Grassland	1.43	1.23	0.97	0.93	1.42	1.00	1.17
Forest NL	1.15	1.55	0.60	0.68	1.00	1.31	1.28
Forest EU	1.31	1.87	0.74	0.66	1.15	1.57	1.37
Grassland Poland	1.75	1.20	1.64	0.99	1.69	1.20	1.79
UK	1.72	2.03	1.00	0.95	1.60	1.78	1.60

Compared to the results presented in the main text (for Full, Present, Mean spline and Raw mean) the extra methods give slightly better results for Fullkernel and Presentkernel compared with respectively the Full method and the Present method. It

can be concluded that adding the kernel method improves the predictions, but on the other hand also complicates the method. Applying this method would only be recommendable if the predictions would be better than the best method, which is by far not the case. The Max spline method gives worse results than the Mean spline method. This could be expected since the prediction of the maximum for the max spline method comes with a larger uncertainty than the prediction of the mean for the Mean spline method. This implies that a significant part of the response curves are skewed. This seems particularly the case in the forest sets (the UK set also contains many forest data). This could indicate that species occurring in forest have a more skewed response.

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Appendix 4. Extra information on the width of the spline.

Table 1. *The number of species responses per standard deviation class (SD) of the response curve and per class of number of presences of the species in the training data set.*

SD/ present	<50	50-100	100-200	>200	Total
<0.5	18	3	1	0	22
0.5-1.0	47	50	30	31	158
1.0-1.5	54	59	32	51	196
1.5-2.0	24	35	24	42	125
>2.0	11	19	9	16	55
Total	154	166	96	140	556

Appendix 5. Calculation of the RMSEP for Ellenberg indicator value 'R'.

The RMSEP for The Ellenberg indicator value for acidity (R, Ellenberg et al., 1991) was calculated by taking the square root of the division of the sum of squares of the residual (Table 1, i.e. the sum of the sums of squares of model 2 and 3 and the residual sum of squares from Table 1 in Wamelink et al., 2002) by the number of degrees of freedom for the residual. It follows from the Table 1 that $RMSEP = (3817.2 / 3536)^{1/2} = 1.039$.

Table 1. Regression analyses of the mean Ellenberg indicator score for acidity (R) on soil pH. The accumulated analysis of variance is shown, with degrees of freedom (d.f.) and sum of squares (s.s.). The data are derived from Wamelink et al. (2002) Table 1.

no	Model	d.f.	s.s.
1	$y = \alpha + \beta x$	1	3043.8
	Residual	3536	3817.2

Literature

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Appendix 6. Mean pH response per plant species for the ‘raw mean’ method.

Scientific name	author	pH
<i>Acer campestre</i>	L.	6.1
<i>Acer pseudoplatanus</i>	L.	5.1
<i>Achillea millefolium</i>	L.	6.1
<i>Achillea ptarmica</i>	L.	5.7
<i>Adoxa moschatellina</i>	L.	5.0
<i>Aegopodium podagraria</i>	L.	5.2
<i>Agrimonia eupatoria</i>	L.	7.3
<i>Agrostis gigantea</i>	Roth	7.2
<i>Agrostis stolonifera</i>	L.	6.2
<i>Agrostis capillaris</i>	L.	5.9
<i>Aira caryophylla</i>	L.	5.7
<i>Aira praecox</i>	L.	5.8
<i>Ajuga reptans</i>	L.	5.8
<i>Alisma plantago-aquatica</i>	L.	7.2
<i>Alliaria petiolata</i>	(Bieb.) Cavara & Grande	5.3
<i>Allium vineale</i>	L.	6.2
<i>Alnus glutinosa</i>	(L.) Gaertner	4.9
<i>Alopecurus geniculatus</i>	L.	5.9
<i>Alopecurus pratensis</i>	L.	6.1
<i>Ammophila arenaria</i>	(L.) Link	6.3
<i>Anemone nemorosa</i>	L.	4.4
<i>Angelica sylvestris</i>	L.	5.4
<i>Anthoxanthum odoratum</i>	L.	5.7
<i>Anthriscus sylvestris</i>	(L.) Hoffmann	6.1
<i>Apera spica-venti</i>	(L.) Beauv.	7.4
<i>Aphanes inexpectata</i>	Lippert	7.4
<i>Apium inundatum</i>	(L.) Reichenbach fil.	6.8
<i>Arnica montana</i>	L.	4.6
<i>Arrhenatherum elatius</i>	(L.) J.& C.Presl	6.9
<i>Arum maculatum</i>	L.	5.3
<i>Aster tripolium</i>	L.	7.5
<i>Athyrium filix-femina</i>	(L.) Roth	4.8
<i>Atriplex prostrata</i>	DC.	6.9
<i>Azolla filiculoides</i>	Lamk.	7.3
<i>Bellis perennis</i>	L.	6.0
<i>Betula pubescens</i>	Ehrhart	4.7
<i>Betula pendula</i>	Roth	4.3
<i>Brachypodium pinnatum</i>	(L.) Beauv.	7.2
<i>Brachypodium sylvaticum</i>	(Hudson) Beauv.	5.6
<i>Briqua media</i>	L.	6.7

Scientific name	author	pH
<i>Bromus hordeaceus</i> subsp. <i>hordeaceus</i>		6.1
<i>Butomus umbellatus</i>	L.	7.7
<i>Calamagrostis canescens</i>	(Weber) Roth	5.1
<i>Calamagrostis epigejos</i>	(L.) Roth	6.4
<i>Callitriche hamulata</i>	Koch	6.6
<i>Callitriche obtusangula</i>	Le Gall	7.7
<i>Callitriche platycarpa</i>	Kuetzing	7.0
<i>Calluna vulgaris</i>	(L.) Hull	4.5
<i>Calystegia sepium</i>	(L.) R.Br.	6.0
<i>Campanula rotundifolia</i>	L.	6.4
<i>Capsella bursa-pastoris</i>	(L.) Medicus	7.1
<i>Cardamine amara</i>	L.	6.0
<i>Cardamine hirsuta</i>	L.	6.9
<i>Cardamine pratensis</i>	L.	5.8
<i>Carex acuta</i>	L.	6.1
<i>Carex acutiformis</i>	Ehrhart	5.9
<i>Carex arenaria</i>	L.	5.8
<i>Carex caryophyllea</i>	Latourr.	6.6
<i>Carex curta</i>	Goodenough	4.9
<i>Carex disticha</i>	Hudson	5.8
<i>Carex elongata</i>	L.	4.8
<i>Carex flacca</i>	Schreber	7.0
<i>Carex hirta</i>	L.	6.0
<i>Carex hostiana</i>	DC.	5.4
<i>Carex lasiocarpa</i>	Ehrhart	5.1
<i>Carex nigra</i>	(L.) Reichard	5.5
<i>Carex ovalis</i>	Goodenough	5.8
<i>Carex panicea</i>	L.	5.5
<i>Carex pilulifera</i>	L.	4.4
<i>Carex pseudocyperus</i>	L.	6.1
<i>Carex remota</i>	L.	4.7
<i>Carex riparia</i>	Curtis	5.9
<i>Carex rostrata</i>	Stokes	5.5
<i>Carex spicata</i>	Hudson	6.2
<i>Carex sylvatica</i>	Hudson	5.7
<i>Carex trinervis</i>	Degland	5.5
<i>Carpinus betulus</i>	L.	4.9
<i>Carum carvi</i>	L.	6.4
<i>Centaurea cyanus</i>	L.	7.2
<i>Centaurea scabiosa</i>	L.	7.2
<i>Cerastium arvense</i>	L.	6.4
<i>Cerastium glomeratum</i>	Thuillier	5.9
<i>Cerastium fontanum</i> subsp. <i>vulgare</i>	(Hartman) Greuter & Burdet	6.2
<i>Cerastium semidecandrum</i>	L.	6.9

Scientific name	author	pH
<i>Ceratophyllum demersum</i>	L.	7.7
<i>Chaerophyllum temulum</i>	L.	5.0
<i>Chenopodium album</i>	L.	7.3
<i>Leucanthemum vulgare</i>	Lamk.	6.3
<i>Cicuta virosa</i>	L.	7.3
<i>Circaea lutetiana</i>	L.	5.7
<i>Cirsium acaule</i>	Scopoli	7.1
<i>Cirsium arvense</i>	(L.) Scopoli	6.4
<i>Cirsium dissectum</i>	(L.) Hill	5.4
<i>Cirsium palustre</i>	(L.) Scopoli	5.5
<i>Cirsium vulgare</i>	(Savi) Tenore	7.0
<i>Clematis vitalba</i>	L.	7.1
<i>Potentilla palustris</i>	(L.) Scopoli	5.4
<i>Convallaria majalis</i>	L.	4.6
<i>Convolvulus arvensis</i>	L.	6.9
<i>Cornus sanguinea</i>	L.	6.8
<i>Ceratocarpus claviculata</i>	(L.) Liden	3.8
<i>Corylus avellana</i>	L.	5.3
<i>Corynephorus canescens</i>	(L.) Beauv.	6.3
<i>Crataegus monogyna</i>	Jacquin	5.9
<i>Crataegus laevigata</i>	(Poiret) DC.	4.3
<i>Crepis biennis</i>	L.	6.6
<i>Crepis capillaris</i>	(L.) Wallroth	6.9
<i>Cynoglossum officinale</i>	L.	7.2
<i>Cynosurus cristatus</i>	L.	6.0
<i>Dactylis glomerata</i>	L.	6.3
<i>Daucus carota</i>	L.	6.9
<i>Deschampsia cespitosa</i>	(L.) Beauv.	5.4
<i>Deschampsia flexuosa</i>	(L.) Trinius	4.6
<i>Drosera intermedia</i>	Hayne	4.9
<i>Drosera rotundifolia</i>	L.	4.8
<i>Dryopteris dilatata</i>	(Hoffmann) A.Gray	4.0
<i>Dryopteris cristata</i>	(L.) A.Gray	4.6
<i>Dryopteris filix-mas</i>	(L.) Schott	4.8
<i>Dryopteris carthusiana</i>	(Villars) H.P.Fuchs	4.3
<i>Eleocharis acicularis</i>	(L.) Roemer & Schultes	7.0
<i>Eleocharis multicaulis</i>	(J.E.Smith) J.E.Smith	4.9
<i>Eleocharis palustris</i> subsp. <i>palustris</i>		5.9
<i>Elodea canadensis</i>	Michaux	7.5
<i>Elodea nuttallii</i>	(Planchon) St.John	7.5
<i>Elymus athericus</i>	(Link) Kerguelen	7.5
<i>Elymus repens</i>	(L.) Gould	6.4
<i>Empetrum nigrum</i>	L.	5.0
<i>Chamerion angustifolium</i>	(L.) Holub	4.9

Scientific name	author	pH
<i>Epilobium hirsutum</i>	L.	6.3
<i>Epilobium parviflorum</i>	Schreber	6.7
<i>Epipactis belleborine</i>	(L.) Crantz	5.9
<i>Equisetum arvense</i>	L.	6.1
<i>Equisetum fluviatile</i>	L.	6.2
<i>Equisetum palustre</i>	L.	6.2
<i>Erica tetralix</i>	L.	4.6
<i>Eriophorum angustifolium</i>	Honckeny	4.9
<i>Erodium cicutarium</i> subsp. <i>cutitarium</i>		7.4
<i>Erophila verna</i>	(L.) Chevallier	6.6
<i>Eryngium campestre</i>	L.	6.7
<i>Eryonymus europaeus</i>	L.	5.5
<i>Eupatorium cannabinum</i>	L.	5.6
<i>Fagus sylvatica</i>	L.	4.3
<i>Festuca arundinacea</i>	Schreber	6.5
<i>Festuca gigantea</i>	(L.) Villars	5.0
<i>Festuca ovina</i>	L.	5.8
<i>Festuca pratensis</i>	Hudson	6.0
<i>Festuca rubra</i> subsp. <i>commutata</i>	Gaudin	5.9
<i>Filipendula ulmaria</i>	(L.) Maximowicz	5.5
<i>Fragaria vesca</i>	L.	6.7
<i>Rhamnus frangula</i>	L.	4.5
<i>Fraxinus excelsior</i>	L.	5.4
<i>Galeopsis tetrahit</i>	L.	4.7
<i>Galium aparine</i>	L.	5.7
<i>Galium saxatile</i>	L.	4.5
<i>Galium mollugo</i>	L.	6.8
<i>Galium uliginosum</i>	L.	5.8
<i>Galium verum</i>	L.	5.9
<i>Genista anglica</i>	L.	5.1
<i>Gentianella germanica</i>	(Willdenow) Boerner	7.2
<i>Gentiana pneumonanthe</i>	L.	4.8
<i>Geranium molle</i>	L.	6.9
<i>Geranium pusillum</i>	L.	7.3
<i>Geranium robertianum</i>	L.	5.4
<i>Geum urbanum</i>	L.	5.4
<i>Glaux maritima</i>	L.	6.9
<i>Glechoma hederacea</i>	L.	6.0
<i>Glyceria fluitans</i>	(L.) R.Br.	6.2
<i>Glyceria maxima</i>	(Hartman) Holmberg	6.6
<i>Gymnadenia conopsea</i>	(L.) R.Br.	7.1
<i>Hedera helix</i>	L.	4.7
<i>Arenula pubescens</i>	(Hudson) Dumortier	7.0
<i>Heracleum sphondylium</i>	L.	6.5

Scientific name	author	pH
<i>Hieracium laevigatum</i>	Willdenow	5.2
<i>Hieracium pilosella</i>	L.	5.7
<i>Hieracium umbellatum</i>	L.	5.8
<i>Hippophae rhamnoides</i>	L.	7.2
<i>Hippuris vulgaris</i>	L.	7.6
<i>Holcus lanatus</i>	L.	5.9
<i>Holcus mollis</i>	L.	5.6
<i>Hordeum secalinum</i>	Schreber	6.3
<i>Hottonia palustris</i>	L.	7.1
<i>Humulus lupulus</i>	L.	5.0
<i>Hydrocharis morsus-ranae</i>	L.	7.5
<i>Hydrocotyle vulgaris</i>	L.	5.6
<i>Hypericum elodes</i>	L.	5.5
<i>Hypericum perforatum</i>	L.	6.5
<i>Hypochaeris radicata</i>	L.	5.7
<i>Ilex aquifolium</i>	L.	4.0
<i>Impatiens parviflora</i>	DC.	4.4
<i>Iris pseudacorus</i>	L.	5.6
<i>Jasione montana</i>	L.	5.3
<i>Juncus acutiflorus</i>	Hoffmann	5.5
<i>Juncus articulatus</i>	L.	6.0
<i>Juncus bufonius</i>	L.	7.0
<i>Juncus conglomeratus</i>	L.	5.3
<i>Juncus effusus</i>	L.	5.6
<i>Juncus alpinoarticulatus subsp. alpinoarticulatus</i>		5.4
<i>Juncus gerardi</i>	Loisel.	6.5
<i>Juncus squarrosus</i>	L.	4.5
<i>Knautia arvensis</i>	(L.) Coulter	7.1
<i>Koeleria macrantha</i>	(Ledeb.) Schultes	6.6
<i>Lamium album</i>	L.	5.0
<i>Galeobdolon luteum</i>	Hudson	4.9
<i>Lathyrus palustris</i>	L.	5.7
<i>Lathyrus pratensis</i>	L.	6.3
<i>Lemna gibba</i>	L.	7.5
<i>Lemna minor</i>	L.	7.3
<i>Lemna trisulca</i>	L.	7.6
<i>Leontodon autumnalis</i>	L.	5.9
<i>Leontodon hispidus</i>	L.	7.1
<i>Leontodon saxatilis</i>	Lamk.	6.0
<i>Ligustrum vulgare</i>	L.	7.0
<i>Linaria vulgaris</i>	Miller	6.7
<i>Linum catharticum</i>	L.	6.9
<i>Listera ovata</i>	(L.) R.Br.	6.2
<i>Littorella uniflora</i>	(L.) Ascherson	6.2

Scientific name	author	pH
<i>Lolium perenne</i>	L.	6.1
<i>Lonicera periclymenum</i>	L.	4.3
<i>Lotus corniculatus</i> subsp. <i>corniculatus</i>		6.2
<i>Lotus uliginosus</i>	Schkuhr	5.8
<i>Luronium natans</i>	(L.) Rafin.	6.1
<i>Luzula campestris</i>	(L.) DC.	5.8
<i>Luzula pilosa</i>	(L.) Willdenow	4.4
<i>Lycchnis flos-cuculi</i>	L.	5.7
<i>Anchusa arvensis</i>	(L.) Bieb.	7.5
<i>Lycopus europaeus</i>	L.	5.7
<i>Lysimachia nummularia</i>	L.	6.2
<i>Lysimachia thyrsoiflora</i>	L.	4.9
<i>Lysimachia vulgaris</i>	L.	5.4
<i>Lythrum salicaria</i>	L.	5.6
<i>Maianthemum bifolium</i>	(L.) F.W.Schmidt	4.1
<i>Matricaria maritima</i>	L.	7.1
<i>Medicago falcata</i>	L.	6.8
<i>Medicago lupulina</i>	L.	7.1
<i>Silene latifolia</i> (subsp. <i>alba</i>)	(Miller) Greuter & Burdet	7.3
<i>Silene dioica</i>	(L.) Clairville	4.7
<i>Mentha aquatica</i>	L.	6.2
<i>Mentha arvensis</i>	L.	6.2
<i>Menyanthes trifoliata</i>	L.	5.8
<i>Milium effusum</i>	L.	4.4
<i>Moehringia trinervia</i>	(L.) Clairville	4.9
<i>Molinia caerulea</i>	(L.) Moench	4.5
<i>Myosotis arvensis</i>	(L.) Hill	7.4
<i>Myosotis laxa</i> (subsp. <i>caespitosa</i>)	(Schultz) Nordh.	5.9
<i>Myosotis discolor</i>	Persoon	5.8
<i>Myosotis ramosissima</i>	Schultes	7.3
<i>Myosotis palustris</i>	(L.) L.	6.8
<i>Myrica gale</i>	L.	4.6
<i>Myriophyllum alterniflorum</i>	DC.	6.9
<i>Myriophyllum spicatum</i>	L.	8.1
<i>Myriophyllum verticillatum</i>	L.	7.5
<i>Nardus stricta</i>	L.	5.0
<i>Rorippa microphylla</i>	(Boenninghausen) Hyl.	7.6
<i>Nuphar lutea</i>	(L.) J.E.Smith	7.2
<i>Nymphaea alba</i>	L.	6.4
<i>Nymphoides peltata</i>	(S.G.Gmelin) O.Kuntze	7.8
<i>Oenanthe aquatica</i>	(L.) Poiret	6.9
<i>Oenanthe fistulosa</i>	L.	7.7
<i>Ononis repens</i> subsp. <i>spinosa</i>	Greuter	6.7
<i>Origanum vulgare</i>	L.	7.4

Scientific name	author	pH
<i>Ornithogalum umbellatum</i>	L.	5.5
<i>Ornithopus perpusillus</i>	L.	6.2
<i>Oxalis acetosella</i>	L.	4.3
<i>Oxyccus macrocarpos</i>	(Aiton) Pursh	5.6
<i>Papaver dubium</i>	L.	7.5
<i>Paris quadrifolia</i>	L.	5.3
<i>Parnassia palustris</i>	L.	5.8
<i>Pedicularis sylvatica</i>	L.	5.2
<i>Lythrum portula</i>	(L.) D.A.Webb	6.5
<i>Peucedanum palustre</i>	(L.) Moench	4.8
<i>Phalaris arundinacea</i>	L.	5.9
<i>Phleum pratense subsp. pratense</i>		6.0
<i>Phragmites australis</i>	(Cavanilles) Steudel	5.9
<i>Picris hieracioides</i>	L.	7.2
<i>Pilularia globulifera</i>	L.	6.2
<i>Pimpinella major</i>	(L.) Hartman	7.0
<i>Pimpinella saxifraga</i>	L.	6.9
<i>Pinus sylvestris</i>	L.	4.4
<i>Plantago coronopus</i>	L.	7.2
<i>Plantago lanceolata</i>	L.	6.0
<i>Plantago media</i>	L.	7.1
<i>Poa annua</i>	L.	6.2
<i>Poa nemoralis</i>	L.	4.6
<i>Poa palustris</i>	L.	5.9
<i>Poa pratensis</i>	L.	6.2
<i>Poa trivialis</i>	L.	6.0
<i>Polygala comosa</i>	Schkuhr	7.1
<i>Polygala serpyllifolia</i>	Hose	4.9
<i>Polygala vulgaris</i>	L.	6.7
<i>Polygonatum multiflorum</i>	(L.) Allioni	4.5
<i>Polygonatum odoratum</i>	(Miller) Druce	7.2
<i>Polygonum amphibium</i>	L.	6.5
<i>Polygonum aviculare</i>	L.	6.3
<i>Polygonum convolvulus</i>	L.	6.9
<i>Polygonum hydropiper</i>	L.	6.3
<i>Polygonum persicaria</i>	L.	6.3
<i>Polypodium vulgare</i>	L.	4.9
<i>Potamogeton acutifolius</i>	Link	7.6
<i>Potamogeton compressus</i>	L.	7.4
<i>Potamogeton crispus</i>	L.	7.6
<i>Groenlandia densa</i>	(L.) Fourreau	7.6
<i>Potamogeton mucronatus</i>	Sonder	7.8
<i>Potamogeton gramineus</i>	L.	7.4
<i>Potamogeton lucens</i>	L.	7.6

Scientific name	author	pH
<i>Potamogeton natans</i>	L.	6.9
<i>Potamogeton obtusifolius</i>	Mertens & Koch	7.3
<i>Potamogeton pectinatus</i>	L.	8.0
<i>Potamogeton perfoliatus</i>	L.	7.8
<i>Potamogeton polygonifolius</i>	Pourret	6.0
<i>Potamogeton pusillus</i>	L.	7.9
<i>Potamogeton trichoides</i>	Chamisso & Schlechtendal	7.7
<i>Potentilla anserina</i>	L.	6.0
<i>Potentilla erecta</i>	(L.) Rauschel	5.1
<i>Potentilla reptans</i>	L.	6.8
<i>Primula elatior</i>	(L.) Hill	5.0
<i>Prunella vulgaris</i>	L.	6.1
<i>Prunus avium</i>	(L.) L.	5.3
<i>Prunus padus</i>	L.	4.6
<i>Prunus serotina</i>	Ehrhart	4.4
<i>Prunus spinosa</i>	L.	6.2
<i>Pteridium aquilinum</i>	(L.) Kuhn	3.8
<i>Puccinellia maritima</i>	(Hudson) Parlato	7.4
<i>Quercus robur</i>	L.	4.6
<i>Ranunculus acris</i>	L.	6.0
<i>Ranunculus aquatilis</i>	L.	7.8
<i>Ranunculus baudotii</i>	Godron	8.1
<i>Ranunculus bulbosus</i>	L.	6.4
<i>Ranunculus circinatus</i>	Sibthorp	7.9
<i>Ranunculus ficaria</i> subsp. <i>bulbilifer</i>	(L.) Lambinon	6.3
<i>Ranunculus flammula</i>	L.	5.8
<i>Ranunculus peltatus</i>	Schrank	7.0
<i>Ranunculus repens</i>	L.	6.0
<i>Ranunculus sceleratus</i>	L.	7.6
<i>Raphanus raphanistrum</i>	L.	7.4
<i>Rhamnus catharticus</i>	L.	6.9
<i>Rhinanthus angustifolius</i>	C.C.Gmelin	5.5
<i>Rhinanthus minor</i>	L.	7.1
<i>Ribes nigrum</i>	L.	4.9
<i>Ribes rubrum</i>	L.	4.8
<i>Ribes uva-crispa</i>	L.	5.7
<i>Rorippa amphibia</i>	(L.) Besser	7.2
<i>Rorippa palustris</i>	(L.) Besser	6.7
<i>Rubus caesius</i>	L.	6.6
<i>Rubus idaeus</i>	L.	4.5
<i>Rumex acetosa</i>	L.	5.8
<i>Rumex acetosella</i>	L.	5.9
<i>Rumex crispus</i>	L.	6.7
<i>Rumex hydrolapathum</i>	Hudson	7.2

Scientific name	author	pH
<i>Rumex obtusifolius</i>	L.	6.5
<i>Sagina procumbens</i>	L.	6.3
<i>Sagittaria sagittifolia</i>	L.	7.6
<i>Salix aurita</i>	L.	5.2
<i>Salix cinerea</i>	L.	4.9
<i>Salix repens</i>	L.	5.6
<i>Sambucus nigra</i>	L.	5.0
<i>Sanguisorba minor</i>	Scopoli	7.1
<i>Sanguisorba officinalis</i>	L.	5.7
<i>Satureja vulgaris</i>	(L.) Fritsch	7.4
<i>Scabiosa columbaria</i>	L.	7.2
<i>Scirpus fluitans</i>	L.	5.9
<i>Scirpus maritimus</i>	L.	7.6
<i>Scleranthus annuus</i>	L.	7.3
<i>Scrophularia nodosa</i>	L.	4.9
<i>Scutellaria galericulata</i>	L.	5.3
<i>Sedum acre</i>	L.	7.0
<i>Senecio aquaticus</i>	Hill	5.8
<i>Senecio erucifolius</i>	L.	7.3
<i>Senecio jacobaea subsp. jacobaea</i>		7.3
<i>Senecio sylvaticus</i>	L.	5.8
<i>Danthonia decumbens</i>	(L.) DC.	5.3
<i>Bernia erecta</i>	(Hudson) Coville	7.4
<i>Solanum dulcamara</i>	L.	5.6
<i>Sonchus asper</i>	(L.) Hill	7.3
<i>Sorbus aucuparia</i>	L.	4.2
<i>Sparganium erectum</i>	L.	7.4
<i>Sparganium emersum</i>	Rehmann	7.1
<i>Spergula arvensis</i>	L.	6.5
<i>Spergula morisonii</i>	Boreau	4.5
<i>Spergularia maritima</i>	(Allioni) Chiovenda	7.4
<i>Spergularia rubra</i>	(L.) J.& C. Presl	7.1
<i>Spirodela polyrrhiza</i>	(L.) Schleiden	7.6
<i>Stachys sylvatica</i>	L.	5.1
<i>Stellaria uliginosa</i>	Murray	5.7
<i>Stellaria graminea</i>	L.	5.8
<i>Stellaria holostea</i>	L.	4.4
<i>Stellaria media</i>	L.	6.1
<i>Stellaria palustris</i>	Retzius	5.8
<i>Stratiotes aloides</i>	L.	7.5
<i>Suaeda maritima</i>	(L.) Dumortier	7.4
<i>Succisa pratensis</i>	Moench	5.5
<i>Symphytum officinale</i>	L.	6.1
<i>Taraxacum laevigatum</i>	(Willdenow) DC.	7.3

Scientific name	author	pH
<i>Teesdalia nudicaulis</i>	(L.) R.Br.	5.1
<i>Thalictrum flavum</i>	L.	5.7
<i>Thymus pulegioides</i>	L.	6.9
<i>Thymus serpyllum</i>	L.	5.9
<i>Trifolium dubium</i>	Sibthorp	6.1
<i>Trifolium fragiferum</i>	L.	6.8
<i>Trifolium pratense</i>	L.	6.1
<i>Trifolium repens</i>	L.	6.1
<i>Triglochin maritima</i>	L.	7.2
<i>Triglochin palustris</i>	L.	5.9
<i>Trisetum flavescens</i>	(L.) Beauv.	6.5
<i>Typha angustifolia</i>	L.	6.3
<i>Typha latifolia</i>	L.	6.9
<i>Ulmus minor</i>	Miller	5.5
<i>Urtica dioica</i>	L.	5.9
<i>Urtica urens</i>	L.	6.9
<i>Utricularia minor</i>	L.	4.9
<i>Utricularia vulgaris</i>	L.	7.4
<i>Vaccinium myrtillus</i>	L.	4.0
<i>Valeriana dioica</i>	L.	5.6
<i>Valeriana officinalis</i>	L.	5.7
<i>Veronica arvensis</i>	L.	7.0
<i>Veronica catenata</i>	Pennell	7.6
<i>Veronica chamaedrys</i>	L.	6.1
<i>Veronicahederifolia</i>	L.	5.1
<i>Veronica officinalis</i>	L.	6.2
<i>Veronica scutellata</i>	L.	5.7
<i>Veronica serpyllifolia</i>	L.	6.1
<i>Viburnum opulus</i>	L.	5.1
<i>Vicia sativa subsp. nigra</i>	(L.) Ehrhart	7.2
<i>Vicia cracca</i>	L.	6.4
<i>Vicia hirsuta</i>	(L.) S.F.Gray	6.9
<i>Vicia lathyroides</i>	L.	7.0
<i>Viola arvensis</i>	Murray	7.3
<i>Viola canina</i>	L.	5.6
<i>Viola hirta</i>	L.	7.3
<i>Viola palustris</i>	L.	5.4
<i>Viola riviniana</i>	Reichenbach	5.3
<i>Zannichellia palustris subsp. pedicellata</i>	(Wahlenberg & Rosen) Arcangeli	8.7
<i>Juncus canadensis</i>	Laharpe	4.2
<i>Festuca ovina subsp. cinerea</i>	(Villars) Duyfjes	4.7
<i>Festuca ovina subsp. tenuifolia</i>	(Sibthorp) Celakovsky	5.7
<i>Galium verum subsp. maritimum</i>	(DC.) Adema	7.0
<i>Agrostis canina</i>	L.	5.5

Scientific name	author	pH
<i>Agrostis vinealis</i>	Schreber	5.0
<i>Bromus racemosus</i>	L.	6.0
<i>Dactylorhiza maculata</i>	(L.) Soo	6.0
<i>Rubus fruticosus</i>	L.	4.5
<i>Salicornia europaea</i>	L.	7.2
<i>Epilobium tetragonum</i>	L.	5.8
<i>Rosa canina</i>	L.	6.3
<i>Centaurea jacea</i>	L.	6.3
<i>Acer platanoides</i>	L.	4.6
<i>Amelanchier lamarckii</i>	F.G.Schroeder	4.1
<i>Quercus rubra</i>	L.	3.9
<i>Asparagus officinalis</i>	L.	7.7
<i>Eleocharis palustris</i>	(L.) Roemer & Schultes	6.8
<i>Erodium cicutarium</i>	(L.) l'Herit	7.0
<i>Festuca rubra</i>	L.	6.1
<i>Lotus corniculatus</i>	L.	6.8
<i>Luzula multiflora</i>	(Retzius) Lejeune	5.6
<i>Scirpus lacustris</i>	L.	6.4
<i>Tragopogon pratensis</i>	L.	6.9
<i>Zannichellia palustris</i>	L.	8.1
<i>Chara aculeolata</i>	Kützing	8.0
<i>Chara globularis</i>	Thuillier	7.4
<i>Chara vulgaris</i>	L.	8.0
<i>Carex oederi</i>	Retzius	5.5
<i>Larix kaempferi</i>	(Lambert) Carriere	4.0
<i>Picea abies</i>	(L.) Karsten	4.1
<i>Pinus nigra</i>	Arnold	4.5
<i>Populus × canadensis</i>	Moench	5.2
<i>Pseudotsuga menziesii</i>	(Mirbel) Franco	3.7
<i>Senecio jacobaea</i>	L.	6.2
<i>Cerastium fontanum</i>	Baumgarten	5.9
<i>Euphrasia stricta</i>	J.F.Lehmann	6.8
<i>Plantago major</i>	L.	6.3
<i>Solanum nigrum</i>	L.	6.3
<i>Arenaria serpyllifolia</i>	L.	7.1
<i>Bromus hordeaceus</i>	L.	6.2
<i>Caltha palustris</i>	L.	5.8
<i>Juncus bulbosus</i>	L.	5.1
<i>Scirpus cespitosus</i>	L.	4.4
<i>Galium palustre</i>	L.	5.8
<i>Phleum pratense</i>	L.	6.6
<i>Arrhenatherum elatius</i> subsp. <i>elatius</i>		7.1
<i>Ranunculus ficaria</i>	L.	4.9
<i>Taraxacum officinale</i> s.s.	Wiggers	5.9

Scientific name	author	pH
<i>Ononis repens</i>	L.	7.0
<i>Atrichum undulatum</i>	(Hedw.) P. Beauv.	5.0
<i>Aulacomnium androgynum</i>	(Hedw.) Schwagr.	4.1
<i>Aulacomnium palustre</i>	(Hedw.) Schwagr.	4.0
<i>Brachythecium albicans</i>	(Hedw.) Schimp.	5.8
<i>Brachythecium rutabulum</i>	(Hedw.) Schimp.	5.2
<i>Bryum argenteum</i>	Hedw.	7.3
<i>Bryum capillare</i>	Hedw.	6.9
<i>Calliergonella cuspidata</i>	(Hedw.) Loeske	6.8
<i>Campylopus flexuosus</i>	(Hedw.) Brid.	4.1
<i>Campylopus introflexus</i>	(Hedw.) Brid.	4.3
<i>Campylopus pyriformis</i>	(K.F. Schultz) Brid.	4.0
<i>Ceratodon purpureus</i>	(Hedw.) Brid.	6.7
<i>Ctenidium molluscum</i>	(Hedw.) Mitt.	7.1
<i>Dicranella heteromalla</i>	(Hedw.) Schimp.	4.0
<i>Dicranoweisia cirrata</i>	(Hedw.) Lindb. ex Milde	3.9
<i>Dicranum montanum</i>	Hedw.	3.8
<i>Dicranum scoparium</i>	Hedw.	4.5
<i>Eurhynchium bians</i>	(Hedw.) Lac.	5.8
<i>Eurhynchium praelongum</i>	(Hedw.) Schimp.	5.0
<i>Eurhynchium striatum</i>	(Hedw.) Schimp.	5.1
<i>Fissidens bryoides</i>	Hedw.	5.7
<i>Fissidens taxifolius</i>	Hedw.	6.4
<i>Hypnum cupressiforme</i>	Hedw.	5.4
<i>Hypnum jutlandicum</i>	Holmen et Warncke	4.1
<i>Isopterygium elegans</i>	(Brid.) Lindb.	3.9
<i>Leucobryum glaucum</i>	(Hedw.) Aongstr.	3.8
<i>Mnium hornum</i>	Hedw.	4.3
<i>Orthodontium lineare</i>	Schwagr.	3.9
<i>Plagiomnium undulatum</i>	(Hedw.) T. Kop.	6.0
<i>Plagiothecium denticulatum</i>	(Hedw.) Schimp.	4.4
<i>Plagiothecium laetum</i>	Schimp.	3.8
<i>Plagiothecium nemorale</i>	(Mitt.) Jaeg.	4.4
<i>Plagiothecium undulatum</i>	(Hedw.) Schimp.	4.0
<i>Pleurozium schreberi</i>	(Brid.) Mitt.	3.9
<i>Pohlia nutans</i>	(Hedw.) Lindb.	4.5
<i>Polytrichum commune</i>	Hedw.	5.0
<i>Polytrichum formosum</i>	Hedw.	3.9
<i>Polytrichum piliferum</i>	Hedw.	5.7
<i>Pseudoscleropodium purum</i>	(Hedw.) Fleisch. ex Broth.	5.6
<i>Rhytidiadelphus squarrosus</i>	(Hedw.) Warnst.	5.6
<i>Tetraphis pellucida</i>	Hedw.	3.8
<i>Tortula ruralis</i>	(Hedw.) Gaertn., Meyer et Scherb.	7.4
<i>Plagiomnium affine</i>	(Bland.) T. Kop.	6.6

Scientific name	author	pH
<i>Polytrichum juniperinum</i>	Hedw.	5.7
<i>Lophocolea bidentata</i>	(L.) Dum.	5.6
<i>Lophocolea heterophylla</i>	(Schrader.) Dum.	4.2
<i>Riccia fluitans</i>	L.	6.9
<i>Agrostis</i>	L.	5.9
<i>Arctium</i>	L.	7.4
<i>Betula</i>	L.	4.8
<i>Callitriche</i>	L.	6.7
<i>Epilobium</i>	L.	6.7
<i>Fumaria</i>	L.	7.4
<i>Rhinanthus</i>	L.	5.8
<i>Rubus</i>	L.	4.2
<i>Salix</i>	L.	5.2
<i>Taraxacum species</i>	Weber	6.1
<i>Sphagnum species</i>		4.5
<i>Cephalozia species</i>		4.7
<i>Cladonia species</i>	Hill ex P. Browne	6.0
<i>Cladonia pyxidata</i> var. <i>chlorophaea</i>		4.7
<i>Cladonia pleurota</i>		4.6
<i>Cladonia floerkeana</i>	(Fr.) Flörke	4.6
<i>Cladonia furcata</i> ssp. <i>furcata</i>		6.4
<i>Cladonia glauca</i>	Flörke	4.6
<i>Cladonia gracilis</i>	(L.) Willd.	4.8
<i>Cladonia macilenta</i>	Hoffm.	4.5
<i>Cladonia portentosa</i>		4.7
<i>Cladonia rangiformis</i>	Hoffm.	7.1
<i>Cladonia subulata</i>	(L.) Weber ex F.H. Wigg.	4.6
<i>Cornicularia aculeata</i> var. <i>aculeata</i>		6.0
<i>Parmelia physoides</i>		4.7
<i>Trapeliopsis granulosa</i>	(Hoffm.) Lumbsch	4.5
<i>Placynthiella uliginosa</i>	(Schrader) Coppins & P. James	4.6
<i>Salix repens</i> var. <i>argentea</i>	Sm.	4.9

**Vegetation succession as affected by decreasing
nitrogen deposition, soil characteristics and site
management: a modelling approach**



4 Vegetation succession as affected by decreasing nitrogen deposition, soil characteristics and site management: a modelling approach

G.W.W. Wamelink, H.F. van Dobben & F. Berendse

Abstract

After many years of increasing nitrogen deposition, the deposition rates are now decreasing. A major question is if this will result in the expected positive effects on plant species diversity. Long-term experiments that investigate the effects of decreasing deposition are not available. Model simulations may yield insight in the possible effects of decreasing nitrogen deposition on the vegetation. Therefore, we developed the vegetation succession model SUMO which is closely linked to the soil model SMART2. In SUMO the biomass development of five functional plant types is simulated as a function of nitrogen availability, light interception and management. The model simulates the change in biomass distribution over functional types during the succession from almost bare soil via grassland or heathland to various forest types. The model was validated on three sites in the Netherlands and one site in the UK. The aboveground biomass of two grassland vegetation types was simulated properly, as well as the above ground biomass of heathlands during succession of sod removal. Some of the stages of forest succession were simulated less well, but the calculated biomass in the older stages agreed with the measured values.

To explore the long-term effect of a decrease in nitrogen deposition we applied the model to a heathland and a pine stand. In the heathland a major change was predicted as a result of decreasing nitrogen deposition in combination with turf stripping. The dominance of grasses changed into a dominance of dwarf shrubs, whereas at continuing high levels of nitrogen deposition grasses remained dominant. In contrast, the simulations indicated only very small effects of a decreasing N deposition in pine forests. This difference is due to the removal of excess nitrogen by management (turf stripping) in the heathland, whereas the more extensive management in the forest hardly removes any nitrogen from the system. The main conclusion from these examples is that a decrease of nitrogen deposition may retard succession, and consequently increase biodiversity in heathland but probably not in forest. The effects of declining N deposition depend on the amount of N that is removed from the system as a consequence of the various management regimes.

Introduction

High atmospheric deposition of sulphur and nitrogen has had an immense impact on vegetation composition and succession in the last century (Hogg et al., 1995; Lameire et al., 2000). Well-known examples are the succession of north-west European heathland dominated by *Erica tetralix* or *Calluna vulgaris* to monospecific stands of the grass *Molinia caerulea* (Berendse and Aerts, 1984; Aerts et al., 1990) and the change in species composition of the understory of forests (Van Dobben et al., 1999; Lameire et al., 2000). Simulation of the nutrient cycle and the competition between plant species can help to understand the processes behind these changes, and can also provide insight into the most effective strategy to reduce human impact. An important driver for vegetation succession is the accumulation of organic matter (Van Andel et al., 1993; Olff et al., 1997; Van der Putten et al., 2000; Prach et al., 2001), which has a large impact on the soil and the plant community (Berendse et al., 1987; Knops et al., 2002), and even on the abundance of animal species (Olff et al., 1997; Van der Wal et al., 2000).

In Western Europe vegetation succession in ‘natural’ areas is strongly affected by management (Bakker, 1989; Uutera et al., 1996; Van Diggelen et al., 1996; Buckley et al., 1997). Management intensity ranges from extensive, e.g. the regulation of grazers in forests by hunting, to intensive, e.g. the mowing of hay meadows several times a year. In areas with high levels of nitrogen deposition, vegetation management is often used to remove nitrogen from the system, and thus to counteract the negative effects of nitrogen deposition. This may be accomplished by e.g. turf stripping or grazing in heathland (Bokdam, 2001).

After decades of increasing nitrogen deposition ((Burns, 2003; Fenn et al., 2003), deposition rates are now slightly decreasing at least in parts of North America and Western Europe (Wright et al., 2001; Kelly et al., 2002). The effects of decreasing nitrogen deposition, after years of high deposition are still unknown. Questions to be answered are: Will reduced nitrogen deposition change the rate of vegetation succession, and how do different management schemes interfere with the effect of the decreasing nitrogen input? Will reduced nitrogen input decrease the large nitrogen pool present in the vegetation and soil and prevent further leaching of nitrogen to the groundwater? Experiments that investigate the effect of decreasing deposition after years of excessive deposition are scarce and the long-term effects are still unknown.

Model simulation may be used in order to answer the questions addressed. Then models to be used should be able to simulate ecosystem development under unprecedented conditions. For this purpose a process model is most appropriate, while statistical or expert models are less suited since they are solely based on historical relationships (Verboom and Wamelink, 1999). As anthropogenic influence on the vegetation is not limited to a single vegetation type or an isolated area, the model should be able to simulate the influence of nitrogen deposition and

management on succession in widely different vegetation types on a regional scale for a majority of the vegetation types.

Apart from management (in the broadest sense, i.e. including grazing) soil processes are among the most important factors that determine vegetation succession (Berendse, 1990; Van Wijnen and Bakker, 1999; Nierop et al., 2001). Therefore, a vegetation succession model should include the simulation of soil processes, or be run in combination with a soil model. For the simulation of soil processes on a regional scale we used the model SMART2 (Kros et al., 1995; Kros, 2002). This model was built to simulate the effect of atmospheric deposition on soil processes, including soil N mineralization and soil acidity. It has for instance been used to calculate critical loads for nitrogen and acidity deposition on a national and European scale (De Vries et al., 1994; Van Dobben et al., 2006). However, in SMART2 the vegetation processes are mostly neglected. There is no interaction between soil and vegetation, and the vegetation development is simulated as either a steady state, or as a logistic growth curve. Only a very small number of vegetation types are distinguished, and vegetation succession is not simulated.

Over the years many vegetation models have been developed. Models like Century (Parton et al., 1987; Parton et al., 1993), NUCOM (Van Oene et al., 1999a), FORGRA, (Jorritsma et al., 1999), MASSIMO (Kaufmann, 2000; Schmid et al., 2006), FORSPACE (Kramer et al., 2003), NICHE (Koerselman et al., 1999) and ForSAFE (Wallman et al., 2005) only simulate a single site or region, and only for one vegetation type (i.e. grassland, heathland, forest or dunes). The Century model was recently modified to be able to simulate forest as well (Kirschbaum and Paul, 2002) but only soil variables were validated. Although the Century model now is equipped for modelling grassland as well as forest, it is still unable to simulate the succession from grassland to forest. Changes in heathland can be simulated with the 'UK heathland' model (Terry et al., 2004). However, this model only simulates a few species and neglects natural succession towards forests. A variety of forest models exists with widely different aims, but these models do not simulate the development from or towards other vegetation types and mostly neglect the effects of the understory on the tree development (e.g. Bugmann et al., 1996; Jorritsma et al., 1999; Kaufmann, 2000; Smith et al., 2001; Porté and Bartelink, 2002; Kramer et al., 2003; Wallman et al., 2005). A model that is valid for all major vegetation types is required for the evaluation of the effects on biodiversity of nation-wide pollution abatement strategies. Although a number of GIS-based models exist that connect vegetation types to abiotic conditions (e.g. Runhaar et al., 1999; Münier et al., 2001; Nabuurs and Schelhaas, 2003), such models are either based on statistical relationships or on expert knowledge whereas dynamic processes are neglected. In such models new environmental conditions cannot be realistically dealt with. For the answering of the questions addressed in this paper a process model that is able to simulate vegetation responses in a changing environment is necessary. The JPL model (Sitch et al., 2003),

also follows the modelling set up chosen here; it includes many vegetation types and functional types. JPL is a carbon driven model and does not include dynamic effects of nitrogen (limitation) on the growth. The combination of the GUESS-LPJ model (Hickler et al., 2003) uses a similar approach, but also here the effect of nitrogen on the growth is neglected.

For this purpose we developed the model SUMO (which is short for SUccession MOdel). In combination with SMART2 this model should be able to evaluate the effects of management and nitrogen deposition on plant competition and on the interaction between soil and vegetation. We used SUMO in combination with SMART2 to explore the effects of a decreasing nitrogen deposition on the vegetation to address the above mentioned questions.

SUMO was built as an extension to the already existing model SMART2 (Kros, 2002). SUMO is based on the same principles as the much more elaborate and plant species specific model NUCOM (Berendse, 1994a, 1994b; Van Oene et al., 1999a; 1999b). Where NUCOM was built and tested for a specific area (the Veluwe in The Netherlands) to simulate the succession from bare soil to oak forest, SUMO is a more general model covering natural areas all over The Netherlands, where in principal many succession schemes are possible. Where NUCOM is a site specific model needing many input data, SUMO is a more general model applicable in many situations. SUMO needs only a limited number of site specific data. Although SUMO operates on the same principles as NUCOM it was totally rebuilt.

First we will give a short general description of SUMO and SMART2, and then we will describe each process in detail, including its parameterisation and validation.

Model description

SUMO is written in the computer language FORTRAN (Compaq Computer Corporation, 1999). It simulates the biomass and nitrogen dynamics in five functional plant types: herbs and grasses, dwarf shrubs, shrubs, pioneer trees, and climax trees. Each functional type is assumed to consist of three organs: root, stem, and leaf. The time step of the model is one year. In each time step the biomass of the five functional types is computed, based on the biomass in the previous time step, biomass growth and death in the present time step, and removal of biomass by management (Equation 1). The growth is in turn calculated on the basis of an assumed maximum growth, which is reduced by nitrogen availability (provided by SMART2) and light interception (Equation 2). The dead biomass (litter with nitrogen content) is returned to the relevant pools in SMART2.

SUMO distinguishes six vegetation types (grassland, heathland, reedland, shrub vegetation, salt marsh and forest). The model equations are parameterised for each combination of functional plant type and vegetation type. Much attention is given to the simulation of competition between the functional types. The competition for

nitrogen and light is assumed to be the driving force for succession. The initial vegetation type is given as input to the model. Apart from biomass growth, SUMO also simulates height growth.

For the functional types herbs/grasses, dwarf shrubs, and shrubs, SUMO simulates the total biomass of all species. For the functional types pioneer tree and climax tree the biomass of a specific tree species is simulated. Each species is given its own set of parameters. The pool of tree species consists of Scots pine (*Pinus sylvestris*), larch (*Larix decidua*), Douglas fir (*Pseudotsuga menziesii*), Norway spruce (*Picea abies*), birch (*Betula pendula* and *Betula pubescens*), ash (*Fraxinus excelsior*), alder (*Alnus glutinosa*), willow (*Salix alba* and *Salix cinerea*), poplar (*Populus spec.*), oak (*Quercus robur* and *Quercus petraea*), northern red oak (*Quercus rubra*) and beech (*Fagus sylvatica*). The dominant tree species included in the model are selected on the basis of soil characteristics.

SUMO simulates the C and N fluxes. The nitrogen that becomes available through mineralization (simulated by SMART2) and atmospheric deposition is partitioned over the functional types and within each functional type over its organs, using fixed percentage distributions per functional type/vegetation type combination. Nitrogen reallocation before litterfall is also simulated.

The vegetation type may change during a model run. When the management (mowing) of grassland is stopped, succession to heathland or forest may occur. The vegetation type is determined on the basis of the biomass present in the five functional types. In grassland, the vegetation type changes into forest if the stem biomass of the functional types shrubs, pioneer trees or climax trees exceeds a threshold value (Table 1). The pioneer tree, the climax tree and the forest type are selected on the basis of the soil type and the groundwater level present at the specific grid (Table 1). Table 1 gives a scheme of all possible succession pathways and the conditions for succession.

The processes modelled in SUMO are based on the descriptions made by Berendse (1994a; 1994b), and are extensively described in Appendix 1.

Table 1. Succession scheme for vegetation types with conditions under which succession takes place (MSL = mean spring groundwater level in m below surface, SP = sand poor, SR = sand rich, SC = sand calcareous, CN = clay non-calcareous, CC = clay calcareous, PN = peat non calcareous and LN = loess non-calcareous), and tree species in the new vegetation. Succession will take place when the total stem biomass of the shrubs and trees is above $0.15 \text{ ton} \cdot \text{ha}^{-1}$.

original type	new type	soil type	MSL in -m	pioneer tree	climax tree
grassland	heathland				
grassland	natural forest	SP, SR, CN, CC, LN	< 0.3	alder	Ash
	pine forest	SP	≥ 0.3	birch	Pine
	natural forest	SR, LN	≥ 0.3	oak	Beech
	natural forest	SC		oak	Beech
	natural forest	CN, CC	≥ 0.3	alder	Poplar
	natural forest	PN	< 0.3	alder	Birch
	natural forest	PN	≥ 0.3	alder	Ash
heathland	natural forest	SP, CN, CC, LN	< 0.3	alder	Ash
	pine forest	SP, SR	≥ 0.3	birch	Pine
	natural forest	SR	< 0.3	birch	Oak
	natural forest	SC		oak	Beech
	natural forest	PN	< 0.3	alder	Birch
	natural forest	PN	≥ 0.3	alder	Ash
	natural forest	LN	≥ 0.3	oak	Beech
reedland	natural forest			alder	Ash
shrubland	natural forest			birch	Oak

Parameterisation

SUMO uses over 1000 different parameters (including the different parameters per organ for five functional types and for ten vegetation types). Almost all parameters are based on extensive literature research (references can be found in Wamelink et al., 2000b; Wamelink et al., 2000a and Appendix 1). The data from literature were stored in a database. The parameters were estimated from the database and used for test runs of SUMO using a test-set of vegetation types. Fine-tuning of the parameters took place until the model produced an acceptable outcome. Fine-tuning was always done within the range of the data found in literature (which was quite wide in some cases), but most of the parameters were left unchanged. Parameters that are fine-tuned are the maximum growth rate (A_{\max} in Equation 2), light interception coefficient (k in Equation 3), minimum (N_{\min} in Equation 6) and maximum nitrogen content (N_{\max}). Maximum growth rate and light interception had to be fine-tuned because for these parameters data are scarce or absent. Parameters involved in the height of the functional type, the influence of moisture on the growth and management were never fine-tuned. The model does not need to be parameterized for different sites.

Validation

The simulation of biomass increment was validated using data collected at two grassland sites, a heathland site and a forest site. The nitrogen content of the leaves was validated on a set of forest stands.

The first grassland site is situated near Wageningen (51°58' N, 5°39' E) and is part of a long-term field experiment started in 1958 on former agricultural land (Elberse et al., 1983). The soil type is clay with a regulated groundwater table suitable for agricultural use. The site is mown once a year and not fertilised. Every year the mown biomass was dried and weighed. The changes in aboveground biomass were simulated using site specific historical deposition data. Due to yearly differences in i.e. rainfall and temperature the measured biomass varies greatly between years, while the simulated biomass does not vary much among the years (Fig. 1). But the slight decline in the simulated biomass is in agreement with the trend of the measured biomasses. The large difference for the first year is probably caused by the former agricultural use of the land, which has led to a relatively high measured biomass. The effects of former agricultural use of grassland or vegetation in general cannot be simulated by SUMO. The decline in the measured and the simulated biomass is caused by the yearly removal of aboveground biomass, while fertilisation has stopped.

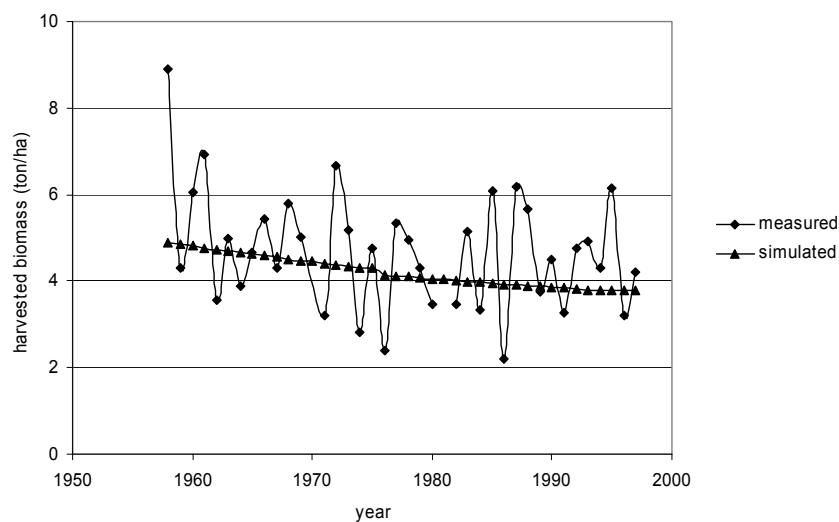


Figure 1. Measured and simulated aboveground biomass for a mown grassland site near Wageningen.

The second grassland site is the Parkgrass experimental site at Rothamsted in the UK. The site was mown twice a year and the harvested biomass was weighed and averaged over ten year periods. The experiment started around 1850 and continues until today. The site is extensively described by i.e. Lawes and Gilbert (1880), Cashen (1947), Thurston et al. (1976), Jenkinson et al. (1994). The site was probably extensively manured just after the start of the experiment, but this treatment stopped after a few years (Jenkinson et al., 1994). The model was initialised with an estimated amount of biomass (Appendix 2). The grassland was assumed to be mown once a year and grazed with a density of 2 sheep per hectare from 1850 until 1852, then mown twice a

year till 1863 and manured with $25 \text{ kg ha}^{-1} \text{ N}$ from 1856 until 1863, and then mown once a year up to present. We used site specific data for sulphur and nitrogen deposition. Both S- and N-deposition increased steadily from the start of the experiment, but decreased in recent years, after c. 1980 and c. 1990, respectively (Appendix 2). The nitrogen deposition was more or less stable between 1900 and 1940, which is accounted for in the model run. The field data were retrieved from Dodd et al. (1994). The results show that the harvested biomass is fairly well simulated by SUMO (Fig. 2). Only the effect of the nitrogen deposition since approximately 1960 is slightly underestimated. But the reduction in biomass harvest in the early years due to exhaustion of the soil, the stabilisation of the harvest when the effect of N deposition compensates for the exhaustion, and the increase of the harvest later on due to the further raise of the deposition is simulated quite well. A part of the discrepancy between modelled and measured biomass may be caused by the changes in plant species composition under contemporary N inputs.

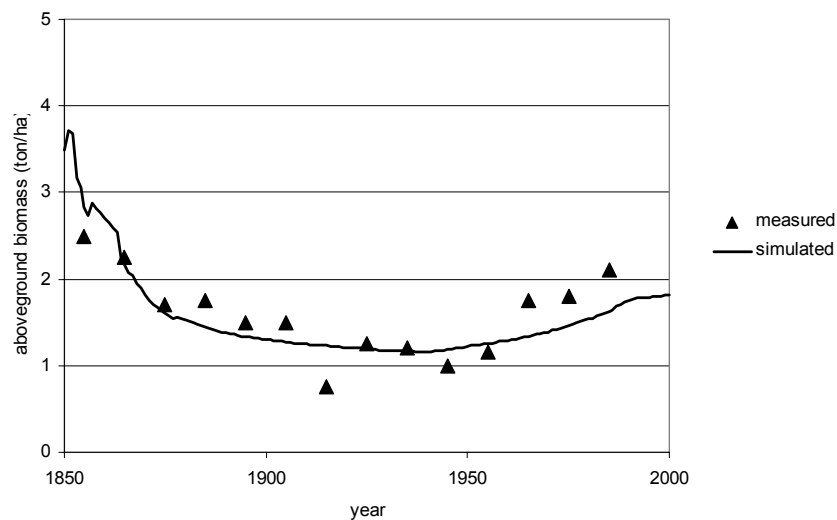


Figure 2. Measured and simulated biomass harvest for the Rothamsted experimental grassland site in the UK.

SUMO was validated for heathland on a site in the south of The Netherlands near Strabrecht ($51^{\circ}23' \text{ N}$, $5^{\circ}37' \text{ E}$, appendix 2), which was studied by Berendse (1990). We compared the biomass in eight plots where turf stripping had taken place in different years. Turf stripping includes the removal of all biomass and the litter and humus layer down to the mineral soil layer after which succession starts on a bare substrate. Above and belowground biomass was harvested in 1984. SUMO was run for each site separately. The runs were started in the year of turf stripping, which differs for each site, and continued up to 1984 when the biomass was measured, using site specific

information on soil type, deposition etc. Aboveground biomass simulated by SUMO was compared with the measured aboveground biomass. In general the aboveground biomass is simulated well, although it is overestimated for the plots where the turf was stripped 16 and 18 years before the field data collection (Fig. 3). For the oldest plot the majority of the simulated biomass is present in grasses. In the field dwarf shrubs are only present as dead biomass in the litter layer in this plot. In all other plots almost all measured and simulated biomass is present in the functional type dwarf shrubs. The results are comparable to those found by Terry et al., (2004) for simulations of heathland development in the UK. They found that above $30 \text{ kg ha}^{-1} \text{ y}^{-1}$ nitrogen deposition the biomass of heath was replaced by biomass of grasses in the long term.

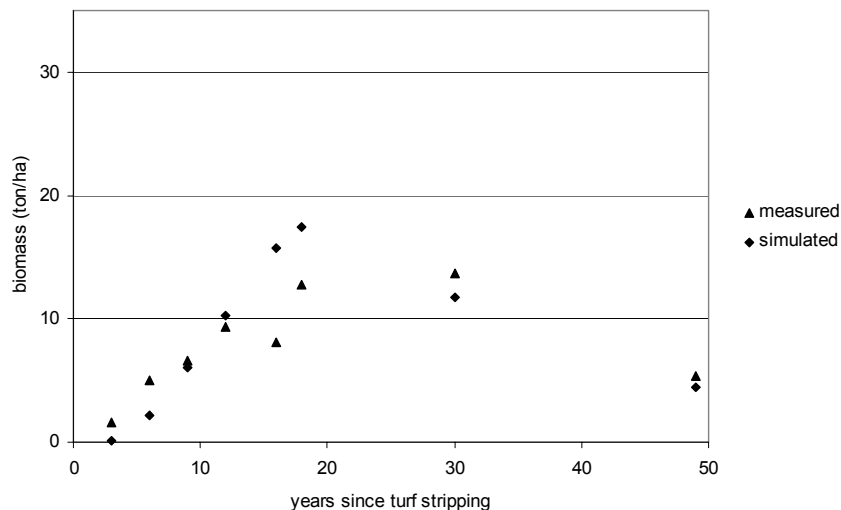


Figure 3. Simulated and measured aboveground biomass for a heathland near Strabrecht in The Netherlands. The simulated biomass is the result of separate independent simulations, starting at the moment of turf stripping, and continuing until the field survey.

The forest site that we used for validation is located in the north of The Netherlands near Sellinger (52°57' N, 7°03' E, appendix 2). Here small forest plots are situated on former agricultural land. This chronosequence consists of ten plots of 0, 14, 25, 32 and 89 years old in 1999 with two independent plots per successional age. At the beginning of each stage trees were planted. One of the 89-years old plots was cut before 1999 and therefore omitted. The remaining stages all have oak (*Quercus robur*) as the dominant tree species. The undergrowth is almost absent in some stages, while in other stages the understory is dominated by grasses. The 0-year stage that is still in agricultural use was used to initialise the simulation. The actual biomass of the trees was estimated on the basis of the diameter at breast height and the height. The above ground biomass of the herbs was harvested and weighed (Van Oene et al., 1999b;

Wamelink et al., 2001). Historic deposition data were used for the simulation. The simulated values were compared with the measured biomass of the sites (Table 2 and Fig. 4). Some of the successional stages are quite well simulated by SUMO; other successional stages are less well simulated. The simulated tree biomass in older forest is too low, but the biomass of other functional types is simulated quite well. An exception is the biomass of the pioneer trees in the 89 year old stage and the biomass of the climax trees in the 25 and 32 year old stage. This difference is probably caused by the thinning regime in the past. Site specific data of the thinning regime are not available.

Table 2. Validation results for the chronosequence Sellinger. Figures are biomass in $\text{ton}\cdot\text{ha}^{-1}$ dry matter per functional type, measured in the field with (standard error) and simulated by SUMO.

age		herbs (s.e.)	dwarf shrubs (s.e.)	Shrubs (s.e.)	pioneer tree (s.e.)	climax tree (s.e.)
14	measured	0.81 (0.11)	0	0	0.02 (0.03)	28.13 (2.35)
	SUMO	0.79	0.11	0.64	0.64	26.50
25	measured	0.37 (0.16)	0	0	0.09 (0.09)	39.03 (0.72)
	SUMO	0.01	0.04	0.59	0.70	47.23
32	measured	0.14 (0.08)	0	0	0	66.96 (0.61)
	SUMO	0.01	0.02	0.58	0.73	48.95
89	measured	0.77	0	0	4.69	111.36
	SUMO	0.01	0.01	0.44	0.29	98.33

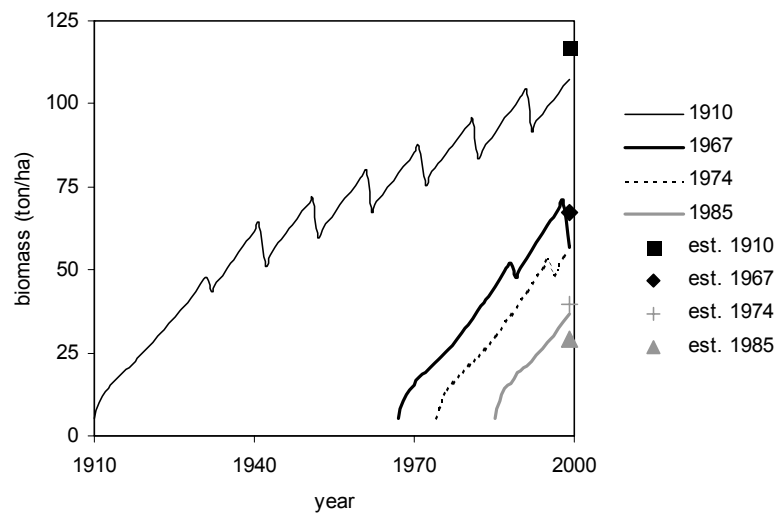


Figure 4. Simulated total biomass increment for four different successional stages at the Sellinger site. The forests were planted in 1910, 1967, 1974 and 1985 on former agricultural land. The biomass of the sites was estimated in 1999 (est. 1910, est. 1967, est. 1974 and est. 1985 giving the estimations for the respective plant years).

SUMO was also validated for the nitrogen concentration in the leaves of planted trees on 169 forest sites on all major soil types situated all over The Netherlands. The simulated N concentrations were regressed on the measured N contents ($R^2 = 39\%$, intercept = 2.1 ± 1.9 ($p = 0.27$), regression coefficient = 0.92 ± 0.09 ($p < 0.001$). When there is no difference between simulated and measured N content one would expect a regression coefficient of 1.0 and an intercept of 0.0. For both the values do not differ significantly ($p = 0.27$ for the intercept and $p = 0.34$ for the regression coefficient). The percentage explained variance indicates that the N contents of the leaves are simulated fairly well.

Analysis of the effect of decreasing nitrogen deposition

Using SMART2-SUMO we explored the effect of decreasing nitrogen deposition on the vegetation for three sites, a planted pine forest ('Zeesserveld', $52^{\circ}03'$ N, $6^{\circ}27'$ E, appendix 3), a heathland ('Edesche heide', $52^{\circ}03'$ N, $5^{\circ}43'$ E, appendix 3) and a grassland (near Renkum, $51^{\circ}58'$ N, $5^{\circ}43'$ E, appendix 3). The three sites are nature reserves where the goal is to enhance or at least preserve biodiversity (Koop and Clerkx, 1995; Van Dobben et al., 2002). In the forest the managers attempt to achieve this objective by cutting 10% of the pine biomass each 10 years, thereby promoting the development of oak and enhancing structural diversity. We initialised the simulation with measured tree biomass values, while the initial biomass of the other functional types was estimated from vegetation relevés. We simulated vegetation development for ten plots. Every 10 years 10% of the dominant trees were cut and the biomass removed. The presented results are the mean of the ten plots. In the heathland it is attempted to preserve biodiversity by turf stripping each 30 years in order to prevent the dominance of grasses over heather. Here we also simulate vegetation development if only shrubs and trees would be removed from the heathland (to prevent succession). The initial biomass per functional type is the measured biomass in a heathland dominated by *Calluna vulgaris* (30 years old) or dominated by grasses (for the degraded stage of heathland, 50 years old). In the grassland the goal is to increase biodiversity by mowing once a year and removing the mown biomass. The initial biomass is the measured biomass of a grassland site situated at the border of a brook valley and a forest on poor sandy dry soil. The grassland was till recently in agricultural use.

To be able to evaluate the effect of management combined with nitrogen deposition decrease we ran two deposition scenarios. The first scenario (1) combines the above-described management with a constant nitrogen deposition rate of $45 \text{ kg ha}^{-1} \text{ y}^{-1}$. The second scenario (2) has a linearly decreasing deposition rate, from $45 \text{ kg ha}^{-1} \text{ y}^{-1}$ in 2000 to $10 \text{ kg ha}^{-1} \text{ y}^{-1}$ in 2090. The models are initialised in the first ten years of the run (1990 - 2000) at a constant deposition of $45 \text{ kg ha}^{-1} \text{ y}^{-1}$.

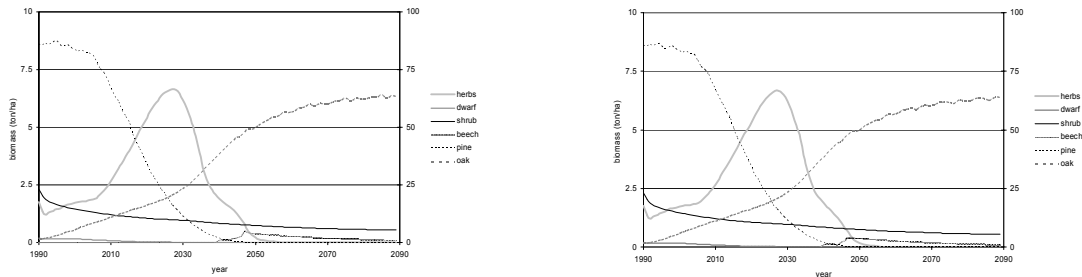


Figure 5. Simulated development of biomass per functional type in the 'Zeesserveld' pine forest under scenario 1 (a, constant deposition of $45 \text{ kg ha}^{-1} \text{ y}^{-1}$) and scenario 2 (b, decreasing deposition from $45 \text{ kg ha}^{-1} \text{ y}^{-1}$ in 2000 to $10 \text{ kg ha}^{-1} \text{ y}^{-1}$ in 2090). The right axis gives the biomass for pine and oak, the left axis for all other functional types.

In the simulation of the development of the forest site we observed a transition from pine to oak. At the end of the simulation period the vertical diversity is still low (Figs 5a and 5b for scenario 1 and 2, respectively). During the transition phase from pine to oak the grasses/herbs become dominant. The shrubs steadily decrease and the dwarf shrubs almost vanish from the site. Around 2040 beech starts to appear, but this species becomes suppressed by oak. In the field beech is often observed to be able to grow under an almost closed oak canopy, which is not taken into account by the model. For this reason the biomass of beech is most likely underestimated. The end of the simulation period shows a dark forest with a strong dominance of oak and little undergrowth. Interestingly, a decreasing deposition has hardly any effect on these processes. This is caused by the relatively high soil N mineralization, despite the decreasing deposition. In the years that deposition rates were high, a large pool of nitrogen was built up in the forest, and this pool is depleted only very slowly, because harvesting of stem wood removes only little nitrogen from the system. The removal of biomass by cutting causes open spots where new tree species such as beech may get an opportunity to grow. In SUMO the biomass is just subtracted from the total biomass and no open spots will be present. This may partly explain why beech is suppressed by oak. This problem may be solved by modelling smaller grid cells, where thinning is achieved by removing all of the trees from some of the cells.

The results for the heathland are totally different from those for the forest (Figs 6a and 6b). At a constant deposition of $45 \text{ kg ha}^{-1} \text{ y}^{-1}$, the grasses/herbs become dominant and the dwarf shrubs start to disappear at the end of the 30 year cutting cycle, and trees (birch and pine) are also becoming more dominant. However, when the deposition decreases the dwarf shrubs are more competitive and become the dominant functional type throughout the cutting cycle. Since with the turf stripping a lot of nitrogen is removed, the availability of nitrogen decreases and a different vegetation type evolves. The last cycle (Fig. 6b) already indicates that when a 30 year

cycle is maintained at low deposition, heather biomass will decrease and an open vegetation type may develop, that in term could even turn into blown sand. This is what actually has happened in historic times when heathland was over-exploited at low deposition rates (Gimingham, 1972). So if the objective is to maintain heathland, the management cycle has to be intensified. Figs 6c and 6d illustrate what would happen when only shrubs and trees are removed. With a constant deposition of $45 \text{ kg ha}^{-1} \text{ y}^{-1}$ the heathland turns into a grassland and will remain so (Fig. 6c), and with a decreasing deposition the vegetation turns into grassland, though with less biomass compared to the situation with high deposition (Fig. 6d). The nitrogen pool in the vegetation and soil remains constant for a very long period. It is clear that if the excess nitrogen is not actively removed a return to a heathland is not likely to occur even when deposition drops.

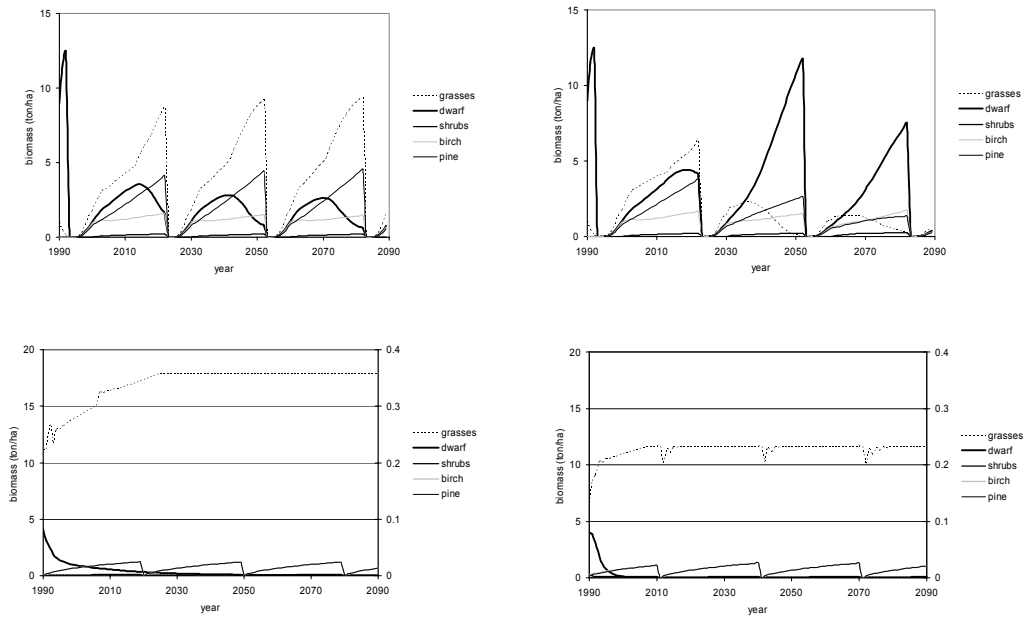


Figure 6. Simulated development of biomass per functional type in the 'Edesche Heide' heathland under scenario 1 (fig. a, constant deposition of $45 \text{ kg ha}^{-1} \text{ y}^{-1}$) and scenario 2 (fig. b, decreasing deposition from $45 \text{ kg ha}^{-1} \text{ y}^{-1}$ in 2000 to $10 \text{ kg ha}^{-1} \text{ y}^{-1}$ in 2090). Fig. c gives the simulation for scenario 1 of a degraded heathland, where only shrubs and trees are removed from the vegetation. Fig. d gives the simulation for scenario 2 combined with shrub and tree removal.

A large difference between the two deposition scenarios is also simulated for the grassland (Fig. 7). At a constant and high deposition the total biomass of the functional type grasses and herbs remains stable during the whole simulated period

(Fig. 7a), although quite a large amount of biomass and thus nitrogen is taken out of the system yearly. Only when the deposition decreases (Fig. 7b) the total biomass decreases as well; almost all standing biomass is halved. The biomass of the other functional types than herbs and grasses is negligible.

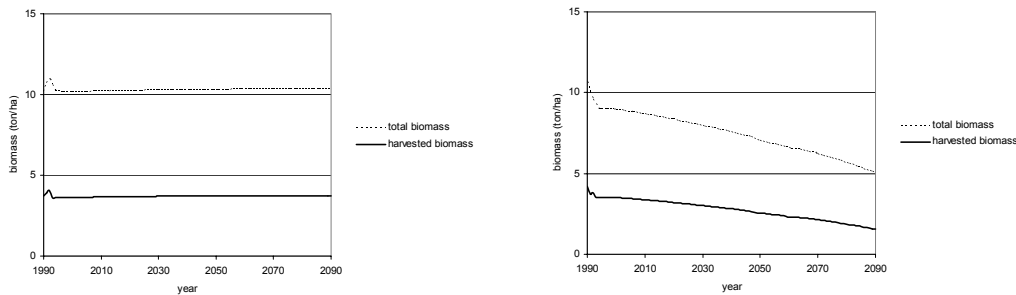


Figure 7. Simulated development of the total biomass and harvested biomass in a grassland near Renkum under scenario 1 (fig. a, constant deposition of $45 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{y}^{-1}$) and scenario 2 (fig. b, decreasing deposition from $45 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{y}^{-1}$ in 2000 to $10 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{y}^{-1}$ in 2090). The grassland is mown once a year, the biomass for the other functional types than grasses and herbs is negligible.

Discussion

We simulated the long-term effect of a decrease in nitrogen deposition under the assumption that the model not only performs well under constant or increasing, but also under decreasing nitrogen deposition. The results for Rothamsted show that at least in grassland (in the earlier years of the experiment, see Figure 2) the effect of a decrease in nitrogen availability is simulated well, and that in grassland that is mown yearly a drop in deposition rate will reduce the total biomass (Fig. 7b). Mowing once a year alone is not sufficient to counteract the effect of deposition. Deposition must apparently decrease to reach a lower total biomass. These results do not agree with measurements in the field during the first years in other grassland sites, where the biomass dropped in the first years after fertilisation stopped (Berendse et al., 1992). Lower biomass production in former agricultural grassland is desirable because it is one of the requirements for the restoration of plant species diversity in grasslands (Al-Mufti et al., 1977; Grime, 1979; Schaffers, 2002; Marriott et al., 2004). At the simulated site the total biomass decreased from approximately 10 to 5 $\text{ton} \cdot \text{ha}^{-1}$, which may lead to an increase in number of species from 25 to 35 (c.f. Schaffers, 2002), if other requirements are fulfilled, including sufficient seed dispersal.

For heathland the biomass distribution over the five functional types changes when nitrogen deposition decreases. Management is an important factor in heathland (Fig. 6). It removes the excess nitrogen that has built up during the years of high nitrogen deposition. Turf stripping in combination with a drop in nitrogen deposition

changes the dominance of the herbs and grasses into a dominance of dwarf shrubs. In natural heathland dominance of dwarf shrubs is strongly correlated with the occurrence of threatened plant species (Gimingham, 1972). If management would only aim at stopping succession by removing shrubs and trees, the soil nitrogen pool would increase even further (see Figure 6d). By removing nitrogen from the system, management not only reduces the total biomass production but also changes the vegetation from dominated by herbs/grasses (e.g. *Molinia caerulea*) to dwarf shrubs (e.g. *Calluna vulgaris* or *Erica tetralix*). It is also clear from the scenario analyses that no increase in biodiversity can be expected if deposition rates do not change; in that case it will even be very difficult to maintain biodiversity at the present level. Moreover Figure 6c shows that when the deposition remains high and only shrubs and trees are removed, the biomass of herbs and grasses is not influenced by the removal of nitrogen from the system.

The effect of declining N deposition in forest is in strong contrast with the effect on heathland and grassland. In forest the differences between the two scenarios are negligible, and with 10% thinning every ten years no real increase in biodiversity can be expected even if deposition drops. Apparently the removal of nitrogen by thinning is too small to remove the excess nitrogen from atmospheric deposition.

Many processes are neglected in SUMO, but at least three of them were considered important enough to be incorporated in the model at a later stage. The first is the effect of moisture availability. The simulated sites are assumed not to be limited by water availability. However, especially in the light of the expected climate change and the associated changes in precipitation, the effect of water availability is important and will be incorporated in an updated SUMO version. Also missing in this first version of SUMO are the effects of phosphorus and base cations on the growth. Under natural circumstances, nitrogen availability is often limiting plant growth, which justifies the choice of basing the biomass growth on the nitrogen availability. However other elements like phosphorus, potassium, calcium and magnesium may also limit growth (Kooijman and Besse, 2002; Wassen et al., 2005). Therefore, the model cannot simulate situations where phosphorus or base cations are solely limiting the growth. The third is the production and decay of dead wood. Although the nitrogen content of dead wood is low, the total amount can be significant. Also, dead wood is considered an important prerequisite for biodiversity in forest (Ohlson et al., 1997; Nilsson et al., 2001). However, the present version of SUMO was tested on sites where dead wood does not play a significant role.

SUMO does not simulate the effects of dispersion of seeds. It is assumed that each vegetation type will occur in any site with suitable abiotic conditions. When single species are important (here only the trees) this is an important limitation of the model. For the other functional types this is less serious since they consist of groups of many species.

The generally poor results of the simulations of the development of forest ecosystems may be due to the lack of sufficient data on the management of the validation sites. A more fundamental problem is that the shorter functional types (grasses and herbs and dwarfshrubs) are underestimated by SUMO during some of the successional stages. The same problem was also encountered by Smith et al., (2001) when testing the GUESS-LPJ models. Here it also appeared to be difficult to simulate the biomass of grass when trees become the dominant functional types. This may be due to a too low simulated availability of light below the tree canopy. A shortcoming of both models is that the functional types compete for nitrogen in one homogeneous soil layer, while in reality the vertical distribution of the roots may differ among the various functional types so that they only partly compete for nitrogen. This problem may be solved by modelling the competition for nitrogen in different soil layers (cf. Berendse, 1979).

We conclude that SUMO can be used to evaluate scenarios of nitrogen deposition reduction after many years of high deposition with or without additional vegetation management. The model shows us that increased nitrogen input in the vegetation will lead to an accelerated increase of the amount of nitrogen in the ecosystem. When the input stops, the nitrogen will remain in the vegetation and litter layer for a long period. We predict that even after the nitrogen input from deposition has been reduced the vegetation will suffer long afterward, especially in forest ecosystems. Restoration of biodiversity is only possible by removing biomass or the soil top layer and thus nitrogen from the system. Vegetation management plays a crucial role in the restoration of vegetation after nitrogen deposition; it removes the excess nitrogen from the system. However, the high management intensity required to compensate for these high levels of N deposition can be costly (Wamelink et al., 2005).

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Appendix 1

The model SMART2 considers linked biotic and abiotic processes in the soil solution as well as in the solid phase. It includes the inorganic soil and two organic soil compartments and simulates the full soil nitrogen cycle. The model consists of a set of mass balance equations, describing the soil input-output relationships and rate-limited and equilibrium soil processes. The soil solution chemistry depends on the net element input from the atmosphere and groundwater, canopy interactions, geochemical interactions in the soil (CO_2 equilibria, weathering of carbonates, silicates and/or Al hydroxides, SO_4 sorption and cation exchange), and nutrient cycling (litterfall, mineralisation, root uptake, nitrification and denitrification). Nutrient uptake by the vegetation and litterfall (including the amount of dead roots and dead wood) are provided by SUMO2. SMART2 delivers the nitrogen availability to SUMO2 as the sum of external N input and mineralisation. Solute transport is described by assuming complete mixing of the element input within one homogeneous soil compartment with a constant density and fixed depth. The time step of the model is one year.

Competition for light

The interception of light is simulated by assuming an exponential decrease of light intensity with decreasing height within the canopy, using the Lambert-Beer equation (Equation 3, cf. Huisman and Weissing, 1994). The light interception per functional type is based on the biomass and position of the leaves. For each functional type the leaves are considered to be equally distributed over the height of the functional type, except for trees higher than 7m, where the canopy does not start at the ground level but at a height of 1.5m. In total five canopy layers are distinguished in which at least one and at most five functional types are present. The highest layer starts at the top of the highest functional type and ends at the height of the second highest functional type. It contains a fraction of the leaf biomass of the highest functional type equal to the thickness of the layer relative to the height of the functional type. The light that is not intercepted passes to the next layer. The second layer consists of two functional types, the highest and the second highest, and this layer ends at the height of the third highest functional type. The leaf biomass of the two functional types in this layer is again computed, and added to give the total leaf biomass for the layer. The light interception computed on the basis of this total biomass is subsequently divided over the two functional types according to their proportion in the total leaf biomass in that layer (Equation 3). The light interception of the functional types in the other three layers is calculated in a similar way. Per functional type the interception of the layers is summed to give the total light interception. The maximum growth of the functional type is reduced by light interception according to Equation 2.

Competition for nitrogen

In SUMO, nitrogen comes from three sources: (1) uptake from the soil, (2) foliar uptake of atmospheric deposition, and (3) internal reallocation from one organ to another.

- (1) The nitrogen release from the soil and litter is simulated by SMART2. The fraction of soil nitrogen absorbed by each functional type is assumed to be equal to the proportion of its root biomass in the total root biomass.
- (2) Atmospheric nitrogen is assumed to be taken up by the canopy, with a rate that declines exponentially with height. For the sake of simplicity the deposition is distributed over the functional types proportional to their light interception and thus dependent on their fraction of total leaf biomass (Equation 4). Data on atmospheric deposition comes from external sources (i.e. deposition models or maps). The actual available atmospheric nitrogen for the vegetation is calculated by SMART2 and depends on the structure of the vegetation (forests catch more deposition than grasslands).
- (3) Before litterfall part of the nitrogen in the litter is reallocated, stored and used for growth in the next year (see below). This reallocated nitrogen remains within the plant and is therefore not available to the other functional types.

The total nitrogen availability for each functional type is calculated by summing (1), (2) and (3) (Equation 5).

The influence of the nitrogen availability on the growth of each functional type is described by a saturation equation based on potential growth, total nitrogen availability, and the minimum nitrogen content per functional type (Equation 6).

In principle, all available nitrogen is taken up, but the nitrogen uptake of each functional type is limited by its maximum growth and maximum nitrogen content. The nitrogen that is not taken up by the roots remains in the soil.

The newly taken up nitrogen is divided over the organs (Equation 7). The nitrogen content in the organs is calculated after adding the new biomass and new nitrogen, and subtracting litterfall and the nitrogen left in it (Equation 8 and 9). The amount of reallocated nitrogen depends on the organ and the nitrogen content of the organ. When the nitrogen content is lower than a threshold value no nitrogen is reallocated (Equation 10).

In the present version of SUMO the effect of moisture availability on the vegetation is neglected. It is assumed that no water shortage occurs that limits the growth and that the growth is not reduced due to high groundwater levels.

Biomass

The biomass of each functional type is computed as the result of the biomass in the previous year, the newly formed biomass, the production of dead biomass and the

amount of biomass removed by management (Equation 1). The newly formed biomass is the result of the reduction of the maximum growth of each functional type by the reduction factors for light interception (Equation 3) and nitrogen availability (Equation 6). Each year, a small amount of biomass is added to each organ of each functional type to simulate seed input ($0.0001 \text{ ton ha}^{-1} \text{ y}^{-1}$). For several processes in SUMO the amount of biomass per organ is required. To this end the newly formed biomass is divided over the organs according Equation 11, where the division over the three organs differs per functional type. The total biomass the biomass per organ is corrected for death and biomass removal, like the total biomass.

Litter

Each year part of the biomass dies. The fraction that dies depends on the organ and the functional type, and varies from 1.0 y^{-1} for leaves of herbs, shrubs and deciduous trees to 0.01 y^{-1} for stems of climax trees (Equation 12). The nitrogen content of the dead organs is calculated by Equation 10. The nitrogen content in litter and dead wood is lower than in living material due to reallocation. However, when the nitrogen content drops below a given threshold value no reallocation takes place. The biomass of dead roots and leaves is transferred to the litter pool and nitrogen release from the dead plant parts is simulated by SMART2. SMART2 assumes that dead stems do not release nitrogen.

Height

The height of the five functional types is calculated yearly. As height growth is assumed to decline with age, SUMO also keeps track of the 'age' (i.e., the number of years since colonisation or plantation occurred) per functional type. For the functional types herbs/grasses and dwarf shrubs the height is based on the biomass present in the functional type (Equation 13).

The height of shrubs is calculated with Equation 14. It depends on the age of the stand. Over the years the height growth is decreasing until the maximum height has been reached.

The computation of the height of the trees is more complicated. It is based on the height in the previous year, the biomass growth in the current year, a minimum and maximum height growth, and the 'age' of the functional type (Equations 15 and 16). The maximum and minimum height growth of the trees is based on growth curves for the Netherlands on rich and poor soil, respectively (Jansen et al., 1996). The realised height growth per tree species per year lies between values determined by the growth curves at the tree's 'age' and the biomass increment in that year, according to Equation 17. The height growth of shrubs and trees is assumed to start at a given threshold biomass (0.15 ton ha^{-1} for the sum of stem biomass of shrubs and trees). These threshold values are equal to the threshold values for succession (Table 1). If

the biomass is below this threshold the height is set to the minimum height given above, and the 'age' is kept at 1 year. A maximum height is explicitly imposed only for dwarf shrubs (1 m). For shrubs and trees the maximum height is determined by parameters k_1 and k_4 in Equations 15 and 16.

Management

Management implies the removal of biomass and therefore nitrogen from the system. In some cases management also influences the height of the functional types. SUMO can simulate four types of management: mowing (grassland), turf stripping (heathland), cutting (forests) and grazing. Grazing may be combined with any other management form.

1. Mowing. In mown grassland the leaf biomass of the functional type grasses/herbs is reduced to 1 ton ha^{-1} . The aboveground biomass of the other functional types is reduced to 0.002 ton ha^{-1} . The biomass of the roots is not reduced. The height of all functional types except for herbs/grasses is reduced to the height of their seedlings. For herbs/grasses the height depends on the remaining biomass according to Equation 13. The age of the shrubs and trees is set back to 1 year.
2. Turf stripping. After turf stripping the total biomass of the functional types is minimised to 0.002 ton ha^{-1} for dwarf shrubs and to 0.0002 ton ha^{-1} for the other functional types. It is assumed that there remains more biomass, especially seeds, of dwarf shrubs in the soil than for the other functional types. Since after turf stripping the humus layer is also removed, SUMO signals SMART2 to remove the humus layer from the system.
3. Cutting. Cutting can influence all functional types. Three different types of forest management are modelled in SUMO. The first is extensive management. In this type of management, every 10 years 10% of the trees are harvested; this is implemented by reducing the biomass of all organs by 10%. The dead roots are transported to the dead roots-pool in SMART2. The rest of the cut biomass is removed from the system. The pool of reallocatable nitrogen is also reduced by 10%. The height of the trees is not influenced by cutting. The second management form is traditional (intensive) forest management with thinning every 5 years and clear-cutting at the end of the management cycle (Equation 18). The amount of thinning depends on the tree species and the age of the stand (after Jansen et al., 1996). The cut biomass and its nitrogen content are removed from the system. In the case of a clear-cut this is the total aboveground biomass and all nitrogen it contains. The biomass of the non-tree functional types is assumed to be destroyed for 90% due to the cutting activities, and added to the litter. The forest is replanted after clear-cutting. The height and age are set back to the height of planted young trees. The third management type is coppicing, which is simulated for a few tree species only: willow, ash, alder and oak. For willow, ash and alder the shoots are

harvested every seven years, for oak every 30 years. For all tree species 80% of the above ground biomass is harvested. A large part of the herbs and grasses is assumed to be destroyed (90%) and is added to the dead roots and litter pools, shrubs are assumed to be actively removed from the system. The height of the remaining stub after management is set to 0.3 m.

4. Grazing. Grazers are modelled as biomass removing objects, similar to the other forms of management. The model does not contain a population dynamic module for the grazers. In SUMO the effect of grazing can be simulated for 15 different grazers (young cattle, domestic cow, 'wild' cow, horse, pony, sheep, wild boar, roe deer, red deer, fallow deer, European bison, moose, moufflon, goose and rabbit). Their effect is that they eat from the three organs, of which a part is returned to the system as manure. The nitrogen in the manure is available for the vegetation in the next year and is handled by SMART2. The model was adjusted for this purpose. The amount of nitrogen in the manure is simply added to the available nitrogen pool which is returned to SUMO. It is assumed that all nitrogen is available in the next year. The grazers differ from each other in the amount of biomass they have to eat and the preference for different organs and functional types. For instance, only wild boar eats roots. The amount of grazers depends on the amount of food that is available. When there is a surplus of food then the amount of grazers will increase gradually, till a maximum of five times the original amount. When the amount of food is not sufficient the number of grazers is adjusted to the amount of available food where the maximum possible increase is halved to correct for generation time. For domesticated grazers it is also possible to fix the amount of grazers. Not all the in principle eatable biomass is available for the grazers. For all functional types there is an organ specific threshold value and of shrubs and trees higher than 1.5m only a limited part of the leaves are available. When the trees are higher than 10m only 10% of this reduced amount is available. All the values are based on expert judgement. To calculate the available amount the leaves are equally divided over the length of the trees and only the biomass that is below the threshold amount is available. Although a preference per grazer is given beforehand it is not fixed, the actually eaten amount of biomass per organ and functional type also depends on the amount of available biomass per organ.

For all Equations: t: time step, j: vegetation type, i: functional type, o: organ, g: tree species

Overall description of biomass

$$B_{i,j,t} = B_{i,j,t-1} + (Aact_{i,j,t} - D_{i,j,t} - M_t + Bs_{i,j,t}) \cdot \Delta t \quad [1]$$

$B_{i,j,t}$: biomass (ton.ha⁻¹)
 $Aact_{i,j,t}$: actual growth (ton.ha⁻¹.y⁻¹)
 $D_{i,j,t}$: actual mortality (ton.ha⁻¹.y⁻¹)
 M_t : actual removal by management (ton.ha⁻¹.y⁻¹)
 $Bs_{i,j,t}$: actual seed biomass (ton.ha⁻¹.y⁻¹)
 Δt : time step (y⁻¹)

Overall description of growth

$$Aact_{i,j,t} = Amax_{i,j} \cdot RI_{i,j,t} \cdot RNav_{i,j,t} \quad [2]$$

$Aact_{i,j,t}$: actual growth (ton.ha⁻¹.y⁻¹)
 $Amax_{i,j}$: maximum growth (ton.ha⁻¹.y⁻¹)
 $RI_{i,j,t}$: reduction factor for light availability (-)
 $RNav_{i,j,t}$: reduction factor for nitrogen availability (-)

Light interception

$$RI_{i,j,t} = \sum_{n=1,5} (fI_{i,t,n-1} \cdot (1 - e^{(-k_{i,j} \cdot fBl_{i,t,n})})) \quad [3]$$

$RI_{i,j,t}$: reduction factor for light interception (-)
 $fI_{i,t,n-1}$: fraction light remaining after interception in canopy layer n-1 (-)
 $k_{i,j}$: interception factor (-)
 $fBl_{i,t,n}$: fraction leaf biomass of functional type i in canopy layer n (-)
 n : number of functional types present in a canopy layer (-)

Nitrogen deposition interception

$$Nint_{i,j,t} = \left(\frac{RI_{i,j,t}}{\sum_{i=1,5} RI_{i,j,t}} \right) \cdot Ndep_t \quad [4]$$

$Nint_{i,j,t}$: actual intercepted nitrogen deposition (ton ha⁻¹ y⁻¹)
 $RI_{i,j,t}$: light interception (-)
 $Ndep_t$: actual nitrogen deposition (ton ha⁻¹ y⁻¹)

Nitrogen availability

$$Nav_{i,j,t} = Nint_{i,j,t} + \sum_{o=1,3} (Nrea_{o,i,j,t-1}) + \left\{ \left(\frac{B_{o=r,i,j,t}}{\sum_{i=1,5} B_{o=r,i,j,t}} \right) \cdot Ns_t \right\} \quad [5]$$

$Nav_{i,j,t}$: actual nitrogen availability (ton ha⁻¹ y⁻¹)
 $Nint_{i,j,t}$: actual intercepted nitrogen deposition (ton ha⁻¹ y⁻¹)
 $Nrea_{o,i,j,t-1}$: actual nitrogen reallocation (ton ha⁻¹ y⁻¹)
 $B_{o,i,j,t}$: actual biomass (ton ha⁻¹ y⁻¹)
 r : root
 Ns_t : actual nitrogen release from the soil (ton ha⁻¹ y⁻¹)

Reduction factor for nitrogen availability

$$RNav_{i,j,t} = \frac{Nav_{i,j,t}}{Nav_{i,j,t} + (Amax_{i,j} \cdot RI_{i,j,t} \cdot Nmin_{i,j})} \quad [6]$$

$RNav_{i,j,t}$: reduction factor for nitrogen availability (-)
 $Nav_{i,j,t}$: actual nitrogen availability (ton ha⁻¹ y⁻¹)
 $Amax_{i,j}$: maximum growth (ton.ha⁻¹.y⁻¹)
 $RI_{i,j,t}$: reduction factor for light availability (-)
 $Nmin_{i,j}$: minimum nitrogen content (-)

New nitrogen mass per functional type

$$Nnew_{o,i,j,t} = Nav_{i,j,t} \cdot fN_{o,i,j} \quad [7]$$

$Nnew_{o,i,j,t}$: actual nitrogen mass uptake (ton ha⁻¹ y⁻¹)
 $Nav_{i,j,t}$: actual nitrogen availability (ton ha⁻¹ y⁻¹)
 $fN_{o,i,j}$: factor for the partitioning of nitrogen (-)

Nitrogen mass organs

$$N_{o,i,j,t} = N_{o,i,j,t-1} - (N_{o,i,j,t-1} \cdot fd_{o,i,j}) + Nnew_{o,i,j,t} \cdot \Delta t \quad [8]$$

$N_{o,i,j,t}$: nitrogen mass (ton ha⁻¹)
 $fd_{o,i,j}$: biomass mortality factor (-)
 $Nnew_{o,i,j,t}$: new nitrogen mass (ton ha⁻¹ y⁻¹)
 Δt : time step (y⁻¹)

Nitrogen content organs

$$NC_{o,i,j,t} = \frac{N_{o,i,j,t}}{B_{o,i,j,t} \cdot fB_{o,i,j}} \quad [9]$$

$NC_{o,i,j,t}$: nitrogen content (-)
 $N_{o,i,j,t}$: nitrogen mass (ton \cdot ha⁻¹)
 $B_{o,i,j,t}$: biomass (ton \cdot ha⁻¹)
 $fB_{o,i,j}$: factor for the partitioning of nitrogen (-)

Nitrogen content litter, dead wood and dead roots

$$NCd_t = \frac{\sum_{i=1,5} \left\langle \sum_{o=1,3} (1 - frea_o) \cdot N_{o,i,j,t} \right\rangle}{\sum_{i=1,5} \left\langle \sum_{o=1,3} (B_{o,i,j,t} \cdot fd_{o,i,j}) \right\rangle} \quad [10]$$

NCd_t : nitrogen content of litter/dead wood/dead roots (-)
 $N_{o,i,j,t}$: nitrogen mass (ton \cdot ha⁻¹)
 $frea_o$: nitrogen reallocation factor (-)
 $N_{o,i,j,t}$: nitrogen mass (ton \cdot ha⁻¹)
 $B_{o,i,j,t}$: biomass (ton \cdot ha⁻¹)
 $fd_{o,i,j}$: biomass mortality factor (-)

Biomass per organ

$$B_{o,i,j,t} = B_{i,j,t} \cdot fB_{o,i,j} \quad [11]$$

$B_{o,i,j,t}$: biomass in a given organ (ton \cdot ha⁻¹)
 $B_{i,j,t}$: biomass (ton \cdot ha⁻¹)
 $fB_{o,i,j}$: factor for the distribution of biomass (-)

Dead biomass

$$D_{i,j,t} = \sum_{o=1,3} (B_{o,i,j,t-1} \cdot fd_{o,i,j}) \quad [12]$$

$D_{i,j,t}$: dead biomass (ton \cdot ha⁻¹)
 $B_{o,i,j,t}$: Biomass (ton \cdot ha⁻¹)
 $fd_{o,i,j}$: biomass mortality factor (-)

Height of grasses and herbs and dwarfshrubs

$$H_{i=(gh,d),j,t} = k \cdot B_{i=(gh,d),j,t} \quad [13]$$

$H_{i,j,t}$: height (m)
 gh : grasses/herbs
 d : dwarf shrubs
 k : regression coefficient; fixed at 1 ($m^3 \cdot kg^{-1}$)
 $B_{i,j,t}$: biomass ($ton \cdot ha^{-1}$)

Height of shrubs

$$H_{i=s,j,t} = H_{max} + (-k_{s1} \cdot (k_{s2})^{[age_{s,t}/\Delta t]}) \quad [14]$$

$H_{i,j,t}$: height (m)
 H_{max} : maximum height; fixed at 3.104 (m)
 s : shrubs
 k_{s1} : regression coefficient 1; fixed at 3.395 (-)
 k_{s2} : regression coefficient 2; fixed at 0.90526 (-)
 $age_{s,t}$: age shrubs (y)
 Δt : time step set at 1 (y^{-1})

Minimum height trees

$$Hmin_{t,g} = k_{1,g} + (-k_{2,g} \cdot (k_{3,g})^{[age_{g,t}/\Delta t]}) \quad [15]$$

$Hmin_{t,g}$: minimum height (m)
 $k_{1,g}$: regression coefficient 1 (m)
 $k_{2,g}$: regression coefficient 2 (-)
 $k_{3,g}$: regression coefficient 3 (-)
 $age_{g,t}$: age trees (y)
 Δt : time step set at 1 (y^{-1})

Maximum height trees

$$Hmax_{t,g} = k_{4,g} + (-k_{5,g} \cdot (k_{6,g})^{[age_{g,t}/\Delta t]}) \quad [16]$$

$Hmax_{t,g}$: maximum height (m)
 $k_{4,g}$: regression coefficient 4 (m)
 $k_{5,g}$: regression coefficient 5 (-)
 $k_{6,g}$: regression coefficient 6 (-)
 $age_{g,t}$: age trees (y)
 Δt : time step set at 1 (y^{-1})

Actual height trees

$$H_{g,t} = H_{g,t-1} + \left\langle H_{grmin_{g,t}} + \left\{ (H_{grmax_{g,t}} - H_{grmin_{g,t}}) \cdot \left(\frac{A_{act_{i=g,j,t}} - B_{min}}{B_{max} - B_{min}} \right) \right\} \right\rangle \cdot \Delta t \quad [17]$$

- $H_{g,t}$: Actual height (m)
 $H_{grmin_{g,t}}$: minimum height growth; difference between $H_{min_{t,g}}$ and $H_{min_{t-1,g}}$ (m y^{-1})
 $H_{grmax_{g,t}}$: maximum height growth; difference between $H_{max_{t,g}}$ and $H_{max_{t-1,g}}$ (m y^{-1})
 $A_{act_{g,j,t}}$: biomass growth for tree species g (ton $ha^{-1} y^{-1}$)
 B_{min} : minimum biomass growth (ton $ha^{-1} y^{-1}$)
 B_{max} : maximum biomass growth (ton $ha^{-1} y^{-1}$)

Tree thinning

If $rt = tt$

$$M_t = B_{i=g,j,t} \cdot kT_{g,t} \quad [18]$$

- rt : runtime (y)
 tt : thinning time (y)
 $B_{i=g,j,t}$: biomass tree species g (ton. ha^{-1})
 $kT_{g,t}$: thinning factor (-)

Parameter values for SUMO

Initial biomass for different vegetation types and (successional) stadia. Note that for some of the validations site specific data were used. For tree species 1 birch is used except for alder where ash is used as tree species 1.

vegetation type		dune shrub	open dune	salt marsh	reed	rough land	grassland	extensive natural	heath land <75%	heath land >75%	peat bog	bare sand	natural land
Root	Herbs	1	1	5	4	3	4	3	1	4	4	0.1	3
	Dwarf shrubs	4	2	2	0.1	0.1	0.1	0.1	3	1	1	0.1	0.1
	Shrubs	0.1	0.1	0.1	0.1	1	0.1	0.1	0.1	0.1	0.1	0.1	1
	tree 1	0.1	0.1	0.1	0.1	1	0.1	0.1	0.1	0.1	0.1	0.1	1
Wood	tree 2	0.1	0.1	0.1	0.1	1	0.1	0.1	0.1	0.1	0.1	0.1	1
	Herbs	0.1	1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
	Dwarf shrubs	7	3	5	0.1	0.1	0.1	0.1	2	1	1	0.1	0.1
	Shrubs	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	1
Leaves	tree 1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	1
	tree 2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	1
	Herbs	1	1	5	4	3	4	3	1	4	3	0.1	3
	Dwarf shrubs	3	2	3	0.1	0.1	0.1	0.1	3	1	1	0.1	0.1
	Shrubs	0.1	0.1	0.1	0.1	1	0.1	0.1	0.1	0.1	0.1	0.1	1
	tree 1	0.1	0.1	0.1	0.1	1	0.1	0.1	0.1	0.1	0.1	0.1	1
	tree 2	0.1	0.1	0.1	0.1	1	0.1	0.1	0.1	0.1	0.1	0.1	1
		0.1	0.1	0.1	0.1	1	0.1	0.1	0.1	0.1	0.1	0.1	1
tree species		oak Northern red oak Northern red oak Northern red oak Northern red oak Beech Beech Beech Beech Douglas Douglas Douglas Douglas											
age class		<40y 40-80y 80-120y >120y <40y 40-80y 80-120y >120y <40y 40-80y 80-120y >120y											
Root	Herbs	1	1	1	1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
	Dwarf shrubs	0.3	0.3	0.3	0.3	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
	Shrubs	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5
	tree 1	1.5	1.5	1.5	1.5	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2
Wood	tree 2	3	3	3	3	3	3	3	3	3	3	3	3
	Herbs	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
	Dwarf shrubs	0.8	2	2	2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2
	Shrubs	2.5	2.5	3	5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5
Leaves	tree 1	11	12	15	19	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2
	tree 2	11	40	80	90	20	50	80	100	20	50	80	100
	Herbs	1	1	1	1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
	Dwarf shrubs	0.3	0.3	0.3	0.3	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
	Shrubs	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5
	tree 1	1.5	1.5	1.5	1.5	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2
	tree 2	3	3	3	3	3	3	3	3	3	3	3	3
		3	3	3	3	3	3	3	3	3	3	3	3

tree species		Oak	Oak	Oak	Oak	Alder	Alder	Alder	Alder	Pine	Pine	Pine	Pine
age class		<40y	40-80y	80-120y	>120y	<40y	40-80y	80-120y	>120y	<40y	40-80y	80-120y	>120y
Root	Herbs	1	1	1	1	1	1	1	1	1	1	1	1
	Dwarf shrubs	0.3	0.3	0.3	0.3	0.1	0.1	0.1	0.1	0.3	0.3	0.3	0.3
	Shrubs	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5
	tree 1	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5
Wood	tree 2	3	3	3	3	3	3	3	3	3	3	3	3
	Herbs	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
	Dwarf shrubs	0.2	1.4	1.8	1.2	0.1	0.1	0.1	0.1	0.2	1.4	1.8	1.2
	Shrubs	2.5	2.2	2.5	6	2.5	1.7	2.5	4.5	2.5	2.2	2.5	6
Leaves	tree 1	10	12	15	20	10	12	15	17	10	12	15	20
	tree 2	15	40	70	80	15	40	70	80	15	40	60	90
	Herbs	1	1	1	1	1	1	1	1	1	1	1	1
	Dwarf shrubs	0.3	0.3	0.3	0.3	0.1	0.1	0.1	0.1	0.3	0.3	0.3	0.3
	Shrubs	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5
	tree 1	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5
	tree 2	3	3	3	3	3	3	3	3	3	3	3	3
tree species		Larch	Larch	Larch	Larch	Poplar	Poplar	Poplar	Willow	Willow	Willow	Willow	
age class		<40y	40-80y	80-120y	>120y	<40y	40-80y	80-120y	<40y	40-80y	80-120y	>120y	
Root	Herbs	1	1	1	1	1	1	1	1	1	1	1	
	Dwarf shrubs	0.3	0.3	0.3	0.3	0.1	0.1	0.1	0.1	0.1	0.1	0.1	
	Shrubs	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	
	tree 1	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	
Wood	tree 2	3	3	3	3	3	3	3	3	3	3	3	
	Herbs	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	
	Dwarf shrubs	0.2	1.4	1.8	1.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	
	Shrubs	2.5	2.2	2.5	6	2	0.7	0.7	2	0.7	0.7	0.7	
Leaves	tree 1	10	12	15	20	7	7	4	7	7	4	3	
	tree 2	20	40	70	90	20	40	70	20	40	60	80	
	Herbs	1	1	1	1	1	1	1	1	1	1	1	
	Dwarf shrubs	0.3	0.3	0.3	0.3	0.1	0.1	0.1	0.1	0.1	0.1	0.1	
	Shrubs	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	
	tree 1	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	
	tree 2	3	3	3	3	3	3	3	3	3	3	3	

Vegetation succession as affected by decreasing nitrogen depositon, soil characteristics and site management

tree species		New forest	clear cut	Alder coppice	Willow coppice	Oak coppice	Ash coppice
Root	Herbs	1	0.1	0.5	0.5	0.5	0.5
	Dwarf shrubs	0.5	0.1	0.1	0.1	0.3	0.3
	Shrubs	1	0.1	0.1	0.1	0.1	0.1
	tree 1	1	0.2	2	2	2	2
	tree 2	1	0.2	2	2	2	2
Wood	Herbs	0.1	0.1	0.1	0.1	0.1	0.1
	Dwarf shrubs	0.5	0.1	0.1	0.1	0.3	0.3
	Shrubs	1	0.1	0.1	0.1	0.1	0.1
	tree 1	1	0.1	12	12	12	12
	tree 2	1	0.1	12	12	12	12
Leaves	Herbs	1	0.1	0.5	0.5	0.5	0.5
	Dwarf shrubs	0.5	0.1	0.1	0.1	0.3	0.3
	Shrubs	1	0.1	0.1	0.1	0.1	0.1
	tree 1	1	0.2	2	2	2	2
	tree 2	1	0.2	2	2	2	2

Parameter values for herbs and grasses, dwarf shrubs and shrubs per vegetation type; k_{int} light interception factor, N_{min} minimal N content of the biomass, N_{max} maximal N content of the biomass and A_{max} maximum growth rate.

Vegetation type	Functional type	k_{int}	N_{min}	N_{max}	A_{max} (ton.ha ⁻¹ .y ⁻¹)
Grassland	Herbs	0.7	0.0085	0.025	24
	Dwarf shrubs	0.7	0.0085	0.023	10
	Shrubs	0.6	0.0085	0.023	16
Salt marsh	Herbs	0.7	0.01	0.02	15
	Dwarf shrubs	0.8	0.01	0.018	20
	Shrubs	0.001	0.01	0.001	10
Reed	Herbs	0.7	0.01	0.02	30
	Dwarf shrubs	0.7	0.01	0.018	8
	Shrubs	0.7	0.01	0.018	18
Heathland	Herbs	0.6	0.01	0.02	18
	Dwarf shrubs	0.7	0.01	0.018	12
	shrubs	0.4	0.01	0.018	13
Shrub	herbs	0.7	0.01	0.025	15
	Dwarf shrubs	0.7	0.01	0.023	12
	Shrubs	0.6	0.01	0.023	13
Forest	Herbs	0.8	0.01	0.025	24
	Dwarf shrubs	0.7	0.01	0.023	10
	Shrubs	0.6	0.01	0.023	14

Parameter values for herbs and grasses, dwarf shrubs and shrubs per vegetation type; f_B new biomass distribution over the organs, f_N new nitrogen distribution over the organs, f_d mortality factor per organ and B_s yearly seed biomass input.

Vegetation type	Functional type	organ	f_B	f_N	f_d	B_s (ton.ha ⁻¹ .y ⁻¹)
Grassland	Herbs	Root	0.49	0.45	1	0.0001
		Wood	0.4	0.41	0.7	0.0001
		Leaves	0.4	0.41	0.3	0.01
	Dwarf shrubs	Root	0.01	0.01	1	0.0001
		Wood	0.2	0.02	0.3	0.0001
		Leaves	0.1	0.02	0.04	0.01
	Shrubs	Root	0.5	0.54	0.9	0.0001
		Wood	0.4	0.57	0.6	0.0001
		Leaves	0.5	0.57	1	0.01
Salt marsh	Herbs	Root	0.49	0.49	0.9	0.0001
		Wood	0.35	0.45	0.8	0.0001
		Leaves	0.4	0.4	1	0.0001
	Dwarf shrubs	Root	0.01	0.01	1	0.0001
		Wood	0.3	0.1	0.2	0.0001
		Leaves	0.1	0.1	1	0.0001
	Shrubs	Root	0.5	0.5	0.7	0.0001
		Wood	0.35	0.45	0.6	0.0001
		Leaves	0.5	0.5	1	0.0001
Reed	Herbs	Root	0.45	0.45	0.8	0.0001
		Wood	0.35	0.42	0.6	0.0001
		Leaves	0.35	0.42	0.6	0.0001
	Dwarf shrubs	Root	0.01	0.01	0.9	0.0001
		Wood	0.2	0.01	0.1	0.0001
		Leaves	0.2	0.01	0.03	0.0001
	Shrubs	Root	0.54	0.54	0.8	0.0001

Vegetation succession as affected by decreasing nitrogen depositon, soil characteristics and site management

Vegetation type	Functional type	organ	fB	fN	fδ	Bs (ton.ha ⁻¹ .y ⁻¹)
Heathland	Herbs	Wood	0.45	0.57	0.6	0.0001
		Leaves	0.45	0.57	1	0.0001
		Root	0.49	0.49	1	0.0001
	Dwarf shrubs	Wood	0.45	0.45	0.6	0.0001
		Leaves	0.4	0.42	0.3	0.0001
		Root	0.01	0.01	1	0.0001
	Shrubs	Wood	0.1	0.05	0.3	0.0001
		Leaves	0.1	0.01	0.04	0.0001
		Root	0.5	0.5	1	0.0001
	Herbs	Wood	0.45	0.5	0.5	0.0001
		Leaves	0.5	0.57	1	0.0001
		Root	0.45	0.45	0.9	0.0001
Shrub	Dwarf shrubs	Wood	0.35	0.42	0.6	0.0001
		Leaves	0.4	0.42	0.7	0.01
		Root	0.01	0.01	1	0.0001
	Shrubs	Wood	0.15	0.01	0.3	0.0001
		Leaves	0.1	0.01	0.1	0.01
		Root	0.54	0.54	0.9	0.0001
	Herbs	Wood	0.5	0.57	0.5	0.0001
		Leaves	0.5	0.57	0.8	0.01
		Root	0.45	0.45	0.8	0.0001
	Dwarf shrubs	Wood	0.35	0.42	0.6	0.0001
		Leaves	0.35	0.42	0.6	0.01
		Root	0.01	0.01	1	0.0001
Forest	Shrubs	Wood	0.15	0.01	0.1	0.0001
		Leaves	0.2	0.01	0.03	0.01
		Root	0.54	0.54	0.8	0.0001
	Herbs	Wood	0.5	0.57	0.5	0.0001
		Leaves	0.45	0.57	1	0.01
		Root	0.45	0.57	1	0.01

Parameter values for tree species; f_B new biomass distribution over the organs, f_N new nitrogen distribution over the organs, f_d mortality factor per organ and B_s yearly seed biomass input.

species	organ	f_B	f_N	f_d	B_s (ton.ha ⁻¹ .y ⁻¹)
Scots pine	Root	0.4	0.41	0.7	0.0001
	Wood	0.25	0.02	0.01	0.0001
	Leaves	0.35	0.57	0.7	0.0001
Larch	Root	0.35	0.41	0.7	0.001
	Wood	0.3	0.02	0.01	0.001
	Leaves	0.35	0.57	1	0.001
Douglas fir	Root	0.3	0.41	0.6	0.001
	Wood	0.25	0.02	0.03	0.001
	Leaves	0.45	0.57	0.6	0.001
Norway spruce	Root	0.35	0.41	0.3	0.001
	Wood	0.2	0.02	0.03	0.001
	Leaves	0.45	0.57	0.6	0.001
Birch	Root	0.4	0.41	0.3	0.01
	Wood	0.15	0.02	0.01	0.01
	Leaves	0.45	0.57	1	0.01
Ash	Root	0.28	0.42	0.7	0.001
	Wood	0.32	0.01	0.01	0.001
	Leaves	0.4	0.57	1	0.001
Alder	Root	0.35	0.41	0.3	0.001
	Wood	0.15	0.02	0.01	0.001
	Leaves	0.5	0.57	1	0.001
Poplar	Root	0.3	0.41	0.3	0.001
	Wood	0.25	0.02	0.03	0.001
	Leaves	0.45	0.57	1	0.001
Oak	Root	0.3	0.42	0.7	0.01
	Wood	0.3	0.01	0.01	0.01
	Leaves	0.4	0.57	1	0.01
Northern red oak	Root	0.3	0.42	0.7	0.01
	Wood	0.35	0.01	0.02	0.01
	Leaves	0.35	0.57	1	0.01
Beech	Root	0.3	0.41	0.7	0.001
	Wood	0.3	0.02	0.03	0.001
	Leaves	0.4	0.57	1	0.001
Willow	Root	0.28	0.42	0.7	0.001
	Wood	0.32	0.01	0.01	0.001
	Leaves	0.4	0.57	1	0.001

Height growth regression coefficients for trees (Formula 15 and 16). All coefficients are derived from Jansen et al., (1996). It is assumed that willow has the same growth characteristics as ash.

Species	k ₁	k ₂	k ₃	k ₄	k ₅	k ₆
Scots pine	14.392	-14.63	0.96952	29.847	-30.5	0.97154
Larch	20.332	-20.992	0.96332	33.616	-34.759	0.96332
Douglas fir	24.49	-24.919	0.972	36	-37	0.965
Norway spruce	21.318	-21.7	0.97742	36.357	-37.18	0.97356
Birch	15.925	-16.2	0.97	31	-31.5	0.977
Ash	18.506	-18.9	0.97	34.13	-34.8	0.97318
Alder	16.414	-16.8	0.96557	29.105	-30.18	0.95754
Poplar	24.293	-25.51	0.9408	40.544	-43.7	0.92
Oak	17.85	-17.95	0.98546	42.47	-42.99	0.98396
Northern red oak	16.283	-16.5	0.97101	30.531	-31.2	0.97
Beech	39.09	-39.18	0.99345	41.7	-42.3	0.97524
Willow	16.414	-16.8	0.96557	29.105	-30.18	0.95754

Parameter values for tree species; k_{int} light interception factor, Nmin minimal N content of the biomass, Nmax maximal N content of the biomass and Amax maximum growth rate.

Species	k _{int}	Nmin	Nmax	Amax (ton.ha ⁻¹ .y ⁻¹)
Scots pine	0.4	0.0085	0.023	15
Larch	0.4	0.005	0.018	13
Douglas fir	0.4	0.01	0.018	17
Norway spruce	0.4	0.01	0.018	17
Birch	0.3	0.0085	0.023	15
Ash	0.8	0.01	0.023	15
Alder	0.3	0.01	0.023	15
Poplar	0.9	0.01	0.018	16
Oak	0.7	0.01	0.018	14
Northern red oak	0.7	0.01	0.018	15
Beech	0.7	0.01	0.023	14
Willow	0.8	0.01	0.018	15

Clear cut cycle for tree species. After the clear cut the same species is assumed to be replanted.

Species	Cycle (y)
Scots pine	85
Larch	70
Douglas fir	85
Norway spruce	60
Birch	75
Ash	75
Alder	80
Poplar	75
Oak	105
Northern red oak	85
Beech	135

Thinning percentages for tree species (after Jansen et al., 1996). Percentages are given for a five year cycle. Thinning starts at the moment more than 25 ton ha⁻¹ dry mass of wood is present for the trees. When the number of management occurrences is higher than here given the last thinning percentage is used.

Scots pine	Larch	Douglas fir	Norway spruce	Birch	Ash	Alder	Poplar	Oak	Northern red oak	Beech
3.57	5.77	35.56	13.46	9.09	20.83	3.85	20.83	10.47	25.86	4.41
18.48	20.62	20.23	17.75	7.69	31.86	10.58	31.86	15.67	16.48	9.84
16.15	31.83	17.28	18.41	18.85	19.57	11.03	19.57	13.74	13.6	17.05
26.79	22.72	14.74	27.24	12.56	16.86	17.55	16.86	22.61	11.68	19.13
20.43	18.57	12.63	18.35	10.87	14.87	16.68	14.87	18.87	37.24	19.41
17.71	15.2	10.69	15.14	10.4	13.39	15.92	13.39	17.38	15.11	19.18
15.02	12.27	9.16	13.19	9.52	11.67	15.04	11.67	15.59	13.42	17.82
12.81	9.88	7.8	12.52	8.65	10.46	13.98	10.46	14.19	11.33	15.43
10.91	8.23	6.62	11.37	7.95	9.35	13.05	9.35	13.43	10.14	18.2
9.33	6.7	5.7	10.12	7.41	8.11	11.62	8.11	12.42	8.71	16.89
7.98	5.61	4.75	9.31	6.99	6.93	10.97	6.93	11.56	7.91	15.51
6.79	4.89	4.14	8.41	6.65	6.4	9.81	6.4	10.73	7.44	14.62
5.71	4.35	3.36	7.53	6.37	5.5	8.94	5.5	10.01	6.79	13.43
5.15	4.13	2.86		5.93	4.97	7.97	4.97	9.01	6.2	12.68
4.62	4.18	2.78		5.76	4.64	7.58	4.64	8.5	5.84	11.8
4.42		2.47		5.07	4.2	6.71	4.2	8.03	5.33	10.89
4.21		2.43						7.65	5.03	10.2
4.16								7.12	4.93	9.46
								6.79		8.67
								6.78		8.07
								6.35		7.63
								6.09		6.89
										6.52
										6.18
										5.65
										5.35
										4.86

Threshold values for available biomass (Ba) for grazers

Functional type	organ	Ba (ton ha ⁻¹)
Herbs	Root	1.0
	Wood	0.01
	Leaves	0.5
Dwarf shrubs	Root	1.0
	Wood	0.2
	Leaves	0.5
Shrubs	Root	1.0
	Wood	0.2
	Leaves	0.1
Pioneer tree	Root	1.0
	Wood	0.2
	Leaves	0.1
Climax tree	Root	1.0
	Wood	0.2
	Leaves	0.1

Amount of biomass to be eaten per grazer (Be), the factor for calculating the amount of manure (\bar{m}) and the N-content of the manure (Ncm).

grazer	Be (ton ha ⁻¹)	\bar{m}	Ncm
Domestic cattle	2.288	0.65	0.007
'wild'cattle	2.490	0.65	0.007
Young cattle	2.450	0.65	0.007
European bison	4.500	0.65	0.007
pony	1.462	0.65	0.007
horse	1.900	0.65	0.007
sheep	0.480	0.65	0.021
moose	2.007	0.65	0.007
Roe deer	0.240	0.65	0.007
Red deer	0.670	0.65	0.007
Fallow deer	0.513	0.65	0.007
mouflon	0.422	0.65	0.007
Wild boar	0.522	0.65	0.007
goose	0.0028	0.65	0.044
rabbit	0.0032	0.65	0.007

Biomass preference factor for grazers (β_p)														
Domestic cattle	wild cattle	Young cattle	European bison	pony	horse	sheep	moose	Roe deer	Red deer	Fallow deer	mouflon	Wild boar	goose	rabbit
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.33	0.0	0.0
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.04	0.0	0.0
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.06	0.0	0.0
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.06	0.0	0.0
0.01	0.01	0.01	0.01	0.01	0.01	0.04	0.01	0.01	0.01	0.01	0.01	0.01	0.0	0.01
0.01	0.01	0.01	0.01	0.01	0.01	0.04	0.01	0.01	0.01	0.01	0.01	0.01	0.0	0.01
0.01	0.01	0.01	0.03	0.01	0.01	0.05	0.10	0.01	0.01	0.01	0.01	0.01	0.0	0.01
0.01	0.01	0.01	0.06	0.01	0.01	0.05	0.15	0.01	0.01	0.01	0.01	0.01	0.0	0.01
0.01	0.01	0.01	0.06	0.01	0.01	0.04	0.15	0.01	0.01	0.01	0.01	0.01	0.0	0.01
0.74	0.50	0.74	0.78	0.84	0.89	0.20	0.28	0.43	0.53	0.21	0.45	0.11	1.00	0.75
0.0	0.01	0.0	0.00	0.01	0.0	0.20	0.00	0.08	0.13	0.0	0.0	0.02	0.0	0.10
0.0	0.03	0.0	0.01	0.0	0.0	0.12	0.10	0.24	0.12	0.45	0.0	0.0	0.0	0.02
0.10	0.15	0.10	0.02	0.05	0.03	0.13	0.10	0.10	0.08	0.14	0.25	0.17	0.0	0.04
0.11	0.26	0.11	0.02	0.05	0.03	0.13	0.10	0.10	0.09	0.15	0.25	0.17	0.0	0.04

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Appendix 2. Data used for the validation of SUMO.

Rothamsted Parkgrass

The initial biomass per organ for SUMO is given in Table 1, the deposition of nitrogen en sulphur is given in Figure 1.

Table 1. Initial biomass per functional type and organ for the Parkgrass site at Rothamsted (UK).

functional type	roots	wood	leaves
herbs and grasses	4	0.1	4
dwarf shrubs	0.1	0.1	0.1
shrubs	0.000001	0.000001	0.000001
tree 1	0.000001	0.000001	0.000001
tree 2	0.000001	0.000001	0.000001

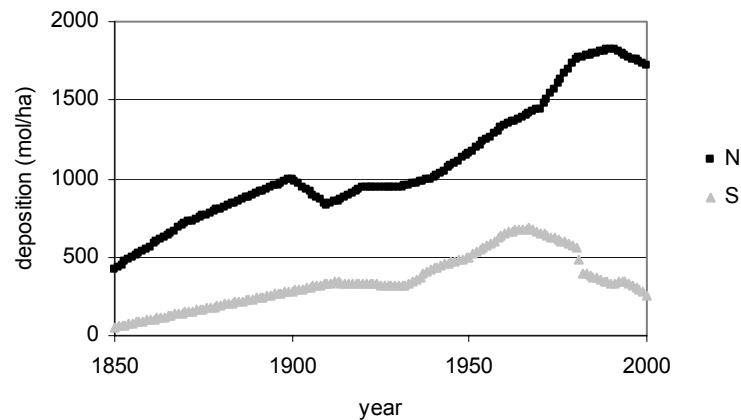


Figure 1. Nitrogen (N) en Sulphur (S) deposition for Parkgrass Rothamsted (UK).

Wageningen

The initial biomass for SUMO is given in Table 2, the deposition of nitrogen en sulphur is given in Figs. 2 and 3. The deposition data are reconstructed from measurements and historic emissions. Deposition rates are estimated for 5*5 km grids and subsequently appointed to the sites SUMO was validated on.

Table 2. Initial biomass per functional type and organ for the grassland site near Wageningen.

functional type	roots	wood	leaves
herbs and grasses	4	0.1	4
dwarf shrubs	0.1	0.1	0.1
shrubs	0.1	0.1	0.1
tree 1	0.1	0.1	0.1
tree 2	0.1	0.1	0.1

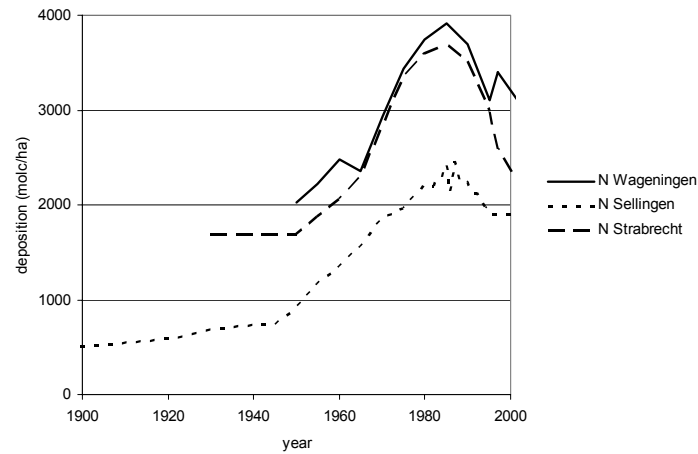


Figure 2. Constructed 'historic' nitrogen deposition for the sites in The Netherlands where SUMO was validated on.



Figure 2. Constructed 'historic' sulphur deposition for the sites in The Netherlands where SUMO was validated on.

Strabrechtse heide

The initial biomass for SUMO is given in Table 3, the deposition of nitrogen en sulphur is given in Figs 2 and 3. The initial biomass for all the different stages after turf stripping are the same, since they are only used to initialise the model SMART2. As soon as the turf stripping takes place at different years in the past the biomass accumulation starts, which is compared to the measured biomass.

Table 3. *Initial biomass per functional type and organ for each heathland site at Strabrechtse beide.*

functional type	roots	wood	leaves	
herbs and grasses	1	0.1	1	
dwarf shrubs	3	2	3	
shrubs	0.1	0.1	0.1	
tree 1	0.1	0.1	0.1	
tree 2	0.1	0.1	0.1	

Sellingen

The initial biomass for SUMO is given in Table 4, the deposition of nitrogen en sulphur is given in Figs 2 and 3. The initial biomasses are for all the sites this chronosequence is composed of the same, the runs just start at different points in time.

Table 4. *Initial biomass per functional type and organ for the grassland site near Sellingen for all age classes.*

functional type	roots	wood	leaves	
herbs and grasses	0.1	0.1	0.1	
dwarf shrubs	0.1	0.1	0.1	
shrubs	0.1	0.1	0.1	
tree 1	0.2	0.1	0.2	
tree 2	0.2	0.1	0.2	

Appendix 3. Data used for the analysis of the effect of decreasing nitrogen deposition.

Zeesserveld

The initial biomass for SUMO is given in Table 1, the deposition of nitrogen en sulphur for both scenarios is given in Figure 1.

Table 1. Initial biomass per functional type and organ for the pine forest site Zeesserveld.

functional type	roots	wood	leaves
herbs and grasses	1	0.1	1
dwarf shrubs	0.1	0.1	0.1
shrubs	1	1	1
tree 1 (birch)	1	1	1
tree 2 (pine)	1	1	1

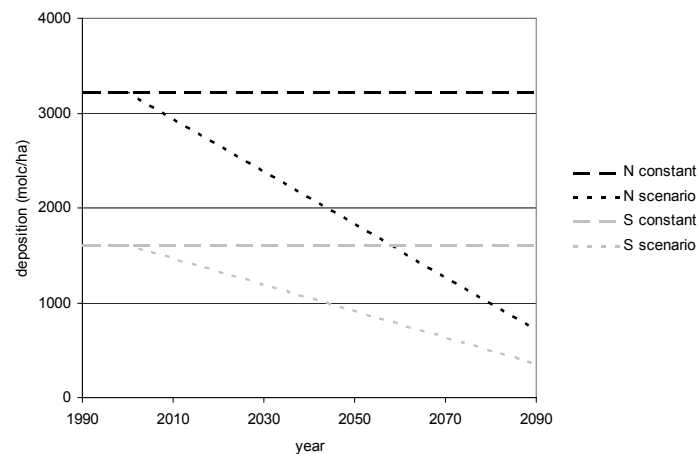


Figure 1. Deposition scenarios of nitrogen (N) and sulphur (S) used for the simulation of Zeesserveld, Edesche heide and Renkum.

Edesche heide

The initial biomass for SUMO is given in Table 2, the deposition of nitrogen en sulphur is given in Figure 1.

Table 2. Initial biomass per functional type and organ for the heathland site Edesche heide.

functional type	roots	wood	leaves
herbs and grasses	1	0.1	1
dwarf shrubs	3	2	3
shrubs	0.1	0.1	0.1
tree 1	0.1	0.1	0.1
tree 2	0.1	0.1	0.1

Renkum

The initial biomass for SUMO is given in Table 3, the deposition of nitrogen and sulphur is given in Figure 1.

Table 3. *Initial biomass per functional type and organ for the grassland site near Renkum.*

functional type	roots	wood	leaves	
herbs and grasses		3.0	0.1	3.0
dwarf shrubs		0.1	0.1	0.1
shrubs		0.1	0.1	0.1
tree 1		0.1	0.1	0.1
tree 2		0.1	0.1	0.1

**Changes in large-scale patterns of plant
biodiversity predicted from environmental
economic scenarios**



5 Changes in large-scale patterns of plant biodiversity predicted from environmental economic scenarios

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Abstract

In the industrialized world large sums of money are spent on measures to preserve biodiversity by improving the environmental quality. This creates a need to evaluate the effectiveness of such measures. In response we developed a model, NTM, that links plant biodiversity to abiotic variables that are under human control. These variables are: vegetation management, and the soil variables groundwater level, pH and nitrogen availability. We used species richness and the criteria of the Red Lists, i.e. the rarity and decline per species as measure for potential changes in biodiversity. NTM uses a statistical approach, and models the potential plant biodiversity based on the above criteria as a non-linear function of the three soil variables. The regression model is calibrated on a data set consisting of 33,706 vegetation relevés. Because field data of vegetation combined with measurements of soil variables are insufficiently available, we used the mean of Ellenberg's indicator values of the species in each relevé as a proxy.

NTM was subjected to both validation and uncertainty analysis. The validation was carried out by comparison with an independent data set. The uncertainty analysis showed that uncertainty in absolute biodiversity values is large, but that comparative scenario studies can be carried out with an acceptable uncertainty. As an example we show the evaluation of the impact of three European economic scenarios on potential plant biodiversity in the Netherlands. Although there were differences per vegetation type and per region, the potential plant biodiversity had a tendency to increase, with the highest increase for the scenario with the highest reduction in atmospheric deposition of nitrogen and acidity.

Introduction

Since the Rio Convention biodiversity has become an important policy issue, even in densely populated and highly industrialised regions like Western Europe. In these regions biodiversity is to a large extent determined by abiotic circumstances within a given pattern of man-made and natural areas, but the entire landscape is under the widespread influence of human activities. Large-scale abiotic patterns are to an

increasing extent anthropogenically determined, and therefore biodiversity can to a certain extent be actively controlled. The past decades have shown a general willingness to invest in measures to promote biodiversity, such as emission control. The political attitude towards such measures, however, is also determined by world-wide economic developments.

Financial investment in measures to promote biodiversity requires methods to determine their effectiveness. We might for example want to compare the effects of a reduction in emission of ammonia with those of an increase in groundwater level. In order to do so one needs a measure for biodiversity that can be linked to abiotic variables like nitrogen and water availability. Existing models can be used to translate policy measures like pollution abatement into patterns of abiotic variables. This approach has been used by e.g. Berdowski et al. (1991), Kros et al. (1995) and van Oene et al. (1999).

Actual biodiversity can be measured in the field, using for instance (abundance-weighted) plant species richness or composite measures (i.e. the Simpson and the Shannon-Weaver index; Huston, 1994), or estimated by remote sensing (Nohr and Jorgensen, 1997; Griffiths et al., 2000). But if one wants to predict the effect of environmental changes, e.g. in land use, nitrogen deposition or groundwater level on biodiversity, a model is necessary. Models have been developed that link productivity (Whisheu and Keddy, 1996; Naeem et al., 1996; Loreau, 1998; Hector et al., 1999), productivity and disturbance (Pollock et al., 1998), disturbance (Angelstam, 1998; Ali et al., 2000), water availability (van Ek et al., 2000) or temperature, geology, landscape diversity and soil (Wohlgemuth, 1998) with biodiversity. But none of these models connect biodiversity with the combined effect of the four main anthropogenically controlled factors in lowland western Europe, namely management (e.g. mowing or forest cutting), soil acidity, and water and nitrogen availability.

In the present paper we concentrate on floristic biodiversity, because the flora is the component of the ecosystem for which sufficient data are available. Floristic biodiversity is highly influenced by environmental factors, both biotic and abiotic, which nowadays are to a large extent determined by human impact. One of the most important ways to manipulate biodiversity is management (Bakker, 1989; Oomes et al., 1996). This management may be fertilising, mowing, grazing, sod cutting (in heathland), forest management (i.e., cutting or planting of trees) or water management (i.e., manipulation of the surfacewater or groundwater level). The other important factor influencing the occurrence of plant species, and therefore floristic biodiversity, is the soil. In large parts of Europe the most important soil factors are moisture availability, soil acidity (soil pH) and nitrogen availability (Ellenberg, 1982). Human activities have had an - in some areas of Europe - immense impact on these soil conditions. Atmospheric deposition influences pH and nitrogen availability, water management influences moisture availability and fertilisation influences nitrogen availability. Other factors influencing biodiversity, not included in this study, are

climatic gradients (Noss, 2001), land use history (Dupre and Ehrlén, 2002) or landscape fragmentation (Foppen, 2001). Although human activities often have a negative impact on the (floristic) biodiversity (Dupre and Ehrlén, 2002; Foppen, 2001; Catto, 2002), certain forms of management can also influence biodiversity positively, for instance low-density grazing, mowing or sod cutting (Bakker, 1989; Oomes et al., 1996).

Our aim was to reveal a statistical relationship between vegetation management and soil conditions on the one hand, and floristic biodiversity on the other hand. For this purpose we developed the NTM model, which relates plant biodiversity to abiotic variables. When such relations have been quantified they can be used to predict the effects on biodiversity of environmental scenarios. For evaluating scenarios that entail changes over time, a dynamic model would be preferable. Unfortunately not enough information is available at present to develop such a model. Therefore we developed a static model, with the disadvantage that under changing conditions, a time-lag in the response of the vegetation is not accounted for. Theoretically, the output of such a model is the final state that is expected after an infinite time period. However, because we used dynamic models to generate the input for NTM, the output presented here is explicit in time (visualized, for the years 1995 and 2020). Therefore the temporal differences presented reflect processes simulated by dynamic models and not by NTM.

NTM is a non-linear regression model in which the potential biodiversity is regressed on the three Ellenberg indicator values (Ellenberg, 1991) for soil conditions: F (for moisture content of the soil), R (for soil acidity) and N (for the soil nitrogen content). The Ellenberg indicator system is based on expert knowledge and for a small part on field measurements, and gives the response of a large set of plant species on an arbitrary (mostly nine point) scale. Although the use and the validity of the Ellenberg indicator values is the subject of a still ongoing debate (Schaffers & Sykora, 2000; Wamelink et al., 2002), we think that these indicators are the best available at the moment. The model is calibrated by means of a training set, which consists of vegetation relevés. The training set can be chosen in relation to the questions to be answered. For instance, it may contain relevés from a specific region or a specific vegetation type, but it may also be a reflection of the most common vegetation types of a large area. In order to account for the effect of management our training set was split into three vegetation structure types that are related to management types. These structure types are forest (no management or extensive management), heathland (sod-cutting or extensive grazing) and grassland (mowing or intensive grazing). We use the floristic conservation value as a measure for biodiversity. In turn, the conservation value is calculated for each relevé in the training set on the basis of the rareness and temporal trend of its constituent species. These are the criteria of the Red Lists (Mace and Stuart 1994). NTM predicts potential plant biodiversity, i.e. the suitability of the (abiotic) environment as estimated from Ellenberg's indicator values, for the

development of an ecosystem containing rare or declining plant species. Whether the predicted potential biodiversity is actually realised, depends also on factors that are not included in the model such as dispersal and the presence of a seed bank.

NTM's input can either be derived from measurements in the field or from other models. For scenario analyses only models can produce the input. The examples given in this paper concentrate on the prediction of nation-wide changes in the pattern of potential biodiversity resulting from three scenarios. Therefore the input has to be derived from other models, which are fully described elsewhere.

Model description

Statistics

NTM makes a link between potential biodiversity and soil parameters estimated as Ellenberg's indicator values through a smooth non-linear regression. The regression is based on spline functions (Hastie & Tibshirani, 1990; Eilers & Marx, 1996) and uses three predictors, namely the Ellenberg indicator values for moisture (F), acidity (R) and nutrient availability (N). The Ellenberg indicator values are used as a proxy for groundwater level, pH and nitrogen availability. Regression based on spline functions avoids the awkward edge-effects of polynomial functions. To fit the model we used the multivariate generalisation of the penalised B-spline approach of Eilers & Marx (1996). We implemented that in the statistical programming language Genstat (Genstat 5 Committee 1993) using the SPLINE procedure by Goedhart (1996). In this generalisation each predictor is replaced by a series of B-splines, the three-dimensional tensor products of which form the actual regressors. In this study we used cubic B-splines with 4 knots, yielding 8 B-splines per predictor and $8 \times 8 \times 8 = 512$ regressors. A least-squares fit would thus take 512 degrees of freedom and would result in a non-smooth regression surface. To obtain a smoother surface, the least-squares criterion is increased with a penalty on the squared second order differences of the parameters. For this, the parameters are arranged in a cube, each side representing a predictor, on the basis of the B-splines that form each regressor. By increasing the penalty the effective number of degrees of freedom (Hastie & Tibshirani, 1990; Eilers & Marx, 1996), can be decreased on a continuous scale from 512 to 8, that is, from a rough and general model to a linear model with interactions. We attempted formal ways to choose the optimal number degrees of freedom to use, such as based on generalised cross validation and Akaike's information criterion (Hastie & Tibshirani, 1990), but these formal methods resulted in regression surfaces that we judged as too rough. In this paper, we chose for an effective number of degrees of about 125 as a good compromise between fit and smoothness. We used penalized B-splines instead of the also possible cubic B-splines, because the penalized B-splines approach is even more powerful than the use of restricted B-splines. Extrapolation till the outer knots is

possible; the splines are so constructed that the extrapolation lines are linear. But extrapolation should be avoided when possible (pers. comm. P. Eilers, 2002).

Calibration

To estimate NTM's regression parameters a large data set is necessary. Ideally, this data set contains vegetation relevés of which the management and the soil variables pH, moisture content and nitrogen availability are known. A sufficiently large data set containing these combinations of relevés and measured soil conditions is not available at the moment. But a large data set of only vegetation relevés made in natural areas is available. To calibrate NTM for the Netherlands we used 33,706 vegetation relevés (Schaminée et al., 1989). This data set represents a balanced overview of the Dutch flora (Latour et al., 1993). We used the Ellenberg (1991) indicator values for F, R and N as an estimate for the soil conditions. Every single Ellenberg indicator value for F, R and N is represented by at least one species in this data set. Out of all 972 (12 (for F)*9 (for R) * 9 (for N)) possible combinations, only 384 combinations are present. This is understandable as under Dutch circumstances some extreme situations do not occur, e.g. very dry and very nutrient rich.

The calibration set was split into three subsets on the basis of vegetation structure: one for forest, one for heathland and one for all remaining vegetation types. These may be salt marsh, peatbog, etc., but since most of them are grasslands we will further refer to them as grassland. The three subsets were chosen so as to reflect the main land use and management types (grassland with mowing and grazing, heathland with sod cutting, forests with forest management). The three subsets also reflect the main structure types: low vegetation without woody species (grassland), low vegetation with woody dwarfshrubs (heath) and high vegetation dominated by woody species (forest). The subsets were used to calibrate NTM, resulting in three submodels. For the number of relevés used for the calibration per subset, see Table 1. Figure 1 shows an example of the submodel grassland for F=1. A further subdivision of the data set into more subsets could be considered, for instance to reflect various management intensities. However, at the moment the data set is not large enough to allow such a subdivision, and the information on management is usually unavailable.

Table 1. Number of relevés (*n*) used for the parameterisation of NTM 3.0.

Vegetation type	n
Forest	5848
Heathland	4759
Grassland	23099
Total	33706

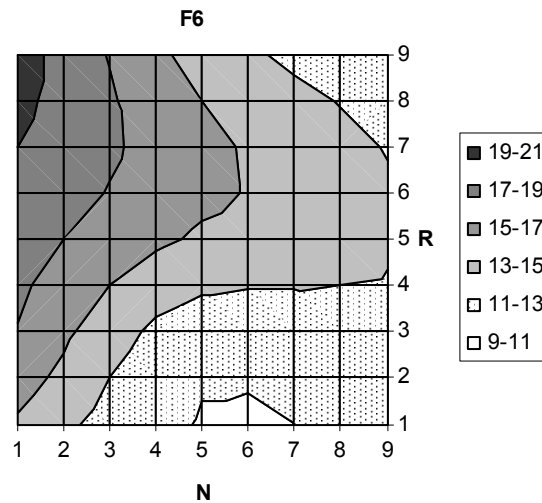


Figure 1. A slice of NTM, calibrated for the structure type forest. It shows the potential biodiversity for the Ellenberg moisture indicator value of 1 ($F=1$), with on the x-axis the Ellenberg indicator value for nitrogen (N) and on the y-axis the Ellenberg indicator value for acidity (R). The lines (estimated by penalized B-splines) connect points with equal potential biodiversity. The potential biodiversity is estimated for a combination of F , R and N value by simple 'looking up' the corresponding potential biodiversity.

A biodiversity value was assigned to each relevé on the basis of its conservation value using the method developed by Hertog & Rijken (1992). This method and its validation are extensively described in a separate paper (van Dobben et al., in prep). Its principle is that each plant species is assigned a conservation value depending on its rarity and temporal trend (the criteria of the red list, Mace & Stuart, 1994) in the Netherlands, and its international rarity (i.e., the national responsibility for the species). The trend is calculated as the percentage 5 by 5 km² squares in the Netherlands on a log-scale where the species has appeared or disappeared. Note that in principle a negative value can be calculated, for instance for invasive species that are becoming a pest (for instance *Prunus serotina* in Dutch forests). The conservation values of the species are used to calculate a biodiversity value per relevé as an abundance weighted sum over the species. Before entering the statistical analysis the biodiversity value is transformed to get an approximately normal distribution (the overall range of the transformed values is 0.0 – 31.2, the mean is 12.3).

In NTM we want to link plant biodiversity to abiotic parameters. To achieve this we have to connect biodiversity value of the relevé with abiotic parameters derived from the relevé. This can be done in several ways. We chose to use Ellenberg indicator values for the estimation of abiotic parameters. There are two possibilities to do this (these are extensively discussed by van Wirdum 1990):

1. The mean Ellenberg indicator values are calculated per relevé. This mean is combined with the biodiversity value of the relevé. This combination is then used for the calibration. The number of data points is equal to the number of relevés.
2. Instead of calculating the mean Ellenberg indicator value of the relevé, the value of each constituent species is used. This value is linked with the biodiversity value of the relevé. In this case the number of data points is equal to the total number of occurrences of the species.

We chose the second method for our model, because in that case more data points are available, especially at extreme values of F, R and N. Therefore, the three dimensional matrix of F, R, N is better ‘filled’. Also, by using the F, R and N values of individual species and not means of the relevé, abiotic heterogeneity within a relevé is accounted for. This method can be considered as a species-by-species approach, where each species’ contribution to biodiversity not only depends on its own value, but also on the values of the species with which it occurs together. A disadvantage of this method is that all three indicator values of the species have to be known. Species with the value ‘indifferent’ cannot be used either. Out of the approximately 1400 species occurring in the Netherlands, 988 species fulfil this criterion.

Validation

To validate the calibration of NTM, the mean Ellenberg indicator values for F, R and N of the calibration data set were calculated per relevé. These means served as input for NTM. The predicted potential biodiversity by NTM was then regressed on the calculated biodiversity of the relevés. The correlation coefficients were 0.65, 0.71 and 0.70 ($p < 0.001$) for the submodels forest, heathland and grassland, respectively.

After NTM was calibrated, a large data set consisting of 106,430 grassland relevés from the Netherlands became available. This data set was used to validate NTM’s grassland submodel. For each relevé the mean Ellenberg indicator values for F, R and N were calculated. These values were used as input for NTM. The predicted biodiversity values were compared with the actually calculated values using linear regression. The correlation between actually calculated biodiversity and the predictions was highly significant ($r = 0.5$, $p < 0.001$).

Application of NTM

Input

In general, the input for NTM has to be obtained from other models. For projections into the future only models can provide the necessary data, e.g., soil parameters. However, models are not always necessary as the input for NTM can also be derived from vegetation relevés. Per relevé the mean Ellenberg indicator values for F, R and N over its species can be calculated. The potential biodiversity of the relevés environment can then directly be estimated by NTM. Even a simple scenario analysis

is possible, for instance a raise of the groundwater level with one Ellenberg indicator unit for F. This type of analyses is particularly interesting when suitable abiotic models like the ones used here are not available.

For this study the models SMART2 (for the prediction of pH and nitrogen availability; Kros et al., 1995) and LGM (for groundwater level; Pastoors 1993) are used. The relation between the models is shown in Figure 2. SMART2 is a model that simulates soil processes. It derives its information from a soil map and deposition scenarios (de Vries et al., 1989; Kros, 2002). LGM predicts the water table on the basis of the topographical, the geological and the soil map, and includes the effects of hydrological scenarios. The predicted values of pH, N availability and groundwater level are translated into the corresponding Ellenberg units using transfer function derived elsewhere (Wamelink & van Dobben, 1996; Ertsen et al., 1998). The models mentioned above use a spatial grid of 250 by 250 m². They calculate single F, R and N values for each cell, which represent the most probable values for that cell. Consequently, the biodiversity predicted for each cell is a single value resulting from the F, R and N values assigned to that cell by the abiotic models.

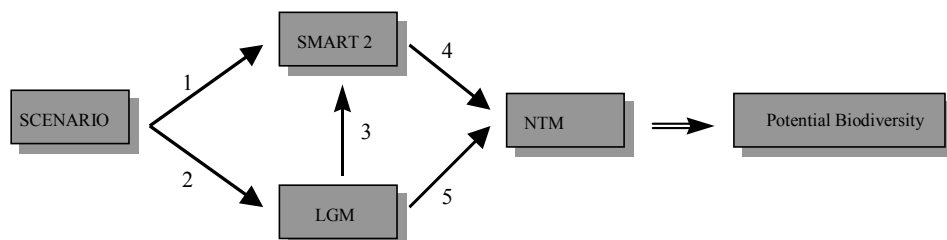


Figure 2. The relationship between the models LGM, SMART2 and NTM. The input for LGM and SMART 2 is water management (influencing groundwater level, for instance water extraction for drinking water or water level management in ditches and canals) and atmospheric deposition, respectively. Three scenarios are used for deposition, for water management there is only one scenario. Finally NTM predicts the potential biodiversity. The arrows represent data flow between models, with (1) deposition, (2) water management, (3) spring groundwater level, (4) nutrient availability and pH and (5) spring groundwater level.

In the present example predictions of potential biodiversity over the Netherlands are made for 1995 and 2020 for three scenarios, using the grid of 250 by 250 m². Predictions are confined to natural areas, which are defined as reserve areas (owned by the government or private organisations), and forests. As the application of NTM in its present form is restricted to the terrestrial environment, no predictions for water are made. The result is visualised on a 1 by 1 km² scale by taking the highest value per 1 km² grid cell of its 16 constituent 250 m cells. This implies that between different model runs, the final value assigned to a 1 km² cell may originate from different vegetation types or different subcells. The predicted potential biodiversity is presented

in three classes, low (value below 8.0), intermediate (value between 8.0 and 13.0) and high (value above 13.0).

Prediction for 1995

The predicted potential biodiversity for 1995 (the 'present' situation, used as a reference for comparison with predictions for 2020 based on scenarios) is shown in Figure 3 for the three types together. For 1995 a high potential biodiversity is predicted for the coastal area (dunes), in the western part of The Netherlands (clay and peat; land below sea level) and in several parts of the east (sand, mainly small-scale landscapes, where high and low biodiversities are mixed). Low potential biodiversity is predicted for large areas in the south (although high values are sometimes present), and in the middle of the Netherlands (for both the soil type is sand). Generally speaking, low values are found in areas with intensive human activities (both industrial and agricultural). On average, the highest values are predicted for the vegetation types heathland and grassland, while lower values are predicted for forests, especially on dry soils.

Predictions for 2020

For the prediction of the potential biodiversity in 2020 we used three scenarios which were used in a national survey conducted for the Dutch government in 1997 (RIVM, 1997). The three scenarios are concisely documented by Centraal Planbureau (1997). The three scenarios are labelled EC (European Co-ordination), DE (Divided Europe) and GC (Global Competition). All three scenarios are denoted as 'realistic', but the EC-scenario is assumed to have the highest probability under certain assumptions. In general, realistic scenarios have the advantage that the outcomes of the predictions are potentially a good representation of the future, however the disadvantage is that the differences between the scenarios in ecologically relevant parameters are small. In all three scenarios acid and nitrogen deposition decrease, but by different amounts. For the DE-scenario the decrease in deposition is largest. For this scenario it is assumed that there is little co-operation between national states. There is less money for nature conservation than at present, but on the other hand the agricultural production decreases. The distribution of land between agriculture and nature remains the same. The EC-scenario gives the best opportunities for natural areas. The world market grows and national policies are well co-ordinated. Government policies cause polluting farms to move away from vulnerable natural areas. The public attitude is environment-friendly. The GC-scenario gives the smallest decrease of the deposition. The market mechanism is dominant and national governments are not inclined to take measures to decrease atmospheric deposition. Growing agriculture activities claim more land and nature is confined to protected areas present before. The public attitude is materialistic.

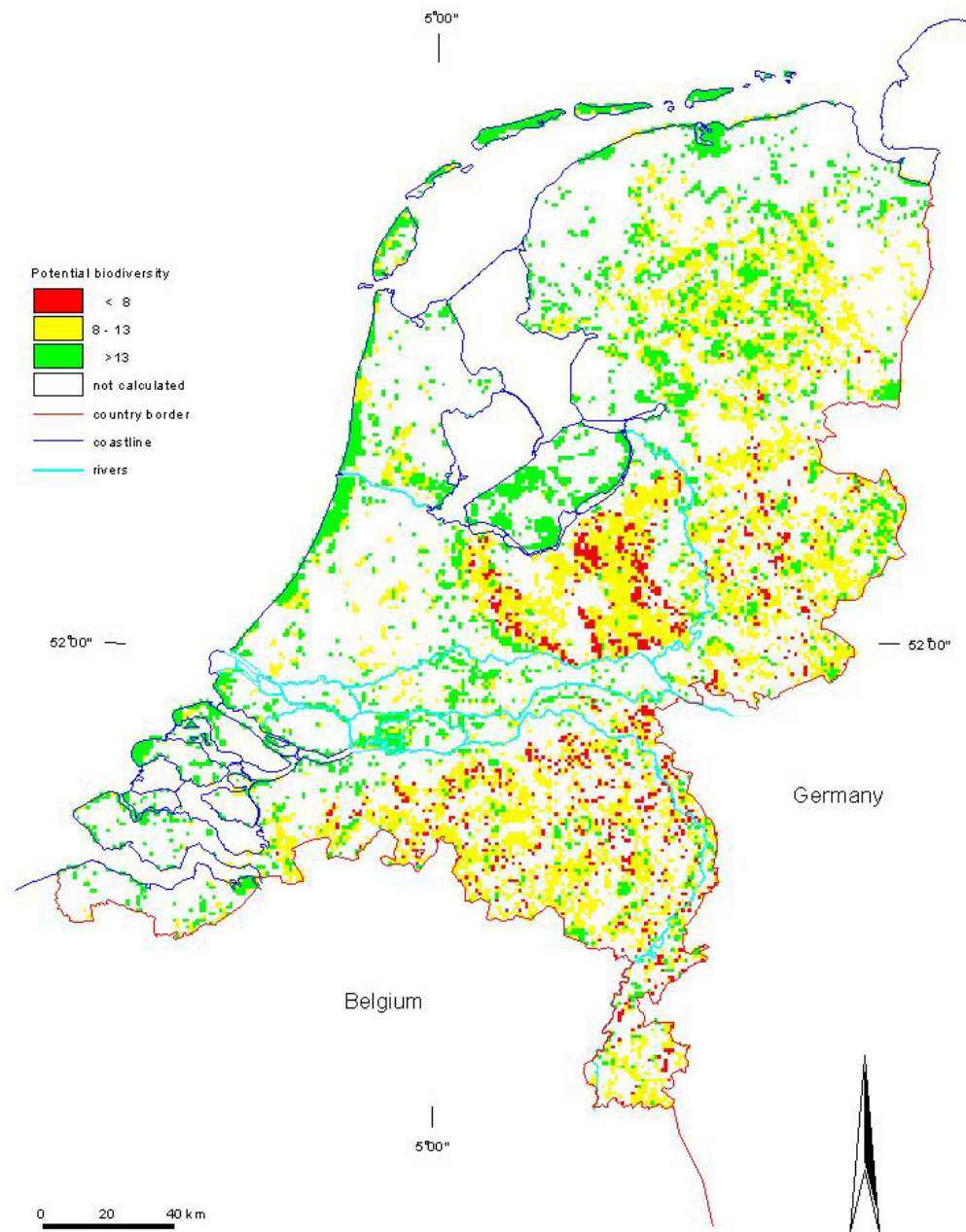


Figure 3. The potential biodiversity for 1995 for the vegetation types heathland, forest and grassland together. The highest potential biodiversity is shown for each km^2 cell. For explanation of the classes see table 3.

The scenarios only govern the atmospheric deposition. The moisture availability also changes over time (generally increasing), but is the same for the three scenarios. The scenario for moisture availability includes local measures to decrease the desiccation caused by agriculture and groundwater extraction.

The predictions for 2020 show that in all scenarios and all vegetation types the potential biodiversity for some grid cells increases whereas it decreases in other cells (Table 2). The mean value increases for all scenarios and all vegetation types. The DE-scenario shows the highest increase, the GC-scenario the lowest. Per vegetation type plant biodiversity increases for forest and grassland, but it decreases for heathland in all scenarios. Table 3 and Figures 4a – 4c show the predictions for the DE-, GC- and EC-scenario for the three vegetation types together. The predictions are rather similar for the three scenarios, and, although there is a general increasing trend in potential biodiversity, patches with increasing and decreasing values occur scattered over the country. For forest and grassland there is a tendency for plant biodiversity to move from the class intermediate to the class high, but for the GC-scenario also from intermediate to low. For heathland plant biodiversity tends to shift from intermediate to high as well as to low values (Table 3).

Table 2. Number of km^2 cells with increasing (+) or decreasing (-) predicted plant biodiversity in 2020, for the three vegetation types and three scenarios (EC= European Co-ordination, GC=Global Competition and DE=Divided Europe), for all types together ('total'), and the difference increasing minus decreasing ('net'), for three scenarios.

Vegetation type		EC	GC	DE
Heathland	+	1222	1185	1248
	-	284	321	258
Grassland	+	3261	3111	3435
	-	3840	3990	3666
Forest	+	4786	4444	5101
	-	2335	2677	2020
Total	+	9269	8740	9784
	-	6459	6988	5944
Net		2810	1752	3840

Figure 5 shows the difference in potential biodiversity between 1995 and 2020 for the EC-scenario. A higher potential biodiversity for 2020 is generally predicted in areas that have a low potential biodiversity in 1995. This is mainly caused by the reduction of the nitrogen deposition, but also by local measures to counteract desiccation. A combination of the two above-mentioned measures creates higher pH levels, which contribute to a higher potential biodiversity in 2020. In the west of the Netherlands, the most urbanised part with a lot of industrial activity, a lower potential biodiversity is predicted in many areas for all three scenarios (see figure 5 for the EC-

scenario). This is caused by a higher NO_x deposition by traffic and industry. For grassland, in the north and north-west a lower potential biodiversity is generally predicted. This is caused by the decrease in acid deposition, and a resulting increase in pH. The higher pH causes an increase of mineralisation of organic matter and hence, of the availability of nitrogen. Higher nitrogen availability generally causes a shift towards lower potential biodiversity. This effect is temporary, but to prevent loss of biodiversity, countermeasures to remove excess nitrogen (e.g. mowing and removing aboveground biomass) may be necessary. In the coastal area (dunes) the plant biodiversity also seems to decrease locally. This is caused by lower pH levels. This happens in stabilised dunes where acidification caused by leaching of calcium is not compensated as in dynamic dunes (Kooiman et al., 1998).

Table 3. Number of km² cells per plant biodiversity class (inter = intermediate potential biodiversity) in 1995 and 2020 per vegetation type and scenario (all scenarios are equal for 1995; EC= European Coordination, GC= Global Competition and DE=Divided Europe) . The minimum predicted value is 3.5, the maximum 19.0, the class low contains values below 8.0, the class intermediate between 8.0 and 13.0 and the class high above 13.0.

Type	year	Scenario	Number of cells		
			low	inter	high
Heathland	1995		10	1052	444
	2020	EC	0	1082	424
		GC	0	1095	411
		DE	0	1062	444
Grassland	1995		0	4904	2197
	2020	EC	0	4421	2680
		GC	0	4511	2590
		DE	0	4340	2761
Forest	1995		1683	3297	2141
	2020	EC	1680	2811	2630
		GC	1761	2759	2601
		DE	1570	2865	2686

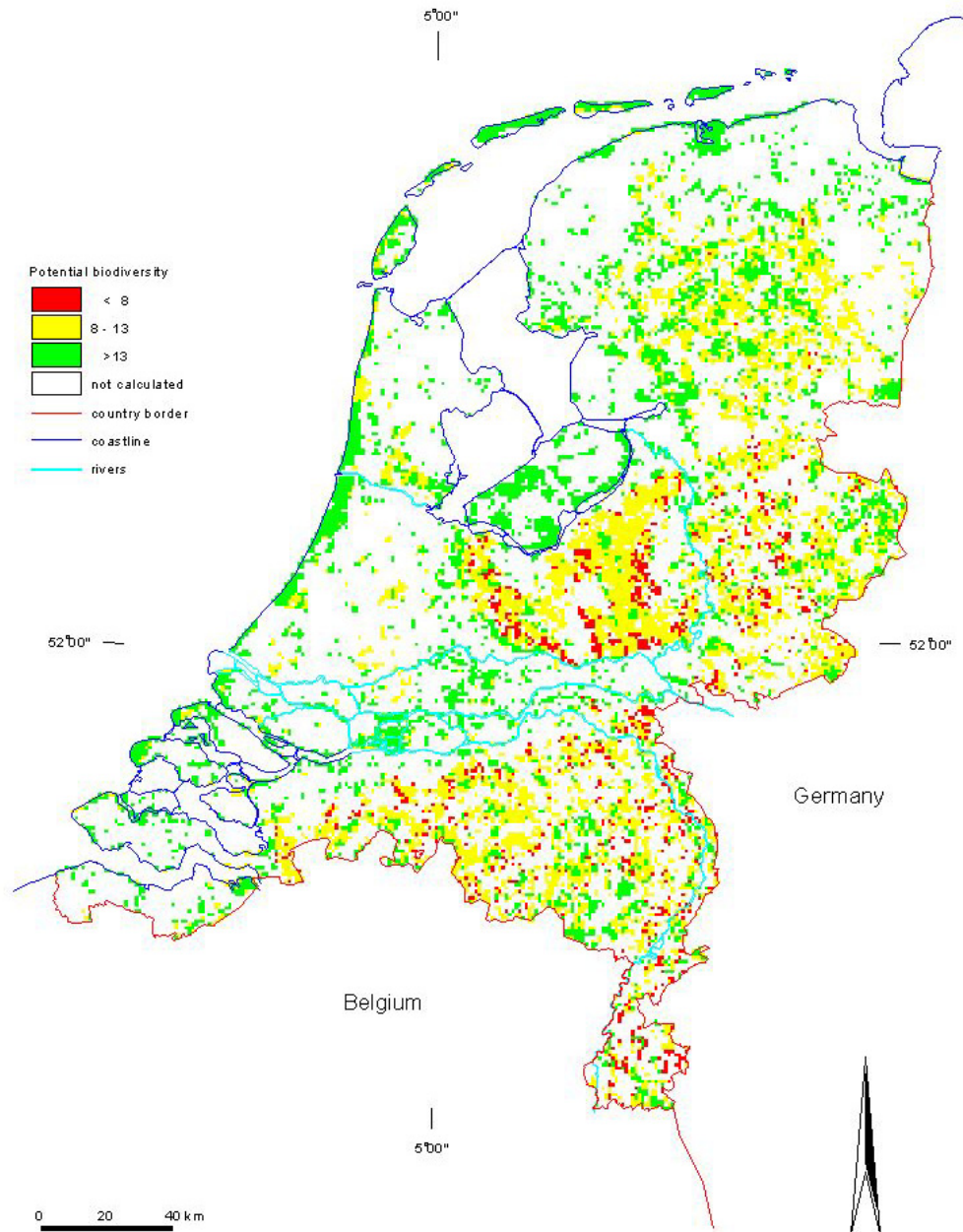


Figure 4a. The potential biodiversity in 2020 per km^2 cell, for the DE-scenario for the three vegetation types together. For explanation of the classes see table 3.

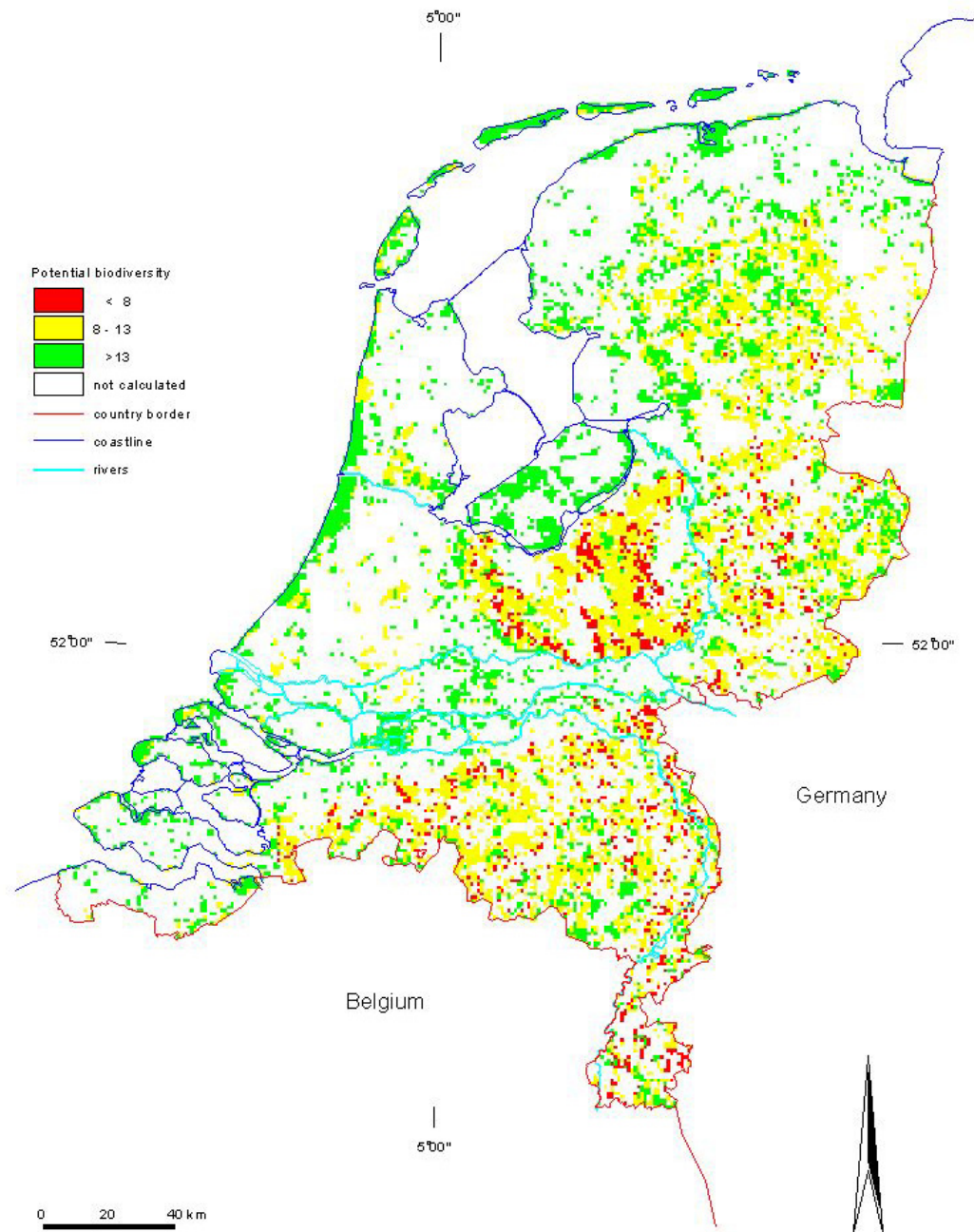


Figure 4b The potential biodiversity in 2020 per km^2 cell for the GC-scenario and for the three vegetation types together. For explanation of the classes see table 3.

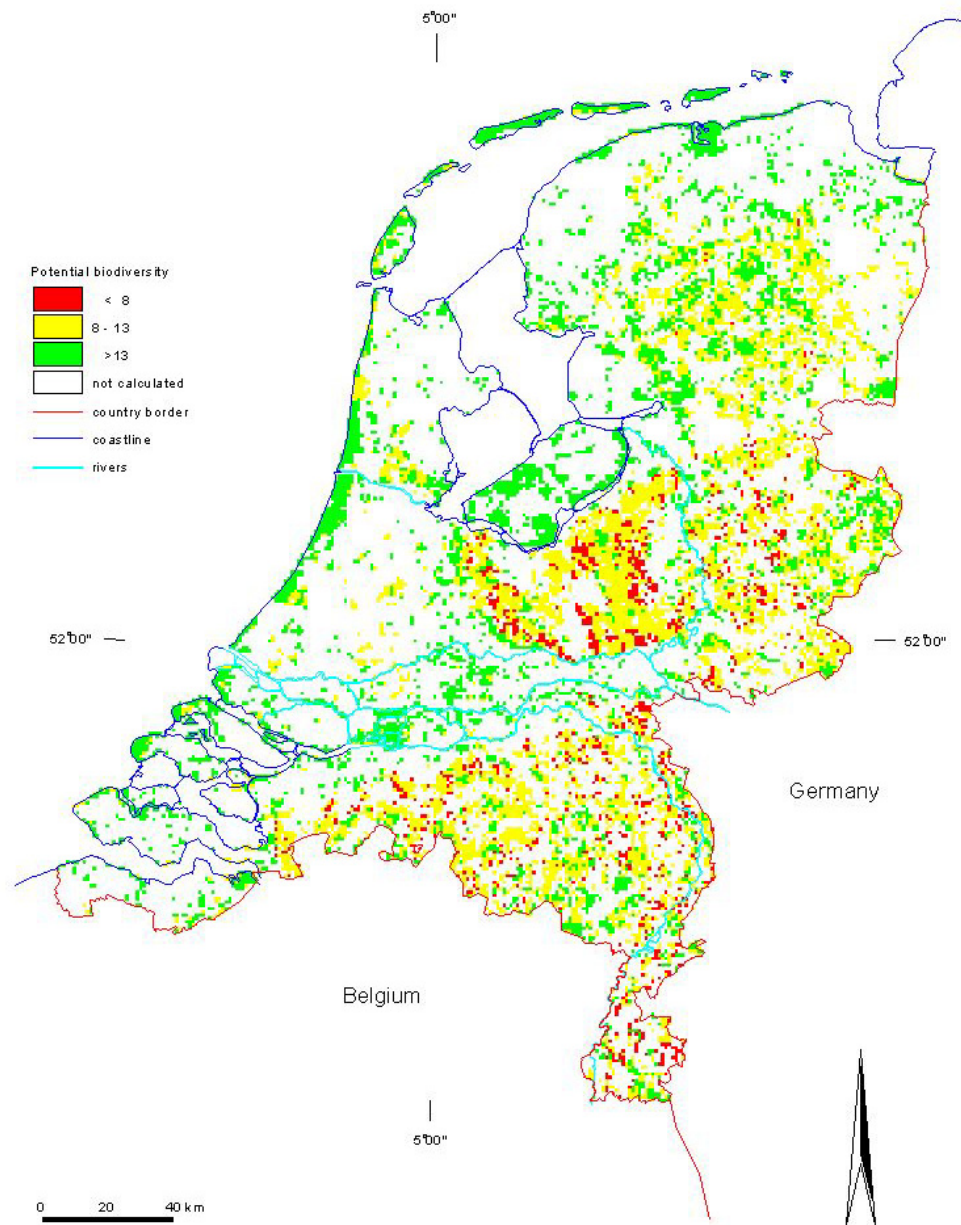


Figure 4c The potential biodiversity in 2020 per km^2 cell for the EC-scenario for the three vegetation types together. For explanation of the classes see table 3.

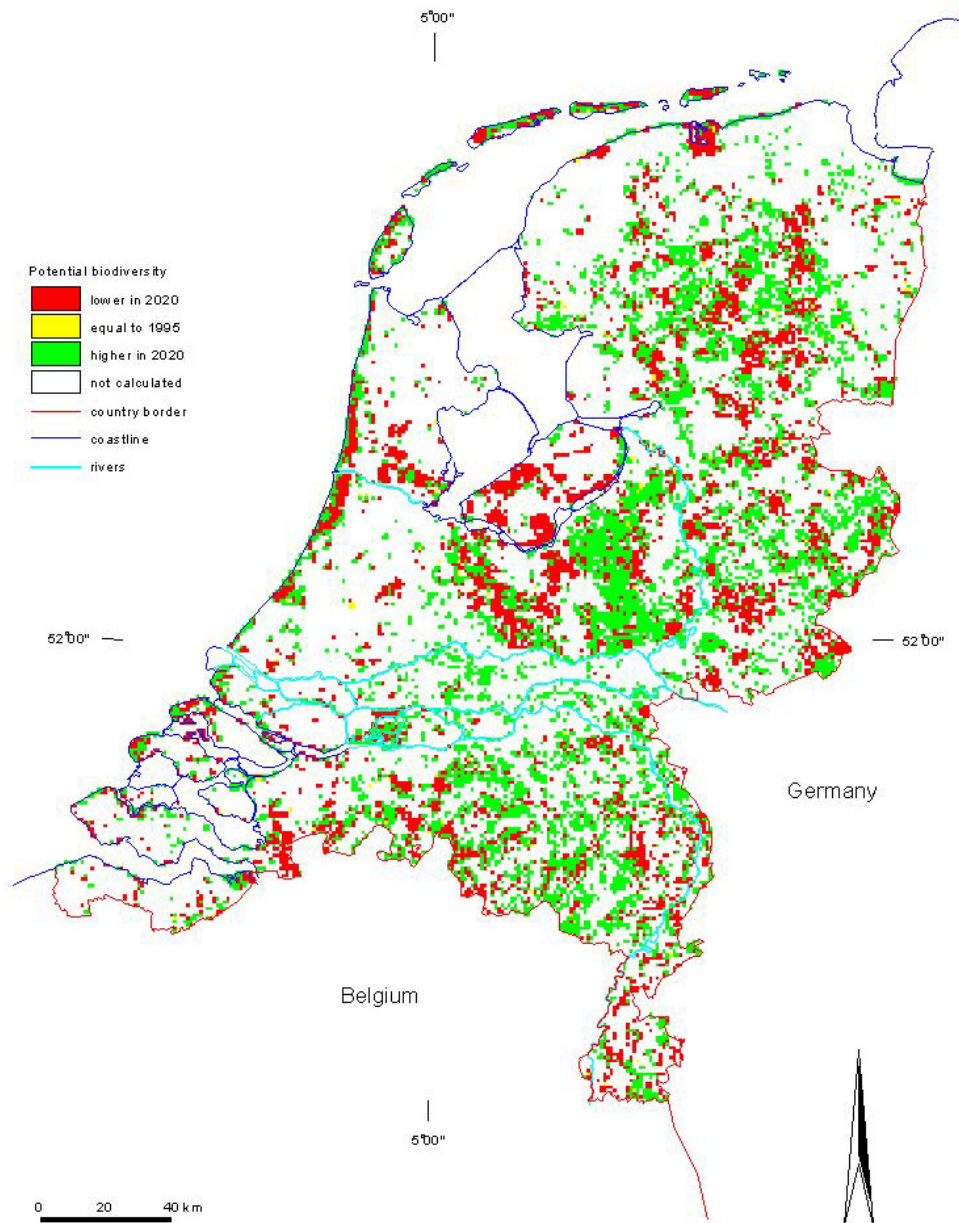


Figure 5. The predicted increase or decrease by NTM of potential biodiversity in 2020 compared to 1995 as the result of the EC-scenario in the Netherlands. Per km^2 cell the highest potential biodiversity in 2020 is compared with the highest potential biodiversity in 1995.

Discussion

This study shows the possibility of making geographically explicit projections of potential plant biodiversity into the future on a nation-wide scale by means of model calculations. When using such models as a tool for policy development the question of uncertainty is a crucial one. As in our case the uncertainty is not only caused by NTM but also by the other models used to calculate the input for NTM, the uncertainty generated by the complete model chain should be considered here.

The effects of using modelled instead of observed input on NTM's predictions and their uncertainty are discussed by Schouwenberg et al. (2000) and Jansen et al. (2000). These authors revealed that for a single point the largest uncertainty in a model chain consisting of SMART2 (Kros et al., 1995), SUMO (Wamelink et al., 2000) and NTM, is caused by NTM itself. This uncertainty mostly consists of the unexplained variance of the regression model due to factors that are not included in the model NTM, for instance the effects of the nearby vegetation, the presence of a seedbank, or dispersal (Geertsema, 2002). The unexplained system variance makes absolute predictions less reliable than comparative predictions (for instance scenarios). When predictions are compared in scenario analyses (as is done in this paper) this unexplained variation is cancelled out, because it works in the same direction, independent of scenarios. So the difference between two scenarios is much more reliable than an absolute prediction. Jansen et al. (2000) showed that for a specific case the variance in the biodiversity value is 2.83 for an absolute prediction, whereas for the difference between two scenarios this is 0.021. Unfortunately these values cannot be used for other model predictions, because they are specific for the case studied, but they can be used as an indicator of the reliability of the predictions of NTM (Jansen et al., 2000).

NTM is calibrated with a data set containing relevés only made in natural or semi-natural areas with low-intensity management. Therefore, the model can only be used in (semi)-natural areas, and not in intensively managed agricultural areas. Extension to these areas could be possible when sufficient data become available, including relevés made in agricultural areas. These could probably be used in a fourth sub-model.

A weak point of NTM in its present form is the use of Ellenberg indicator values. Although they are still widely used (e.g. Hawkes et al., 1997, van der Maarel, 1993, ter Braak et al., 1994, Hill and Carey, 1997), they are also widely discussed, both the values themselves and their validity in general (Thompson et al., 1993; Diekmann & Falkengren Grerup, 1998; Hill et al., 2000; Wamelink et al., 2002). The input for NTM is given as physical values (groundwater level, pH and nitrogen availability), which have to be translated into Ellenberg indicator values. Probably this is the step that introduces the greatest amount of uncertainty in the model chain (Schouwenberg et al., 2000). Wamelink et al. (2002) showed that each phytosociological class (after

Schaminée et al., 1989) needs its own translation of physical values into Ellenberg indicator values. By using three submodels, a part of the uncertainty in the translation is avoided. But to overcome this problem we should be able to use indicator values in physical units instead of Ellenberg indicator values, but these are presently not available on a sufficient scale.

For many grid cells an increase in potential biodiversity was found. This may seem strange in a nation where every inch is managed. However, as was argued before, certain types of management (and more specifically, those applied in natural areas) have a beneficial effect on biodiversity. Secondly, the present biodiversity is generally low, with many species decreasing or extinct. This is mainly caused by land use, lowering of the groundwater table, and deposition of acidifying and eutrophying compounds. Our scenarios assume an improvement of both water management and atmospheric deposition, which in turn is resulting in an slow but steady increase in potential plant biodiversity. It should be stressed that the scenarios used in this study are specific for the Netherlands, but may also be applicable in other Western European countries where the landscape is strongly under human influence. In countries where human influence is less predominant, the same scenarios might show a decrease of potential biodiversity.

In the estimation of conservancy value per species (van Dobben et al., in prep.), invasive species that become a pest, get a negative value. But species that are migrating in a natural way, for instance as a result of global warming, also would get a negative conservation value, because their trend in the countries where they arrive would be increasing. This is unwanted in the light of species conservation. This problem has to be solved before NTM can be used in studies where species are expected to migrate into the studied area.

By our knowledge NTM is the first model that connects floristic biodiversity with three soil factors that are both crucial for the vegetation, and under a strong anthropogenic influence. It is therefore more suitable to predict the complex effects of economic scenarios and resulting change in atmospheric deposition, on floristic biodiversity than models that base biodiversity on only one parameter (e.g. productivity, Whisheu & Keddy 1996, Naeem et al., 1996, Loreau 1998 & Hector et al., 1999; or disturbance, Angelstam, 1998 & Ali et al., 2000; or water availability, van Ek et al., 2000; or dead wood; Larsson, 2001). NTM links biodiversity indirectly with soil parameters and management. Compared to the model MOVE (Latour et al., 1993) NTM skips the problem of predicting probability of occurrence per species, thus avoiding the need for an extra translation step from individual species through vegetation types to potential biodiversity.

Although NTM is calibrated for the Dutch situation, the model is in principle suitable for other countries when a suitable calibration set can be found. Also, in situations where other abiotic parameters are important (e.g. temperature), these can

be incorporated in the model as extra predictors, or can replace the existing predictors.

Acknowledgements

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**Decreasing deposition will reduce costs for
nature management**



6 Decreasing deposition will reduce costs for nature management

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Abstract

In this paper we present a method to estimate the additional costs made by nature reserve managers to mitigate the effects of atmospheric deposition. Theoretically these extra costs may be saved when deposition levels drop. The costs were calculated per Nature Target Type (NTT) and management intensity for both the current (high) and reduced deposition levels. The resulting ecological quality was estimated in both cases. We calculated the difference in costs based on the management intensities required to maintain ecological quality at the current and reduced nitrogen deposition levels. For the NTTs within the clusters grassland, reed and rough land, and heathland we used dynamic simulation models. For forests and moorland pools we used expert knowledge to estimate the reduction in management costs due to a decrease in deposition. The total amount of money that may be saved because of the reduction of deposition rates is estimated on 42 million euro per year for the period from 2000 till 2020 for the assessed NTTs. The highest savings can be made in grasslands; 28 million euro. On average the savings were 80 €/ha/y, which ranged from 5 €/ha/y for forest to 299 €/ha/y for reed and rough land.

Introduction

Many natural areas in Europe are under pressure due to human activities. Among the most important pressures are land use change, climate change and the deposition of acidifying and nitrogenous compounds (Dale et al., 1994; Bobbink et al., 1998; Sala et al., 2000; Gaston et al., 2003; Hannah et al., 2002; Pielke et al., 2002; Hungate et al., 2003; Lindborg & Eriksson, 2004). In the Netherlands, where the deposition of both acidifying and nitrifying compounds was very high, measures were taken to prevent the release of these compounds at the source, and to counteract their effects in natural areas. The former measures are for instance the installation of filters in power plants, the latter are extra measures to undo or limit the effects of deposition on the vegetation, mainly by removing nutrients from the system. Both types of measures are costly. Where the measures at the source are focusing on reducing the amount of released acidifying and nitrogenous compounds, the measures in the field are mainly

focusing on preserving the still present biodiversity. Now that measures at the source begin to take effect (Kelly et al., 2002; Tarason et al., 2003), it is expected that the management measures in the field can be reduced in the near future. Therefore, savings on management measures can then be made. Whether or not this will actually happen is still uncertain (van Dobben et al., 2002b).

This study focuses on direct savings that can be achieved on the management of natural areas in the Netherlands. Reduction of deposition may also affect human health (Small & Kazimi, 1995; Williams, 2002), and therefore possibly the costs for health care, but this is not taken into account. Natural areas also have an economic and intrinsic value in themselves, but the influence of a reduced deposition on this is not incorporated in this study either (Wilson & Carpenter, 1999; Fromm, 2000; Macmillan et al., 2002).

The relation between atmospheric deposition and management costs on a nationwide basis for all types of natural vegetation has not yet been assessed. However, Carpenter et al. (1998) considered in a similar way the cost and benefit of the management of non-point pollution in lakes. Nuppenau (2002) modelled the relation between humans and nature in a broad sense; here we focus on the influence of deposition on the costs of nature management. For the Seychelles the costs of nature restoration by management were estimated (Henri et al., 2004) based on labour costs, planting costs, weeding costs, etc. Management costs to develop and maintain natural areas have been estimated for the cape floristic region in South Africa (Frazee et al., 2003) and for a grassland in Germany (Röder et al., 2002). Hampicke et al., (2004) investigated the costs and profits for several nature management scenarios for the cultivation of rye. The effects on the income of the farmer and his management regime to prevent atmospheric deposition were studied by Zebbartha et al., (1999). They showed that management practices at the source could be effective, but raise the costs for the farmer who has to implement measures to reduce nitrogen emission. Similar results were found by Cowella & Apsimon (1998). In this paper we will show that the management of nature areas in turn will be cheaper when emission reduction by farmers, cars, industry etcetera is achieved.

The aim of this study was to estimate the costs that can be saved on nature management when the deposition decreases. To this end we used a nation-wide application of a method we developed earlier (Wamelink et al., 2005). This study represents the first step towards the development of a new perspective on acidification policy, to provide the government with information on savings resulting from atmospheric deposition abatement.

Material and Methods

General approach

We used a nationwide but site-specific approach, i.e. calculations are made for 250*250m² grid squares where natural areas occur, using the local deposition, hydrology, and soil conditions. To account for the different vegetation types and management regimes we adopted the nature target types system (NTTs, Bal et al., 1995). To estimate the nationwide costs linked with deposition we selected 180 representative sites. We calculated the effect on the vegetation development of management measures that were specific for site conditions, using a constant deposition scenario as well as a gradually decreasing deposition scenario. The NTTs were afterwards clustered into five vegetation types: heathland, grassland, reed and rough land, forest, and moorland pools. The decreasing deposition was combined with decreasing management intensity: theoretically, the less deposition the less intense the management has to be to counteract the effects of the deposition. The constant deposition scenario was combined with the standard management for the NTTs (Table 1). The expected decrease in deposition was combined with the standard management and a decreasing management intensity for which the resulting protection level was calculated. The protection level of a site is defined as the percentage of plant species that may occur of the total number of species defined for a NTT (Wamelink et al., 2005). The Protection level of the NTTs for the constant deposition scenario was compared with the combination of the other deposition and varying management intensity scenarios. The effects of the scenarios on the NTTs were simulated using the models SMART2-SUMO2-MOVE3 (Latour et al., 1997; Kros et al., 1999; Wamelink et al., 2000; Kros, 2002) resulting in a protection level for each NTT.

The management costs were calculated for all scenarios using the model output. For the management scenario for the decreasing deposition that yielded the same protection level as the constant deposition scenario the difference in management costs was calculated. For forest and moorland pools this modelling approach cannot be applied (Wamelink et al., 2003; Wamelink et al., 2005). For these vegetation types we estimated the additional management costs based on subsidies paid by the Dutch government to nature managers to counteract the effects of the increased deposition. For forests and moorland pools we assumed that the extra management costs due to the excess deposition would decrease linearly with the decrease of the deposition until the critical load for the vegetation type is reached (Achermann and Bobbink, 2003; van Dobben et al., 2002a).

Table 1 *Management scenarios and costs for the vegetation clusters. Each NTT within the cluster has its own management scenario and variation in management intensity. The costs are linked to the scenarios and thus varying with management intensity. For labour and rented equipment costs see Table 2.*

Vegetation cluster	Management	Variation in management intensity	Costs/benefits included for	specification
Heathland	Turf stripping + removal of shrub and tree seedlings	Once every 20 - 60 years, depending on the NTT	Specially designed machines for large scale stripping (50%) ^{1,2} , labour, machinery	See Table 2
			Small scale stripping using an excavator (50%)	
			Composting the heather sods (90%)	Rate of 22 €/ton fresh weight
			Local use of sods in agriculture (10%)	Rate of 7.50 €/ton fresh weight
Grassland	Turf stripping + sheep grazing	For turf stripping see above. 0.1 till 0.5 sheep/ha	Transportation of sods	Distance 20 km for composting, 6 km for local use
			For stripping see above;	
			Herded grazing (30%)	Total net costs 0.52 €/grazing day ^{3,4}
			Fenced grazing (70%)	Total net costs 0.31 €/grazing day ^{3,4} plus 19.25 €/ha/y for fencing
	Grazing (young) cattle	0 till 0.5 cows/ha	Renting out land; only for dry and moist grass land. Proportion of land rented out depending on biomass production.	Benefit of 10 €/ ton eatable biomass ⁵
			Grazing Supervision	Benefits of 0.15 € /grazing day ^{3,6}
			Fencing	0.59 € /grazing day ^{6,7}
			Renting out land. See above	27.23 € /ha ⁶
	Mowing	Once a year till once every four years	See above ⁵	
			Harvesting grass, using regular equipment for dry grassland, using special equipment for wet grassland and using both methods for 50% in moist grassland.	See Table 2
			Disposal of harvested grass, for dry grassland for agricultural use (100%), for moist grassland for composting (50%) and agricultural use (50%), wet grassland for composting (100%)	Benefits of 10 €/ton dry weight for agricultural use, Costs 32.65 €/ton fresh weight for composting

Vegetation cluster	Management	Variation in management intensity	Decreasing deposition will reduce costs for nature management	
			Costs/benefits included for	specification
Reed and Rough land			Transport	Distance 2 km for agricultural use, 20 km for composting
	Mowing and grazing	Mowing once a year and 0.2 cow/ha till mowing once every two years and no grazing	For mowing and grazing see above	
	Mowing	Once a year till once every four years	Mowing once a year or less using special equipment and composting (60%) or using a single axis tractor and burning or piling in the field (40%) ⁸	See Table 2
Forest			Transportation of vegetation	Transport distance 20 km ⁸
	Addition of lime/nutrient	Once every 20 years till not	Composting	Costs 40.50 €/ton fresh weight ⁸
	Selective thinning	30% of the forest surface over the period 2000 – 2020, till no selective thinning	Applied on 20% of the forest surface every 20 years	Costs of 335 € per time ^{9,10,11}
	Transformation		– Costs for subsidised tree selection	Costs of 85 € /ha ²
Moorland pools			Replanting	Costs of 3000 €/ha ²
	Clear cutting	Once every 50 years till once every 100 years	Applied for 0.1% of the forest surface over the period 2000 – 2020	
	Dredging and catchment liming	Once every 20 years till not	A frequency of once every 100 years for depositions below the critical load and once every 50 year for depositions above the critical load; applied to 1% of the forest surface on sandy soils Disposal of organic matter by turf stripping (see turf stripping) Applied for 27% of the pools, once every 20 years for the present deposition (year 2000), when the deposition is below the critical load this management is not longer necessary	Time consumption of 11 days/ha ¹² and labour and equipment costs as in Table 2 Removal of 600 ton/ha ¹² Costs of 30,000 €/ha. ¹³

* Costs that are not influenced by the decrease of nitrogen deposition are never included, i.e. hydrological measures, recreation, wild life management etc.

¹ Pers. comm. State forest service, ² Pers. comm. Unie van Bosgroepen, ³ Vink & Wolbers (1997), ⁴ Elbersen et al., (2003), ⁵ Pers. comm. nature managers, ⁶ Van Haperen (1997), ⁷ Anonymous (1983), ⁸ De Jong et al., (2003), ⁹ Heij & Schneider (1991), ¹⁰ Kreutzer (1995), ¹¹ Tamm et al., (1999), ¹² Klap & Schmidt (1995), ¹³ Arts et al., (2002).

Nature target types

In the Netherlands 132 so-called nature target types (NTTs) have been defined for policy and management purposes (Bal et al., 1995). The NTTs are based on plant species communities and may consist of several related vegetation types (associations in the sense of Braun-Blanquet, 1964). Each NTT consists of target species, i.e. species which may ‘naturally’ occur in the defined habitat. Based on inventories for the whole of The Netherlands every distinguishable natural area was assigned to a NTT. We assumed that this inventory was complete and that all NTTs were actually present. Calculations were made for all NTTs which are influenced by atmospheric deposition and for which management measures can be carried out to reduce the effects of excessive deposition. This excludes non-managed NTTs, even though effects of atmospheric deposition may be present, such as parts of the coastal dunes. Fertilised NTTs, such as grasslands with an agricultural main function and commercially managed reedlands are also excluded, as were freshwater and marine ecosystems (but moorland pools were included). This resulted in 27 NTTs that matched the above criteria.

The number of sites was based on a pilot study where we investigated if the variance of the costs was depending on its mean and how we could minimize the variance of the calculations. This resulted in a minimum sample size of three sites per NTT, even for the NTT that cover only a small area. We assumed proportionality between the variance and the mean for optimal allocation (Cochran, 1977). The sample size for the NTTs with higher surface areas is based on its area and the a priori estimated management costs (de Jong et al., 2004). This resulted in a optimal number of sites of 180. To estimate the effects of deposition on the management costs we randomly selected the 180 sites, with known NTT, for the 27 NTTs.

The NTTs included in this study are clustered into five major vegetation types for practical reasons and because they are assumed to have the same management, namely:

1. Heathland
2. Grassland
3. Reed and rough land
4. Forest
5. Moorland pools

The first three clusters are evaluated using the ‘Nature Planner’ approach. Our earlier study (Wamelink et al., 2005) showed that model simulations could not be used for forest, because the nitrogen availability and therefore the costs for biomass removal were not influenced by management. The models are not suited to simulate the effects of management in moorland pools either. For these two vegetation types we used a static method to estimate the management costs due to deposition.

Models

We applied the “Nature Planner” set of modelling instruments (Latour et al., 1997), an interface including several models, to simulate the effects of deposition on the NTTs (Fig 1). We used three models, SMART2, SUMO2 and MOVE3 of the Nature Planner, which are briefly described here. For more detailed information, see Kros et al., (1999) and Kros (2002) for SMART2, Van Dobben et al. (2002b) and Wamelink et al. (2000) for SUMO2 and Latour et al. (1997) for MOVE3.

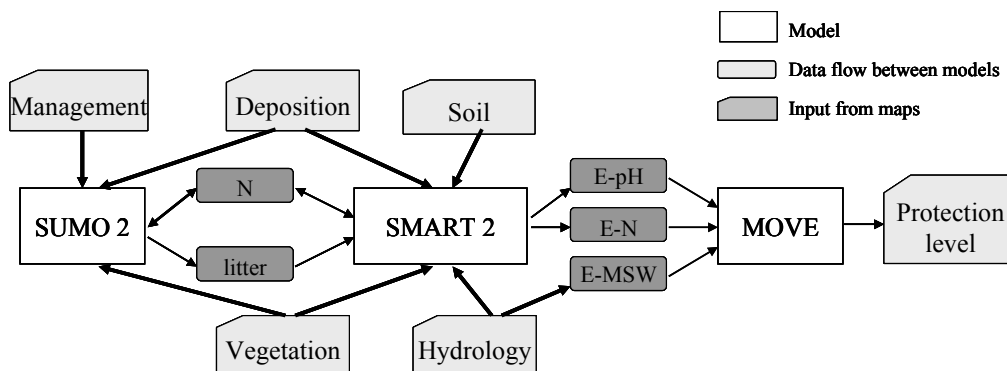


Figure 1. Flow chart of the models SMART2, SUMO2 and MOVE including their main input. With N: nitrogen, E-pH: translation of acidity into the Ellenberg indicator value for acidity, E-N: translation of nitrogen availability into the Ellenberg indicator value for nutrient availability and E-MSL: translation of the mean spring groundwater table into the Ellenberg indicator value for moisture.

The SMART2 model simulates processes in the litter and the uppermost mineral layers. It consists of a complete nutrient cycle, including nitrogen and base cation cycles. The simulated nitrogen availability and soil acidity (pH) values are input for the model MOVE3.

The SUMO2 model is integrated in the SMART2 model and simulates the nutrient cycle in the vegetation. It uses factors like nitrogen availability (from SMART2) and light availability to simulate biomass development for five ‘functional plant types’: grasses and herbs, dwarf shrubs, shrubs and two different tree species. The simulated biomass increment is affected by management (mowing, grazing, sod cutting and forest management at various levels of intensity). Management removes biomass from the system, and hence nitrogen (and in the case of sod-cutting also acid). Both SMART2 and SUMO2 are dynamic process models that produce site-specific output.

The MOVE3 model is based on response curves for individual plant species. The response values, expressed as the likelihood of a particular plant species to occur at a given combination of abiotic factors, are based on Ellenberg’s indicator values

(Ellenberg et al., 1991) for moisture (F), acidity (R) and nutrient availability (N). Based on the likelihood of individual plant species, MOVE3 also calculates the likelihood of particular NTTs to occur. The number of species that can occur is expressed as a percentage of the total number of species defined for the particular NTT. This percentage is denoted as the protection level of a NTT, and is used as an indicator for the ecological quality of each NTT.

SMART2, SUMO2 and MOVE3 each require their specific inputs; the most important of these are described below. The input for SMART2 consists of a map that provides data on soil type, water table and the quantity and quality of seepage. SMART2 also needs data on acidifying and nitrogenous deposition, which are site- and year-specific. The soil map is derived from the national soil-mapping project (Kros et al., 1995; Kros et al., 1999) and the deposition map from Beck et al. (2004). The ground water table is used to calculate the mean spring groundwater level (MSL), which is used by SMART2, SUMO2 and MOVE3. During the simulated period the groundwater levels are constant over time, but site-specific.

The input map for SUMO2 consists of the vegetation type and the type and intensity of management. The type and intensity of management were varied for the NTTs assessed (see Table 1). Management includes mowing, grazing, turf stripping or forest management, as appropriate for each NTT. The main input for MOVE3 is the output of SMART2-SUMO2, that is, nitrogen availability, pH and spring groundwater level. Regression equations are used to convert these values into the Ellenberg indicator values for F, R and N respectively (Ertsen et al., 1998; Wamelink et al., 2002).

Scenarios

Two types of scenarios are used for the modelling. The first concerns the deposition, the second the management. We used two deposition scenarios for the models. The first represents the deposition in the year 2000 and remain constant during the modelled time period (from 2000 – 2020). The deposition is site specific and thus varies considerably between the 180 selected sites. The deposition is also vegetation type specific, for instance forests catch more deposition than grasslands due to their larger roughness (van Jaarsveld, 1995). This scenario combined with the standard management is used as a reference for the second deposition scenario and management scenarios.

The second deposition scenario is based on the EU directive on emissions for The Netherlands (EU, 2001). The scenario consist of a linear reduction of the deposition from 2000 until 2010 and a constant deposition afterwards (up till 2020; Beck et al., 2004). An example of the two deposition scenarios for two different sites can be found in Figure 2. On average the nitrogen deposition decreases from 2312 mol/ha/y in 2000 to 1304 mol/ha/y in 2010. For forest and moorland pools deviating deposition scenarios were used; the deposition for the year 2000 is the

country-wide average, this remains either constant, or decreases linearly until 2010 and stays constant afterwards.

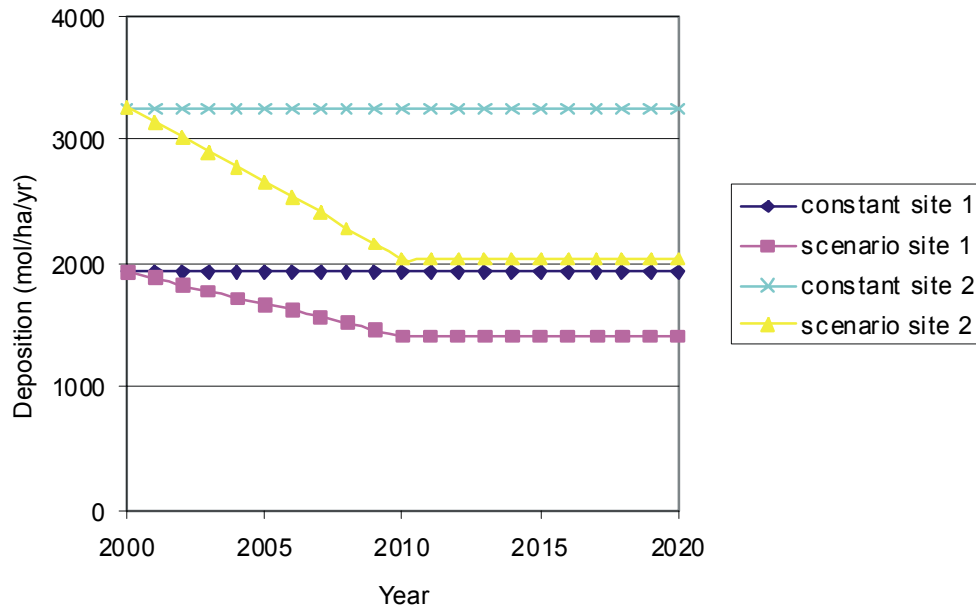


Figure 2. Deposition scenarios for two sites in The Netherlands.

In total there are four different management intensity scenarios for each management type, one of them (the most intensive) being the present management. Each NTT has its own management that consists of different (combinations of) measures (Table 1). The management intensities per NTT for the current deposition scenario are based on the present management. The constant deposition scenario is only combined with the present management intensity (reference). For the decreasing deposition scenario, four different management intensities (one of which is the present management) were simulated for each NTT and location. The mowing frequency was varied from once every year to once every four years, grazing intensity was varied from no grazing to a maximum of 0,5 cows per ha and from 0,1 to 0,5 sheep per ha, and the sod cutting frequency was varied from once every 20 years to once every 60 years (Table 1).

Estimation of costs

The costs for the management scenarios are mainly based on time standards and standard rates (Staatsbosbeheer, 2000a; IMAG DLO, 2001). Time standards are based on field measurements and include allowances for ancillary tasks such as moving from one site to another, personal care, tool maintenance, short breaks and short deliberations (Tables 1 and 2). The standard rates are based on standardised methods for the calculation of machinery and labour costs (Staatsbosbeheer, 2000a; de Jong et al, 2003). The rates for machinery include costs for depreciation, interest, fuel,

maintenance, insurance, and garage. The labour costs include salaries, wages, contributions, allowances and overhead costs.

Table 2. *Labour costs and equipment costs. All costs include 20% overhead.*

	Costs (€/h)
Labour	29.39
Hand tools	0.31
Tractor 70 kW	16.17
Tractor 85 kW	19.85
Single axis tractor	11.24
Rotary mower	3.43
Hay tedder	3.56
Forage harvesters	15.67
Truck with loader	29.74
Excavator	16.80
Chain saw	5.31
Regular sod cutting machine	93.60
Small sod cutting machine	25.30
Dumper	9.30

Costs are only calculated for measures that vary according to the deposition level, e.g. sod cutting, mowing or grazing. These variable costs are based on the intensity of measures simulated in SMART2-SUMO2, and on results of these measures such as the amount of biomass removed and the grazing density. Fixed costs, i.e. costs which do not depend on the level of management or the level of atmospheric deposition are excluded from the calculations. These include: costs of measures not implemented for the direct aim of vegetation development, costs of peripheral management, monitoring and general management planning, hydrological measures, costs for infrastructure and levies and property related taxes. The costs calculations are based on the price level of 2004. For the simulations (2000 to 2020) costs are corrected for 2% inflation per year.

Comparison of protection levels and costs

The model simulations for the current deposition level, combined with the current management scenario, result in a protection level per NTT and location. The protection levels of the different locations per NTT are averaged to calculate the mean protection level per NTT, which is used as the reference. The four management scenarios combined with the decreasing deposition scenario result in four different protection levels. The protection levels of the different locations are averaged to calculate the protection level of each NTT for each of the four management scenarios

as described above. From these four different protection levels per NTT, the mean protection level which equals the protection level under the current deposition and management is derived by interpolation. The management intensity (and management costs) required to maintain the current protection level at a lower deposition rate can then be estimated.

When comparing the four different management scenarios at decreased deposition levels per NTT, three situations may occur:

1. The protection level at a reduced deposition level is lower than the reference protection level for some management intensities and higher for others (situation 1);
2. The protection level at a reduced deposition level is lower than the reference protection level for all management intensities (situation 2);
3. The protection level at a reduced deposition level is higher than the reference protection level for all management intensities (situation 3).

In the first case the management intensity that leads to a protection level equal to the reference level was derived by interpolation. In the second case the scenario that leads to the highest protection level was used for the calculation of management costs at the decreased deposition level for this NTT. Here we accepted a lower protection level for the reduced deposition level compared to the current deposition level, while costs are reduced. In the third situation, the scenario with the lowest management intensity was used for the calculation of the costs. This leads to a higher protection level for the reduced deposition level compared to the current deposition level, while costs are reduced.

Results

The simulated deposition reduction led to an increase of the protection level in 2020 in 60% of the evaluated area at constant management intensity (Tables 3 and 4). This means that for decreasing deposition the management intensity could be reduced, while maintaining or exceeding the protection level at the current deposition. For several NTTs higher protection levels are predicted even at the lowest management intensity.

For 6% of the area the protection level for the decreased deposition level and reduced management intensity was equal to the protection level at the current deposition level. However, for 34% of the area the protection level for the decreased deposition level for all management intensities was lower than the protection level at the current deposition level (Table 4). So even with the same management intensity the protection level dropped. Apparently, the drop in nitrogen deposition level has a negative influence on the protection level. However, 29 percent point of this 34% reached a protection level that was just 2 percent point below the protection level at the current deposition and can be regarded as equal to the current deposition level and

thus of no real consequence. The remaining 5 percent point reached a slightly lower protection level, but not lower than 4 percent point below the protection level at the current deposition level.

Table 3. *Average protection level per NTT (over the sites per NTT) in 2020, for the current deposition level scenario and management intensity (current) and the reduced deposition level scenario with a less intensive management (reduced). In the last row the area weighted average for both combinations of deposition level and management intensity are given.*

NTT	Description	Area (ha)	Current (%)	Reduced (%)
Hl-3.4	Dry grassland on loess soils	545	6.0	11.0
Hl-3.5	Dry grassland on loess soils	392	17.7	17.7
Hl-3.6	Dry grassland on loess soils	2,543	26.3	40.0
Hz-3.3	Reed and rough land on sandy soils	6,336	20.3	27.8
Hz-3.5	Dry grassland on sandy soils	9,975	17.3	17.3
Hz-3.6	Dry flower rich grassland on sandy soils	23,130	6.6	32.7
Hz-3.7	Nutrient poor moist grassland on sandy soils	24,173	4.9	12.1
Hz-3.9	Dry heath and open sand on sandy soils	28,744	46.8	45.9
Hz-3.10	Moist heathland on sandy soils	16,850	11.5	10.3
Ri-3.3	Reed and rough land on river clays	4,504	37.0	44.0
Ri-3.4	Wet grassland on river clays	9,290	2.4	12.6
Ri-3.5	Dry grassland on river clays	7,479	0.7	7.7
Lv-3.3	Reed and rough land on peat	8,648	11.6	25.2
Lv-3.4	Wet grassland on peat	12,295	10.4	19.8
Lv-3.5	Dry grassland on peat	15,617	17.5	37.3
Zk-3.4	Reed and rough land on sea clays	6,424	34.3	40.0
Zk-3.5	Wet grassland on sea clays	4,571	43.9	52.3
Zk-3.6	Dry grassland on sea clays	15,314	46.2	45.5
Du-3.4	Reed and rough land in the dunes	215	23.0	27.7
Du-3.5	Wet grassland in the dunes	821	51.0	51.0
Du-3.6	Dry flower rich grassland in the dunes	1,238	73.3	72.0
Du-3.7	Dry grassland in the dunes	9,460	33.5	31.3
Du-3.8	Dry heath and open sand in the dunes	530	66.3	62.3
Du-3.9	Moist grassland in the dunes	1,113	17.7	17.7
Az-3.4	Reed and rough land on former sea inlets	911	30.7	28.3
Az-3.5	Dry grassland on former sea inlets	904	38.7	42.0
Weighted average protection level			21.4	28.8

The protection levels of both grasslands and reed and rough land increased in most cases (Table 3). The protection levels of grasslands and reed and rough land in the coastal regions decreased in most cases, for three types of grassland only an equal protection level could be reached. The protection levels of both dry and wet heathland types remained more or less constant. The weighted average protection level for the current deposition levels is 21.4 while for the decreased deposition level the weighted

average protection level is 28.8 (Table 3). This means that the protection levels increased for decreased deposition levels compared to the current deposition levels, even though a less intensive management is used.

Table 4. *Effect of reduction of deposition level and management intensity on the protection level of NTTs.*

Difference in protection level	Area (ha)	Portion (%)
Higher protection level	130,019	60
Equal protection level	11,188	6
Lower protection level, with a maximum difference of 2 percent point	62,146	29
Lower protection level, with a difference of larger than 2 percent point	10,901	5

In total 42 m€/y can be saved on management costs when the deposition decreases according the used scenario for the whole of The Netherlands while achieving a higher protection level (Table 5). This is on average over all the vegetation types 80 €/ha/y. The results show that there is a large variation between the vegetation clusters in the costs that can be saved nation-wide as well as per hectare. Nationwide the largest savings are reached for grassland and the lowest for forest. Per hectare the savings are largest for reed and rough land while also moorland gives slightly higher savings per hectare than grassland. Again forest gives the lowest savings per hectare.

By varying the costs involved in nature management by taking the highest and the lowest price assumptions for all the individual costs that are made we gained insight in the uncertainty of the total savings (Table 5). The uncertainty is quite large for grassland and moorland pools (over 50%), while for forest the uncertainty is almost negligible. However, the uncertainty in the total savings is quite large because grasslands make up a large part also. Nevertheless it is clear that a significant amount of money can be saved when a reduction of deposition can be achieved.

Table 5. *Differences in costs for nature management for the current and the decreased deposition level and management level (averaged over the period 2000 – 2020). Lowest and highest cost scenarios are given between brackets by varying the costs for labour etc. between highest and lowest estimation of the costs.*

Cluster	costs at current deposition level m€/y		costs at decreased deposition level m€/y		Difference in costs m€/y		Difference in costs per ha €/y/ha
Heathland	27.3	(11.2-47.8)	23.7	(9.7-41.4)	3.6	(1.5-6.4)	78
Grassland	45.2	(24.3-70.8)	17.2	(8.5-27.8)	28.0	(15.8-43.0)	197
Reed and rough land	21.2	(16.7-27.2)	13.1	(10.4-16.7)	8.1	(6.3-10.5)	299
Forest	2.1	(1.9-2.4)	0.6	(0.5-0.7)	1.6	(1.5-1.7)	5
Moorland	1.5	(0.8-2.4)	0.9	(0.5-1.4)	0.6	(0.3-1.0)	200
Total	97.3	(54.9-150.5)	55.3	(29.5-88.0)	41.9	(25.4-62.5)	80

Discussion

This study shows clearly that the reduction of deposition not only costs money, for instance for farmers (Cowell and Apsimon, 1998; Zebbartha et al., 1999), but also will save money. The savings on nature management alone are estimated on 42 m€/y for The Netherlands. In 1989 the Dutch government started a programme to mitigate the negative effects of acidification and eutrophication on nature. The total amount of money spent in this programme in the period 1989-1999 was estimated at 33 million euros. In 2004 The Dutch government and the major non-governmental nature conservation organisation spent approximately 160 – 190 m€/y on nature conservation. This indicates that the possible savings due to lower deposition rates can give a significant cost reduction on nature management in the future. However, these savings can only be achieved when the deposition rates decrease. Moreover, in the first years the savings will be lower, since the deposition rates will decrease gradually and the still present excess nitrogen will have to be removed before nature values will increase (van Dobben et al., 2002b).

The restoration costs of the forests on the Seychelles estimated by Henri et al., (2004) ranged from 400 to 2700 \$/ha. The estimated costs in our study to counteract the effects of deposition in forests is much lower, only 5 €/ha. This is of course largely determined by the present state of the forests. On the Seychelles this state is much farther removed from the target and much more effort has to be put into the restoration. However, both studies used the same approach by setting targets for nature development and calculating the costs necessary to meet that target. Where our study only focuses on the atmospheric deposition, the research for the Seychelles takes all necessary management into account, thus also arriving at higher costs per hectare. The costs we estimated for the management of the natural grassland areas are of the same magnitude as the estimates by Röder et al. (2002) and Hampicke et al. (2004) for a meadow in Germany; we estimated the costs on approximately 318 €/ha/y, while they estimated it on 450 to 875 €/ha/y (depending on the management). Our estimate should be lower than theirs, because we only took the costs into account which can be saved when the deposition drops, while they estimated all costs.

To gain insight in the effect of the assumptions a sensitivity analysis was carried out on the management costs. It revealed that most changes in the assumptions only lead to a small difference in the results of this study. However, some of the assumptions have a relatively large effect on the results. An increase of dry matter content of harvested grass to 30% (from 25%) results in a decrease of the overall savings of € 4.5 m/yr (on average over 2000 - 2020), which is a difference of more than 10%. Other important factors are the portion of organic matter from wet grasslands that is composted, the benefits from hay and renting out land, and the

portion of heather sods that can be used on agricultural land (and thus does not have to be composted).

For quite a large part of the area (34%) the protection level for the decreased deposition level was lower than the protection level at the current deposition level, although the major part (29 percent point of this 34%) had protection levels just 2% below the protection level at the current deposition, and can be regarded as within the uncertainty limits of the calculated protection level. This is an unexpected result, because we would expect that with decreasing deposition the protection levels would increase or at least remain constant. We have identified three mean reasons for this unexpected result:

- 1) For technical reasons we used an older version of the NTT system. New NTTs are available at the moment, where more attention was paid to the internal coherence of the species per NTT and the relation of the species with the abiotic conditions. Since we think that one of the problems is that the old NTTs are situated on soils with unsuitable abiotic conditions, using new NTTs may solve part of the problem.
- 2) Although improved, the translation from physical units (output from SMART2-SUMO2) into Ellenberg indicator values still has a large contribution to the uncertainty (Wamelink et al., 2002), especially for nitrogen availability into Ellenberg N. Together with the uncertainty in the occurrence of plant species at low N Ellenberg indicator values this results in the drop of the protection level of several NTTs at low N availabilities.
- 3) The NTTs consist of several vegetation types which gives diversity within the NTTs. This may result in more than one optimum for the percentage species protected for nitrogen availability in the soil.

In this research we included only a part of the Dutch nature (Table 6). Important groups that were left out are:

- All natural and semi-natural NTTs (where no management is put into effect).
- All waters.
- Multifunctional nature except some of the forests (multifunctional NTTs, mainly grasslands, are often fertilised and therefore not taken into account).

Roughly one third of all nature in the Netherlands is taken into account. This does not mean that NTTs which are not taken into account will not benefit from a decreasing deposition, most likely the natural and semi-natural NTTs will. Since no direct (management) costs are made in these areas to mitigate the effects of deposition, it is unclear if there will be a financial gain as well. It should be noted that only the effect of reduced deposition and management on plant species and vegetation types is investigated in this study. The effects on for instance insects, bacteria, fungi or birds were not taken into account, but we expect that they will be affected positively as well.

Table 6. Surface area of natural areas in the Netherlands. Only a part of them was included in the study.

vegetation group	included	Surface (* 1000ha)
Grassland	yes	142
Heathland	yes	46
Reed and rough land	yes	27
Moorland pools	yes	3
Forest	yes	305
Grassland and heathland not on NTT map	no	8
Multifunctional 'nature'	no	66
Natural areas	no	267
Semi-natural areas	no	186
Water	no	497
Total		1547

We have assumed that nature management is the tool to counteract the effects of high deposition. Besides, there is the possibility to take measures at the source. However, nature management can not solve all problems. For instance when grasslands are mown more than once a year, more nitrogen is taken out of the system, but this may lead to loss of species that do not tolerate intensive mowing. The opposite may also occur, mowing once every four years may be possible when the deposition decreases (yielding the highest savings), but that frequency may be too low; consequently species will disappear and succession to rough land may take place. Another well known problem is sod cutting. To maintain the heath, turf stripping once every 20 years is necessary at the moment. For some species the time to return after sod cutting is longer than that period and species will be lost due to high management intensity.

The hydrology within the nature target types is regarded constant within this study. It is commonly assumed that there is a close relationship between changes in availability of nitrogen and acid and hydrology. It is recommended to do further research on the relationship between reduction of deposition, protection level, costs of management and hydrology.

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Effect of nitrogen deposition reduction on biodiversity and carbon sequestration



7 Effect of nitrogen deposition reduction on biodiversity and carbon sequestration

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Abstract

Global warming and loss of biodiversity are among the most prominent environmental issues of our time. Large sums are spent to reduce their causes, the emission of CO₂ and nitrogen compounds. However, the results of such measures are potentially conflicting, as the reduction of nitrogen deposition may hamper carbon sequestration and thus increase global warming. Moreover, it is uncertain whether a lower nitrogen deposition will lead to a higher biodiversity. In this study we forecast that a gradual decrease in nitrogen deposition from 40 to 10 kg N ha⁻¹y⁻¹ in the next 25 years will cause a drop in the net carbon sequestration of forest in The Netherlands to 27% of the present amount, while biodiversity remains constant in forest, but may increase in heathland and grassland.

Introduction

Human activities have led to a worldwide decrease in biodiversity (Chapin et al., 1998; Swift et al., 1998; Smith et al., 2000; Dobson, 2005), often caused by land use change (Vitousek et al., 1997; Swift et al., 1998; Zebisch et al., 2004). Intensified land use caused an increase of reactive nitrogen in the atmosphere and soil in agricultural areas, but atmospheric reactive nitrogen also increased due to more intense traffic (Hogg et al., 1995; Kelly et al., 2000; Lameire et al., 2000; Wright et al., 2001; Tarasón et al., 2003). Moreover, industrial activities have lead to an increase of CO₂ in the atmosphere, which may lead to higher temperatures causing an even higher pressure on biodiversity. Whether or not a higher CO₂ concentration will affect biodiversity directly still remains uncertain (Peterson & Melillo, 1985; Smith et al., 2000; Malcom et al., 2002; Chapin et al., 2000; Thomas et al., 2004). These global issues have been the subject of several international conferences where many countries have agreed on countermeasures to prevent further loss of biodiversity and to stop global warming (e.g. the Rio and Johannesburg conferences and the Kyoto conference leading to the Kyoto protocol). Main targets resulting from the conferences are to stop further decrease of biodiversity and to stop global warming. The latter may be reached by a reduction of CO₂ release into the atmosphere or by an increase of carbon sequestration. In areas that are densely populated or have an intensive agricultural use biodiversity may be enhanced by a reduction of the nitrogen release. These areas can

be found mainly in Western Europe, e.g. England, Belgium, Denmark, Germany and the Netherlands, and some parts of the U.S.A. The policy goals, however, could be conflicting since a decrease in nitrogen deposition may negatively affect carbon sequestration. Experimental research has revealed a positive relation between N addition and growth, and thus carbon sequestration, in Scandinavian forests where nitrogen strongly limits growth (Tamm et al., 1999). The relation between N addition and biodiversity has also been experimentally tested (Aerts et al., 2003; Reich et al., 2001; Bobbink et al., 1998; Bobbink & Roelofs, 1995; Thomas et al., 1999) and showed that N addition leads to a decrease in biodiversity. However, research into the combined effect of nitrogen deposition on both carbon sequestration and biodiversity is scarce, especially on a regional scale (Reich et al., 2001; Huston & Marland, 2003).

Measures to reduce nitrogen emission have begun to take effect, and deposition has a downward trend at least in some areas (Kelly et al., 2002; Tarasón et al., 2003). But the deposition is still high; for instance the average deposition in Western Europe is approximately 18 kg-ha⁻¹ N, whereas the estimated background deposition is approximately 3 kg ha⁻¹ N (Galloway et al., 1982, Galloway et al., 1984, Vries, 1994, Tarasón & Schaug, 2000). Several sources claim that increased N deposition will enhance carbon sequestration, although the extent of this effect shows a great deal of variation (Peterson and Melillo, 1985; Nadelhofer et al., 1999; Townsend et al., 1996, Holland, 1997), and some of these studies suggest that it is only of minor importance (Nadelhofer et al., 1999; Townsend et al., 1996). Although there is ample evidence that increased N deposition results in a decrease of floristic diversity, at least in grassland and heathland communities (Aerts et al., 2003; Bobbink et al., 1998; Aerts et al., 1990; Stevens et al., 2004; Roem & Berendse, 2000), it is not certain whether a decrease in deposition will also lead to an immediate return of lost species. This may depend on e.g. the presence of diaspores in the seed bank or in the neighbourhood for recolonisation. However, a decrease in N deposition will lead to improved environmental conditions for these species in terms of soil pH and N availability.

In view of the above, the big questions are (a) whether or not the biodiversity will improve after a decrease of nitrogen deposition and (b) how a decrease of nitrogen deposition will influence the carbon sequestration. To answer these questions, we explored the effect of nitrogen deposition on carbon sequestration in combination with its effect on potential floristic diversity by scenario analyses using the model chain SMART2-SUMO2-NTM3 (Kros, 2002; Berendse, 1994; Van Dobben et al., 2002; Wamelink et al., 2003) on a regional scale. We choose floristic diversity because nitrogen deposition has a close effect on the occurrence of plant species; rare species tend to get locally extinct when deposition rates increases. The effects of climate change (raised temperature and carbon dioxide) on the growth of the vegetation are not included in this research.

Material and Methods

Models

The SMART2 (Kros et al., 2002; Kros, 2002) model simulates soil processes, SUMO2 (Berendse 1994; Van Dobben et al., 2002) simulates vegetation processes and succession, whereas NTM3 (Wamelink et al., 2003) predicts the 'potential floristic diversity' based on groundwater level, nitrogen availability and pH (the latter two simulated by SMART2-SUMO2). SMART2 and SUMO2 are dynamic process models that include complete nitrogen and carbon cycles, based on time steps of one year.

The model SMART2 (Kros et al., 2002; Kros, 2002) considers linked biotic and abiotic processes in the soil solution as well as in the solid phase. It represents the inorganic soil and two organic soil compartments. The model consists of a set of mass balance equations, describing the soil input-output relationships and rate-limited and equilibrium soil processes. The soil solution chemistry depends on the net element input from the atmosphere and groundwater, canopy interactions, geochemical interactions in the soil (CO_2 equilibria, weathering of carbonates, silicates and/or Al hydroxides, SO_4 sorption and cation exchange), and nutrient cycling (litterfall, mineralisation, root uptake, nitrification and denitrification). Nutrient uptake by the vegetation and litterfall (including the amount of dead roots and dead wood) are provided by SUMO2. SMART2 delivers the nitrogen availability to SUMO2 as the sum of external N input and mineralisation. Solute transport is described by assuming complete mixing of the element input within one homogeneous soil compartment with a constant density and fixed depth.

Like SMART2, SUMO2 (Berendse, 1994; Wamelink et al., 2005) is a process-oriented model that simulates vegetation succession and biomass production for time steps of one year. The biomass development is simulated for five functional types (FT), herbs and grasses (1), dwarf shrubs (2), shrubs (3), and two tree species (4 and 5). The five FT compete with each other for nitrogen (including nitrogen deposition), light, and moisture. Competition for nitrogen is based on the relative biomass present in the roots of the FT. Competition for light is simulated as a result of the height and the leaf biomass of the FT. Actual biomass growth of each FT is the result of a reduction of the maximum growth by moisture, nitrogen and light availability. The biomass can also be reduced as a result of management (mowing in grassland, sod cutting in heathland, thinning in forest). Mowing, sod cutting and thinning implies the removal of biomass and thus carbon and nitrogen from the system. SUMO2 requires information on soil type and groundwater level, the initial vegetation type and the management. Management is usually unknown and is therefore derived from the vegetation type. In this study grassland is mown once each year, sod cutting takes place in heathland every 30 years and in forest trees are thinned depending on the tree species and the biomass growth. The initial biomass (and nitrogen content) is derived per vegetation type and age class from a standard database containing biomass and

nitrogen content for an average stand in The Netherlands. The model is initialised for 10 years to adjust the biomass and nitrogen content to the local circumstances.

NTM3 (Wamelink et al., 2003) is a regression model based on the criteria of the red list, i.e. the rarity, the temporal trend and the size of the distribution area of each species. It is a regression model that predicts the potential floristic diversity at given values of the soil characteristics nitrogen availability, soil pH and moisture availability. The nitrogen availability and soil pH are simulated by SMART2, the moisture availability as spring groundwater level is derived from a hydrological map. A nature conservation value (NCV) was assigned to the vascular plant species occurring in The Netherlands, based on the red list criteria, rarity, temporal trend and size of the distribution area (Mace & Stuart, 1994). The rarity was based on the occurrence of the species in the Dutch national 5km grid, and the trend is based on the change of occurrence of the species on the national grid between 1950 and 1990. The distribution area indicates the importance of the occurrence of the species in The Netherlands for its total distribution area. Rare and decreasing species that have their major distribution in The Netherlands get a high value, common species get a low value or even a negative value when they are increasing (i.e. invasive species).

A data set containing 160,000 vegetation relevés was used as a training set to relate NCV to soil properties. As direct measurements of soil conditions are scarce, these conditions were estimated per relevé on the basis of the mean Ellenberg (Ellenberg et al., 1991) indicator values for moisture, pH and nutrient availability of the constituent species. The Ellenberg values were related to actual soil conditions using a separate training set of relevés where these conditions had been measured. A regression analysis using p-splines was used to smoothen the relationship between the soil characteristics and the NCV's of the species. The potential floristic diversity is predicted in an arbitrary scale, where values > 15 indicate a high probability of occurrence of red list species, and values < 12 indicate a low floristic diversity with a very low probability of occurrence of red list species. The lowest possible potential biodiversity is approximately 7 and the highest approximately 19. To account for differences in management, the model was calibrated four times, for heathland, for deciduous forest, for coniferous forest and for grassland. The model estimates the probability of occurrence for red list species at any given combination of groundwater level, nitrogen availability and pH, based on the assumption that sufficient recolonisation can take place if conditions improve. This is why we use the term *potential* floristic diversity.

Study area and scenarios

We used the Netherlands as study area because many data are available. We selected all 250m*250m grid cells with either deciduous forest (38707 cells), coniferous forest (109374 cells), unfertilised grassland (15362 cells) or heathland (558 cells) in the Netherlands. Information about the groundwater table, soil type, tree species and

stand age per grid cell were used as input for the models. It covers all major soil types and groundwater tables in The Netherlands. The models were run for all stands with eight constant nitrogen deposition levels at 5, 10, 20, 30, 40, 50, 60 and 70 kg ha⁻¹ y⁻¹ N. The simulations were run for 25 years using the system state in 2000 as starting point. The average net carbon sequestration in living biomass, litter and dead wood in forest was inspected in the last year of the 25 year period (2025). Potential floristic diversity was predicted for the end of this period in all vegetation types.

Results

Carbon sequestration

The simulated average net carbon sequestration (in living biomass, litter and dead wood) increases from approximately 0 and 0.4 ton ha⁻¹ y⁻¹ to 1.1 and 2.2 ton ha⁻¹ y⁻¹ for coniferous and deciduous forest respectively (Figure 1), between the lowest (5 kg ha⁻¹ y⁻¹) and the highest nitrogen deposition level (70 kg ha⁻¹ y⁻¹). We assumed that the effect of nitrogen deposition on the C-sequestration in grassland and heathland is negligible. The average simulated increase is 20-30 kg carbon per kg nitrogen deposition. The difference between deciduous and coniferous forest is caused in part by the difference in maximum growth rate. These figures are well in agreement with experimental results from Sweden (Tamm, 1999) with increases of 18 and

28 kg C kg⁻¹ N depending on the site. The increase is also very similar to that estimated by Nadelhoffer et al. (1999). They based their estimate on ¹⁵N tracer experiments, showing that approximately 5% of the added N ends up in stem wood with an average C/N ratio of 500, leading to an assumed accumulation of 25 kg C kg⁻¹ N if the C/N ratio remains constant.

In our results the variation is large for both coniferous and deciduous forest, caused by a wide variation in soil types, groundwater tables and age classes. Net emitters of carbon exist for both forest types (actually the older stands). Since Dutch forests are relatively young the amount of older stands will increase over time, especially because clearcutting is no longer practised. This may lead to a decrease in C sequestration over time. In deciduous forest the carbon sequestration levels off at higher nitrogen deposition levels, indicating that other factors besides nitrogen become growth limiting. Coniferous forests do not show such a decline. Field experiments show that in boreal areas nitrogen limitation of forest growth is becoming less important around a nitrogen addition of 60 kg ha⁻¹ y⁻¹, which agrees with our results for deciduous forest (Tamm, 1999).

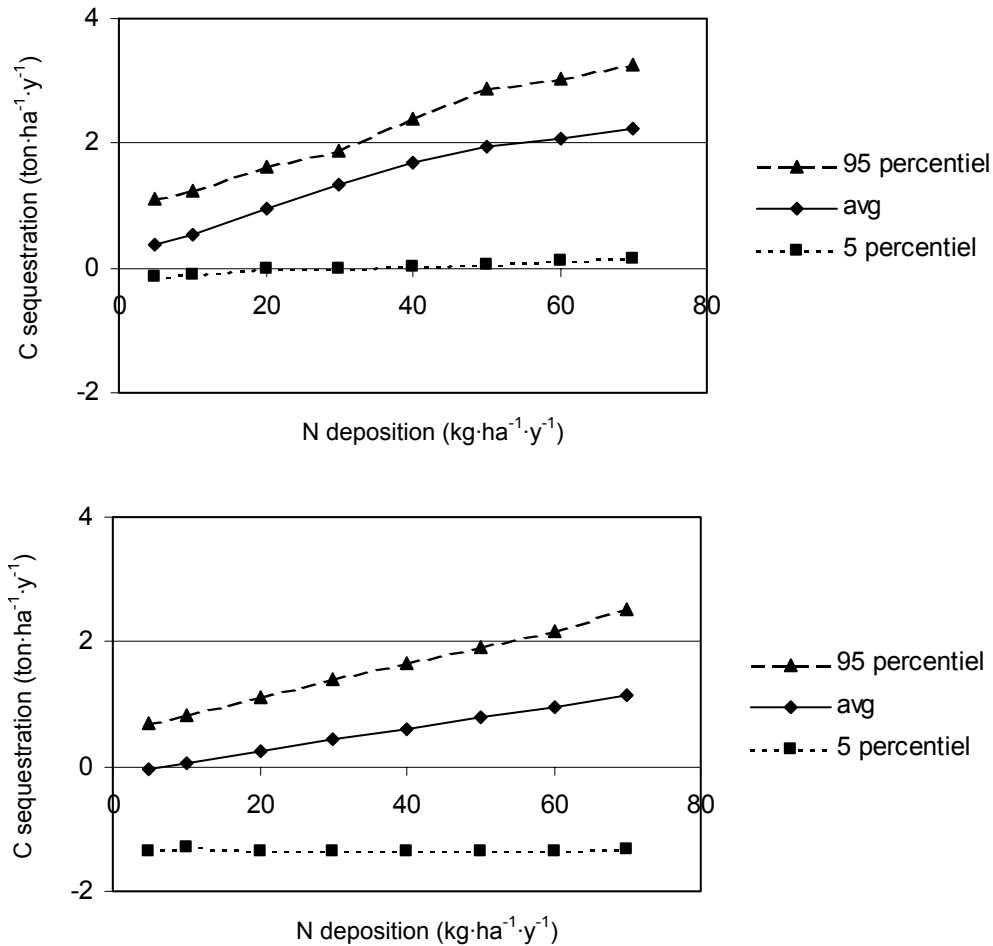


Figure 1 Simulation of the mean carbon sequestration (living biomass + dead wood + litter) with its 5- and 95-percentile realised in deciduous (dec.) and coniferous (con.) forest at five nitrogen deposition levels for all forest in The Netherlands after 25 years.

Potential floristic diversity

The simulated potential floristic diversity decreases with increasing nitrogen deposition, the effect being most prominent for grassland followed by heathland and deciduous forest, whereas the effect is very limited in coniferous forest (Figure 2). The simulated large decrease in potential floristic diversity with nitrogen deposition in grassland, and to a lesser extent in heathland is in agreement with experiments as well as field surveys (Bobbink & Roelofs, 1995; Bobbink et al., 1998; Roem & Berendse 2000; Aerts et al., 2003; Stevens et al., 2004), as is the impact on deciduous forest (Thomas, 1999; Dobben et al., 1999). Like for carbon sequestration, the variation in

simulated potential floristic diversity is large. At low nitrogen deposition levels there are relatively many stands with high values, whereas at high nitrogen deposition levels many stands occur with very low values, as can be seen from the 5- and 95-percentile lines (Figure 2). In contrast to deciduous forest, the effect of nitrogen deposition on the potential floristic diversity is almost absent in coniferous forest (Figure 2) although the 95-percentile indicates that a higher diversity may occur at very low nitrogen deposition levels. Most of the coniferous stands are plantations with only widespread and common species in their ground vegetation layer, although under conditions of very low nitrogen availability rare species may occur e.g. lichens (van Dobben et al., 1999; Ericsson et al., 2005; Gustafsson et al., 2005).

The above results suggest that a decrease in nitrogen deposition will lead to a decrease in carbon sequestration. In order to make a more realistic prediction this observation was further explored in a scenario where nitrogen deposition gradually decreases from 40 kg·ha⁻¹·y⁻¹ N in 2000 to 10 kg·ha⁻¹·y⁻¹ N in 2025. The 40 kg·ha⁻¹·y⁻¹ N is approximately the average deposition in 2000 in The Netherlands and some other areas in western Europe (Tarasón, et al., 2003). When a transition to more sustainable agriculture has been established a deposition of 10 kg·ha⁻¹·y⁻¹ N in 2025 may be achievable.

Table 1 shows the total net carbon sequestration in 2025 for the decreasing and for two of the constant nitrogen deposition scenarios. The results show that under the decreasing scenario carbon sequestration in 2025 will drop to approximately 27% of the sequestration at a constant deposition of 40 kg·ha⁻¹·y⁻¹. Floristic diversity on the other hand will increase in deciduous forest (Table 1). The floristic diversity in coniferous forest increases just slightly, while the carbon sequestration drops dramatically, both in agreement with the results for the constant deposition levels. The largest increase in potential floristic diversity is predicted for heathland and grassland. This increase is much larger than for forest, although not as large that it reaches the floristic diversity for the constant low deposition. As Dutch forests are almost all plantations, the results are likely to be applicable to most plantation forests in temperate Europe (e.g. Germany, UK or Poland), but not to the semi-natural forests in the boreal region where floristic diversity may be more sensitive to nitrogen deposition because of the occurrence of the relatively sensitive bryophytes and lichens.

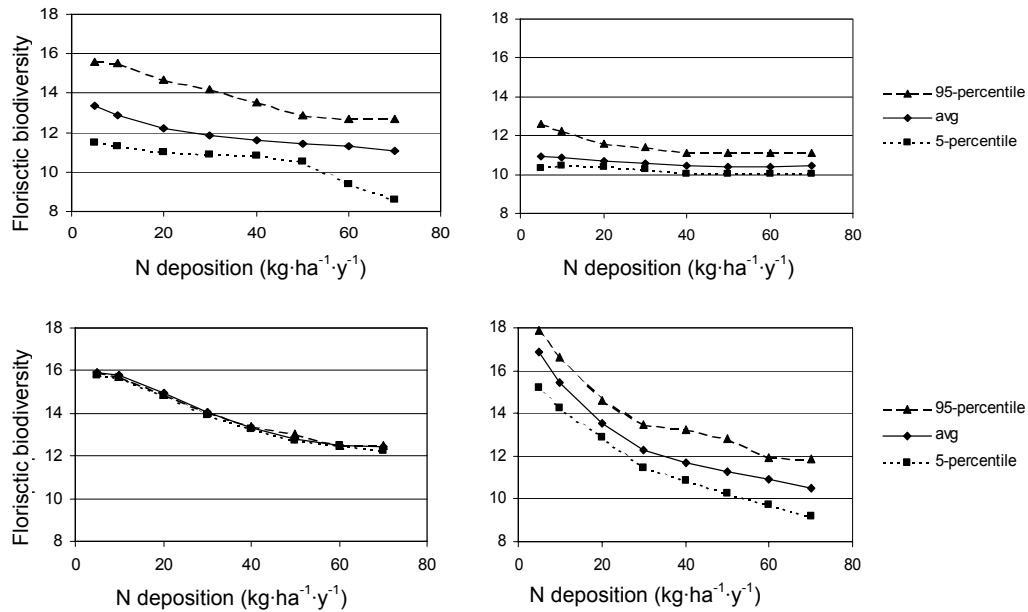


Figure 2 Prediction of the mean potential floristic diversity with its 5- and 95-percentile for deciduous forest (top left), coniferous forest (top right), heathland (bottom left) and grassland (bottom right) in The Netherlands at eight nitrogen deposition levels after 25 years. The potential floristic diversity is predicted in an arbitrary scale, where values > 15 indicate a high floristic diversity with a high probability of occurrence of red list species, and values < 12 indicate a very low probability of occurrence of red list species.

Table 1 Total carbon sequestration (living biomass + dead wood + litter) and mean potential floristic diversity (in arbitrary units, cf. Figure 2) in the Netherlands after 25 years for three nitrogen deposition scenarios (N-dep.) and four vegetation types.

N-dep 2000 kg·ha ⁻¹ ·y ⁻¹	N-dep 2025 kg·ha ⁻¹ ·y ⁻¹	C sequestration (kton·y ⁻¹) in 2025			Floristic diversity In 2025			
		Deciduous forest	Coniferous forest	All forest	Deciduous forest	Coniferous forest	Grass- land	Heath- land
10	10	17.9	-1.6	16.4	12.9	10.9	15.5	15.8
40	10	26.2	-1.9	24.2	12.5	10.8	14.2	15.2
40	40	56.7	30.5	87.3	11.6	10.5	11.7	13.3

Discussion

The presented simulations suggest that a decrease in nitrogen deposition may substantially increase floristic diversity in grassland and heathland, thus fulfilling Rio/Johannesburg requirements. However, this may also lead to a substantial decrease in carbon sequestration in both coniferous and deciduous forest, which would

jeopardise the fulfilment of the Kyoto protocol. These results are probably applicable for large parts of Europe, where forests play a role in C-sequestration and important natural grasslands and heathlands are present, and nitrogen deposition is high at present. Forest fertilisation, as suggested by Oren et al. (2001), may compensate for the reduction in carbon sequestration but will also negatively affect floristic diversity, at least in deciduous forest where the potential gain in C sequestration is largest. The negative effect of reduced N deposition on C sequestration may be partly offset by a reduction in the emission of the greenhouse gas nitrous oxide. Taking the standard IPCC assumption that 1% of the deposition input is returning to the atmosphere as N₂O with a warming potential of 300 times that of CO₂, its effect would be equivalent to 3 kg CO₂ ha⁻¹y⁻¹, i.e. less than 1 kg C ha⁻¹y⁻¹. Thus, this effect is likely to be very limited.

It is difficult to compare the importance of carbon-sequestration on the one hand and floristic diversity on the other hand, but in the end we believe that the good news of increased floristic diversity with decreasing nitrogen deposition outweighs the bad news of the decrease in carbon sequestration. This is especially true since the total contribution of carbon sequestration in existing forest is only a minor part of the total carbon that is released at the moment (Tarasón et al., 2003). Moreover, plantation of new, fertilised forest may compensate for the loss of carbon sequestration, financially stimulated by the government to fulfil the targets set in the Kyoto protocol.

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Summary



Summary

Human activities led to major changes in earth's atmosphere. One of these changes is the increase of reactive nitrogen compounds due to agriculture, industry and transport, especially in Europe and North America. The raised nitrogen supply led to a decrease of plant species diversity. Countermeasures to reduce the nitrogen input into the vegetation have begun to take effect. Atmospheric nitrogen deposition has started to decline. Whether or not this will lead to restoration of plant biodiversity remains uncertain. I investigated whether the reduction in nitrogen deposition will lead to an increase in biodiversity. To this end two models were developed to simulate vegetation development and diversity, respectively. To feed these models I used information from published data and field measurements.

One of the possible approaches to examine changes in the soil due to for instance nitrogen deposition is by using expert systems that link species composition to soil conditions. The advantage of such a system is that it avoids expensive chemical analysis and the environmental conditions can be instantly estimated in the field. The expert system I examined was the Ellenberg indicator system (Chapter 2). This system is widely used in vegetation science to estimate the environmental variables from plant species. For proper use the system has to be validated and its uncertainty has to be quantified. Earlier studies showed an adequate relation between indicator values and measurements. However, the uncertainty appeared to be large. I tested the hypothesis that the uncertainty is due to a vegetation type dependent bias. For that purpose I set up a database containing vegetation relevés where soil pH (3631 records) or mean spring groundwater level (MSL, 1600 records) were measured. These data are probably a good representation of the site conditions encountered in the Netherlands.

All relevés were assigned to vegetation types by an automated procedure. The field data were regressed on the Ellenberg indicator values for acidity (R) and for moisture (F) for soil pH and mean spring groundwater level (MSL) respectively. Percentages explained variance were similar to values that were reported earlier (for R on pH $R^2 = 0.44$ and for F on MSL $R^2 = 0.26$), though the explained variance for F is on the lower end. When I added the syntaxonomic class as an explanatory factor the explained variance increased dramatically (for R on pH $R^2 = 0.751$ and for F on MSL $R^2 = 0.750$). Separate regression lines per vegetation type were estimated, many of which were significantly different from each other. In most cases, the intercepts were different, but in some cases, their slopes differed as well. The Ellenberg indicator values for acidity and moisture appeared to be biased towards the values that experts expect for the various phytosociological classes. Based on these results, I recommend using Ellenberg indicator values only for comparison within the same vegetation type. This makes the Ellenberg system less suitable for application in vegetation modelling.

Therefore, I investigated the possibility to replace the Ellenberg indicator value system by a new system based on physical data instead of expert judgement (Chapter 3).

For this purpose, I used the same database that I used for the above described validation. Based on the data for measured soil pH values, I developed a method to estimate species responses, which could be used in vegetation modelling. I also developed a method to predict abiotic conditions from the vegetation composition using these responses. This method was tested for soil pH.

I was able to estimate the pH response of 556 species of the Dutch flora. These species were used to estimate the soil pH for the relevés (back prediction) using seven different methods. The species responses were estimated using curve fitting and by calculating the mean of the pH values at sites where the species was observed. The estimated curves (splines) were used to estimate the pH following five different approaches. The simplest method yielded the best prediction of pH:

- (1) The indicator value of a species is the average of the soil pH values of the sites where it was observed.
- (2) The predicted pH of a new site is the average of the indicator values of the species occurring there.

The estimated species responses were validated on independent Dutch and European data sets, giving similar results inside and outside The Netherlands. Older successional stages were predicted better than younger stages. Moreover, the validation for a European forest data set showed that in general the prediction error in Northern European countries was low, whereas in Southern European countries the prediction error was largest. The latter may be due to the limited number of species that occur in both Southern Europe and The Netherlands. The average prediction error for the European forest data set was 0.5 pH units.

Finally, I compared the newly developed method with the popular Ellenberg indicator system, which showed that the developed method performed better for the Dutch data set. Therefore, when more data become available on a European scale (also on other abiotic factors than pH, e.g. water availability), the method may replace the Ellenberg system.

Experiments to test the long-term effects of decreasing nitrogen deposition are not available. Therefore, model simulations provide the only possibility to get insight into the effects of decreasing nitrogen deposition on the vegetation. I developed the vegetation succession model SUMO that is linked to the soil model SMART2 (Chapter 4) to simulate the effects of nitrogen deposition on the vegetation. SUMO models the biomass development of five functional plant types, herbs and grasses, dwarf shrubs, shrubs, pioneer tree and climax tree, as a function of nitrogen availability, light availability and management. In the model a distinction is made between the nitrogen content of roots, wood and leaves. The functional types compete for nitrogen. The partitioning of the available nitrogen is calculated on the basis of the root biomass of the competing functional types. The acquired nitrogen is

divided over the organs. Every year a fraction of the biomass dies. Nitrogen is reallocated after which the amount of dead biomass per organ and the nitrogen content is passed on to SMART2. Management intervenes in the biomass and nitrogen cycle by removing biomass and thus nitrogen from the system. The management intervention may be grazing, mowing, sod cutting or forest management. The successional stage of the vegetation is determined on the basis of the biomass distribution over the functional types. The stage can vary from almost bare soil via grassland or heathland to various forest types.

The model was validated on four sites, three in The Netherlands and in one the UK. The aboveground biomass of two grassland vegetation types was simulated properly, as well as the aboveground biomass of heathlands in several stages of development. The older stages of a forest chronosequence were also simulated well, but the simulation of some of the younger stages showed less agreement between simulated and measured values. The simulations of the model were also validated on 169 forest site with a known leaf nitrogen content which gave satisfying results; the relation between simulated and measured nitrogen content was highly significant ($R^2 = 0.39$).

To explore the long-term effect of a decrease in nitrogen deposition I applied the model to a heathland and a pine stand. In the heathland a major change was simulated as a result of a decreasing nitrogen deposition in combination with management (turf stripping). The dominance of grasses changed into a dominance of dwarf shrubs. At a constant and high nitrogen deposition, the grasses remained dominant. The simulation of the changes in the pine forest indicated only a very small effect of a decrease in nitrogen deposition. The different behaviour of the simulated heathland is due to the removal of excess nitrogen by management, whereas the extensive management in the forest hardly removes any nitrogen from the system. These examples show that a decrease of nitrogen deposition may retard succession, and consequently increase biodiversity in heathland but probably not in forest.

Large sums of money are spent on measures to preserve biodiversity by, amongst others, the improvement of environmental quality. This creates the need to evaluate the effectiveness of such costly measures. However, simulation of succession in terms of vegetation structure and biomass is not sufficient to predict possible changes in biodiversity. Currently, dynamic vegetation models that operate on the level of plant species are not feasible. Therefore, I developed a static model, NTM3 that links plant biodiversity to abiotic variables (Chapter 5). These variables are vegetation management, and the soil variables groundwater level, pH and nitrogen availability. I used species richness and the criteria of the Red Lists, i.e. the rarity and decline per species as proxy for potential changes in plant biodiversity. NTM3 is based on statistical relations, and models the potential plant biodiversity based on the above criteria as a non-linear function of the three soil variables. The regression model is calibrated on a data set consisting of 33,706 vegetation relevés. Since vegetation data

combined with measurements of soil variables are insufficiently available, at least for nitrogen availability, I used the average of Ellenberg's indicator values of the species in each relevé as a proxy.

NTM3 was subjected to both validation and uncertainty analysis. The uncertainty analysis showed that the uncertainty is large for individual biodiversity values, but that comparative (i.e., scenario) studies can be carried out with an acceptable uncertainty. Validation of NTM3 was carried out by comparison with an independent data set, which showed that the relation between calculated and predicted potential plant biodiversity was highly significant. As an example, I evaluated the impact of three European economic scenarios on potential plant biodiversity in the Netherlands. Although there were differences per vegetation type and per region, the potential plant biodiversity had a tendency to increase over time, with the highest increase for the scenario with the highest reduction in atmospheric deposition of nitrogen and acidity. Regional differences between the scenarios were mostly due to regional differences in deposition.

Nature reserve managers make additional costs to mitigate the effects of atmospheric deposition. Theoretically, these extra costs may be saved when deposition levels drop. Costs were calculated per Nature Target Type (NTT; they are a combination of phytosociological vegetation types) and management intensity for both the current (high) and reduced deposition levels. The resulting plant diversity was estimated for current and reduced nitrogen deposition levels. I calculated the difference in costs based on the management intensities required to maintain plant diversity at both deposition levels. For the NTTs within the clusters grassland, reed and rough land, and heathland I used the models SMART2-SUMO and MOVE3. For forests and moorland pools, we used expert knowledge to estimate the reduction in management costs due to a decrease in deposition. Results show that for a majority of the vegetation types an increase in plant diversity will be reached when nitrogen deposition drops. Thus, lower costs can be made to maintain the same level of plant diversity. Only for a small part of the vegetation types lower plant diversity was simulated when the deposition drops. The total amount of money that may be saved because of the reduction of deposition rates is estimated to be 42 million Euro per year for the period from 2000 to 2020 for the assessed NTTs for the whole of The Netherlands. The highest savings can be made in grasslands: 28 million Euro. On average the savings were 80 € ha⁻¹·y⁻¹, which ranged from 5 € ha⁻¹·y⁻¹ for forest to 299 € ha⁻¹·y⁻¹ for reed and rough land.

To evaluate the effects of nitrogen deposition on carbon sequestration on the one hand and plant biodiversity on the other hand I used the models SMART2, SUMO and NTM3 to evaluate several nitrogen deposition scenarios (Chapter 7). Global warming and loss of biodiversity are among the most urgent environmental problems of our time. Large sums are spent to reduce their causes, the emission of CO₂ and nitrogen compounds. However, such measures could lead to conflicting

results, as the reduction of nitrogen deposition may hamper carbon sequestration and thus increase global warming. Moreover, it is uncertain whether a lower nitrogen deposition will lead to a higher biodiversity. In this study, I explored whether the goals set by the Kyoto protocol and the biodiversity targets are conflicting. I simulated the carbon sequestration by all Dutch forests for nitrogen deposition rates varying from 5 $\text{kg}\cdot\text{ha}^{-1}\cdot\text{y}^{-1}$ up to 70 $\text{kg}\cdot\text{ha}^{-1}\cdot\text{y}^{-1}$ N. Obviously, a higher deposition led to a higher carbon sequestration in forests. For the low deposition rates, the forest in The Netherlands would even become a net emitter. The potential plant diversity in forests simulated by NTM3, while soil and light conditions were simulated by SMART2-SUMO, does not significantly change at the different levels of nitrogen deposition. Only at very low rates for some forest types a high plant diversity is predicted. However, for the major other vegetation types, grassland and heathland, higher levels of plant biodiversity are predicted at lower nitrogen deposition. The model simulations forecast that a decrease in nitrogen deposition from 40 to 10 $\text{kg}\cdot\text{ha}^{-1}\cdot\text{y}^{-1}$ N, a government target, will cause a drop in the net carbon sequestration of forests in The Netherlands to 27% of the present amount. The plant biodiversity remains constant in forest, but is predicted to increase tremendously in heathland and grassland. The decrease in carbon sequestration due to the reduction of nitrogen deposition may jeopardise the goals set for carbon sequestration.

Samenvatting



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Door de intensivering van de landbouw, maar ook door het toegenomen wegverkeer en de industrialisatie is er steeds meer stikstof terecht gekomen in de bodem van Nederland en grote delen van Europa en Noord Amerika. De landbouw importeert voedsel en daarmee stikstof vanuit de rest van de wereld naar Nederland als voedsel voor het vee. Dit vee produceert niet alleen vlees maar ook grote hoeveelheden mest met daarin, vaak ruikbaar, ammoniak, een vorm van stikstof. Ook olie en gas worden geïmporteerd en verbrand in fabrieken, woningen en auto's. Hierbij komt ook stikstof in de vorm van stikstofoxiden vrij. Deze stikstofvorm is reukloos. Beide stikstofvormen zijn gasvormig en komen overal terecht, ook in natuurgebieden. Ammoniak en de stikstofoxiden (ofwel nitraten) zijn voedsel voor planten. Echter niet alle plantensoorten reageren op dezelfde manier op die extra stikstof. Sommige soorten kunnen beter omgaan met de extra stikstof dan andere. Ze gaan harder groeien en verdringen daarbij andere plantensoorten die daardoor zeldzamer worden en soms zelfs zijn verdwenen uit Nederland. Daarnaast kan ammoniak de bodem verzuren wat ook tot belangrijke veranderingen in de plantensoortensamenstelling kan leiden. De effecten van stikstof op planten en ecosystemen is het belangrijkste onderwerp van dit proefschrift.

In de vegetatie-ecologie wordt veel gebruik gemaakt van zogenaamde indicatorwaarden. Zij geven de ecoloog informatie over bijvoorbeeld de voedselrijkdom van de bodem door gebruik te maken van kennis over de aanwezige plantensoorten, die elk hun eigen aanwijzingen geven over het milieu, zonder dat er directe metingen aan de bodem worden gedaan! Een veel gebruikt systeem is het Ellenberg-indicator systeem. De ecoloog Ellenberg deelde plantensoorten in op een negen (of twaalfdelige) schaal. De soorten werden ten opzichte van elkaar gerangschikt naar hun voorkeur voor milieuomstandigheden. Soorten die bijvoorbeeld onder zure omstandigheden groeien gaf hij een lage waarde op de schaal voor zuurgraad en soorten die onder meer neutrale omstandigheden groeien een hogere waarde. Het Ellenberg-systeem is een typisch expertsysteem, dat vooral is gebaseerd op veldkennis van de opsteller en niet of nauwelijks op metingen. Ik heb dit systeem getest op zijn betrouwbaarheid en bruikbaarheid voor de modellering van het voorkomen van plantensoorten (hoofdstuk 2). Het Ellenberg-systeem vormt een belangrijke schakel tussen de modellen die verderop worden beschreven.

Als eerste stap is er een grote database opgezet met vegetatieopnamen en gemeten abiotische bodemgegevens, zoals pH, grondwaterstand, stikstofgehalte enzovoort. Voor elke vegetatieopname is de gemiddelde Ellenberg-waarde voor zuurgraad en vocht berekend op basis van de aanwezigheid van soorten. Door middel van regressie zijn de gemeten bodem-pH en gemiddelde voorjaarsgrondwaterstand vergeleken met de gemiddelde Ellenberg-indicatorwaarden voor zuurgraad en vocht

(voor respectievelijk 3631 en 1600 waarnemingen). De regressies gaven redelijk goede resultaten te zien en de verklaarde varianties waren acceptabel (voor zuurgraad $R^2=0.44$ en voor vocht $R^2=0.26$). Wanneer ze echter worden gebruikt voor voorspellingen betekent dit dat je vaak een foute voorspelling doet. Ook opvallend is de grote spreiding rond de regressielijn. Mijn stelling was dat dit wordt veroorzaakt door een systematische fout in de Ellenberg-indicatorwaarden die er toe heeft geleid, dat soorten met een relatief hoge waarde een nog hogere waarde hebben gekregen en soorten met een relatief lage waarde een nog lagere waarde. Ik heb getoetst of deze fout vegetatietype afhankelijk is. Daarvoor is elke opname toegekend aan een vegetatietype (namelijk de 'plantensociologische klasse'). Vervolgens is die klasse in de regressie gebruikt als extra verklarende variabele. Hierdoor ging de voorspellende kracht van de indicator waarden sterk omhoog, en is de fout bij voorspellingen veel kleiner geworden (voor zuurgraad en voorjaarsgrondwaterstand $R^2=0.75$). Regressies per vegetatietype zijn daarom noodzakelijk.

In hoofdstuk 3 heb ik een alternatief ontwikkeld voor het Ellenberg-systeem. Hiervoor is wederom gebruik gemaakt van de dataset met vegetatieopnamen en veldmetingen van bodemfactoren. Het ontwikkelde systeem bestaat uit twee delen:

1. Schatting van de responsie van plantensoorten op bodemcondities.
2. Terugschatten van de bodemcondities van een opname op basis van de soortresponsies.

Bovenstaande is verder uitgewerkt voor bodem-pH. De responsies van de plantensoorten zijn geschat door middel van 'splines'. Deze regressietechniek geeft de mogelijkheid om een grote vrijheid te gebruiken bij het schatten van responsies: van een lineaire respons (een rechte lijn) tot een respons met verschillende 'toppen'. Het geeft veel meer mogelijkheden dan de klassieke klokvormige Gausische response-functie. De responsies per soort zijn geschat op basis van het percentage van de opnamen met de betreffende pH-waarde waarin die soort voorkomt. Op die manier kan voor elke soort een 'responsiekromme' geconstrueerd worden die de kans op voorkomen geeft als functie van de bodem-pH. In totaal konden op deze manier responsies voor 556 soorten worden geschat (ruim éénderde van de Nederlandse flora). Vervolgens zijn verschillende methoden gebruikt om de pH van de vegetatieopnamen terug te schatten, onder andere op basis van de aanwezige soorten maar ook op basis van de aanwezige en de afwezige soorten. Tot mijn verrassing bleek de simpelste methode de beste resultaten op te leveren:

1. Bepaal het optimum (de top) van responsiekromme van elke soort.
2. Bepaal het gemiddelde van de optima van de aanwezige soorten in de opname. Dit is dan de geschatte pH.

Deze methode is vervolgens gebruikt om schattingen te maken van de bodem-pH voor niet eerder gebruikte datasets met opnamen en gemeten pH-waarden in zowel Nederland als Europa. Er bleek een redelijke overeenstemming tussen gemeten en voorspelde waarden, die groter was dan bij schattingen op basis van de Ellenberg-

getallen. De pH werd voor oudere successiestadia beter geschat dan voor jongere successiestadia en voor bossen weer beter dan voor andere vegetatietypen. De gemiddelde afwijking van de voorspelling van de pH voor een dataset over Europese bossen was 0.5 pH eenheid, waarbij moet worden opgemerkt dat vooral in Zuid Europa de voorspellingen slecht waren, maar voor de rest van Europa goed. In potentie lijkt het hier ontwikkelde systeem het veelgebruikte Ellenberg-systeem te kunnen vervangen.

Hoewel een deel van het effect van stikstof op de groei nog steeds niet bekend is, is wel duidelijk dat de stikstofbeschikbaarheid grote invloed kan hebben op het voorkomen van plantensoorten, maar ook op het functioneren van ecosystemen. Daarnaast heeft het invloed op de snelheid van successie van vegetaties. Door de toename van de stikstofdepositie zijn ecosystemen de laatste honderd jaar sterk beïnvloed. De stikstofdepositie is echter de laatste jaren voor het eerst op sommige plaatsen gedaald als gevolg van maatregelen in de landbouw. Om de invloed van de stikstofimpact en de effecten van maatregelen te evalueren is het vegetatiesuccessie-model SUMO ontwikkeld (hoofdstuk 4). Het model is geïntegreerd in het bodemmodel SMART2 en wisselt daarmee op jaarbasis informatie uit. In SUMO worden vijf functionele typen gemodelleerd: grassen en kruiden, dwergstruiken, struiken, pionierbomen en climaxbomen. Voor de laatste twee worden specifieke boomsoorten gemodelleerd. Voor elk functioneel type worden drie organen gemodelleerd: wortels, tak/stam en blad. De functionele typen concurreren elkaar om stikstof en licht, terwijl beheer de biomassagroei beïnvloedt door het verwijderen van biomassa (en dus stikstof) uit het systeem.

SUMO is gevalideerd voor grasland, heide en bos. De groei van de bovengrondse biomassa kan goed worden gesimuleerd voor graslanden die jaarlijks gemaaid worden, zowel voor grasland in de buurt van Wageningen als voor het Parkgrass experiment in Rothamsted (Engeland) dat al sinds 1856 loopt. Daarnaast is SUMO gevalideerd voor de Strabrechtse heide, waar de biomassaontwikkeling na plaggen is vergeleken voor verschillende heidestadia. Tot slot is SUMO gevalideerd voor bos door de simulaties te vergelijken met een chronosequentie bij Sellingen, waar op verschillende momenten in het verleden bos is aangeplant op voormalig landbouwgrond. Vooral de ontwikkeling voor de oudere bossen werd goed gemodelleerd. De simulatie van de ondergroei vormde echter voor alle stadia een probleem. Deels is dit waarschijnlijk te wijten aan een gebrek aan kennis over het beheer in het veld (dunnen). Naast de biomassagroei is ook de modellering van het N-gehalte in de bladeren van bomen voor bossen in Nederland gevalideerd. De resultaten waren bemoedigend, er was een significante relatie aanwezig tussen het gemeten en gesimuleerde N-gehalte ($R^2=0.39$).

Omdat geconcludeerd kan worden dat SUMO bevredigende resultaten geeft is het model samen met SMART2 gebruikt om het effect van een dalende stikstofdepositie op de vegetatieontwikkeling te onderzoeken voor een heideveld en een grove dennenbos. Voor de heide worden grote veranderingen gesimuleerd. Als de

heide elke dertig jaar wordt geplagd dan zullen, bij een dalende stikstofdepositie, op den duur de dwergstruiken weer gaan domineren en blijft de vergrassing achterwege. Als echter de depositie op het huidige hoge niveau blijft dan zal de heide blijven vergrassen. Door het beheer wordt er in combinatie met een daling van de stikstofdepositie genoeg stikstof afgevoerd om de heide duurzaam in stand te kunnen houden. De simulaties geven aan dat op den duur de plagintensiteit ook lager kan worden. Voor het grove dennenbos is er nauwelijks verschil te zien tussen het dalende stikstofscenario en het scenario met een blijvende hoge stikstofdepositie. Het beheer in de vorm van dunnen zorgt niet voor een zodanige afvoer van stikstof uit het systeem dat er merkbare verschillen optreden.

Hoewel successie en biomassa belangrijke factoren zijn die onder andere de biodiversiteit bepalen, is er vaak behoefte aan een eenduidige maat voor de botanische diversiteit. Hiervoor is het model NTM3 ontwikkeld (hoofdstuk 5). Dit model kan worden gekoppeld met de modellen SMART2 en SUMO en berekent de geschiktheid van de bodem voor zeldzame plantensoorten. Met het model kan direct worden geschat wat het effect van bijvoorbeeld beheermaatregelen zal zijn op het voorkomen van in Nederland zeldzame plantensoorten. Het is daarmee een model dat een maat geeft voor de potentiële botanische diversiteit in Nederland.

Het model is gebaseerd op 33706 vegetatieopnamen die representatief worden geacht voor de Nederlandse natuur. Om de opnamen een waardering te geven is gekeken naar de soortensamenstelling van de vegetatieopnamen. Hiervoor heeft elke in Nederland voorkomende plantensoort een waarde gekregen. Deze waarde is gebaseerd op de rode lijst criteria: de zeldzaamheid van de plantensoort (hoe zeldzamer, hoe hoger de waardering), de trend van de soort (gaat de soort achteruit een hoge waarde, gaat de soort vooruit een lage waarde) en het belang van het voorkomen van de soort in Nederland (heeft de soort Europees gezien een belangrijke niche in Nederland). De waarden van de soorten worden per opname gemiddeld tot een waarde voor die opname. Die waarde is weer aan de afzonderlijke soorten van elke opname toegekend en is gecombineerd met de Ellenberg-indicatorwaarden voor zuurgraad, vocht en nutriënten van elke soort. Alle vondsten (soort/opname combinaties) zijn vervolgens in een driedimensionale matrix geplaatst op basis van de drie Ellenberg-indicatorwaarden. Hierop is met de eerder genoemde 'spline' techniek een regressie uitgevoerd. Door de uitkomst van SMART2-SUMO (pH en stikstofbeschikbaarheid) en de voorjaarsgrondwaterstand om te rekenen naar Ellenberg-getallen en deze als invoer voor de matrix te gebruiken wordt er een waarde voor de botanische diversiteit verkregen. Feitelijk is dit een maat voor de kans op het voorkomen van rode lijst soorten bij de gegeven abiotische condities. Het model is toegepast in samenhang met SMART2-SUMO om drie beleidscenario's te evalueren in het kader van de Natuurverkenningen op landelijke schaal. De scenario's bleken geringe verschillen te geven, maar voor alle scenario's werd er een vooruitgang in de botanische diversiteit berekend. Daarbij moet worden opgemerkt dat alle scenario's er

van uitgaan dat de stikstofdepositie daalt in Nederland. Daarnaast gaat het om een gemiddelde waarde, in een deel van Nederland gaat de botanische diversiteit wel achteruit.

Een hoge stikstofdepositie heeft aantoonbare negatieve effecten op de natuur. De samenstelling van de vegetatie verandert er door, meestal van een soortenrijke vegetatie in een soortenarme. De vegetatie wordt door de 'bemesting' met stikstofverbindingen vaak gedomineerd door een paar soorten. Om dit verlies van soorten en dus biodiversiteit teniet te doen worden vegetaties intensiever beheerd dan anders nodig zou zijn. Heide wordt nu bijvoorbeeld elke twintig à dertig jaar geplagd in plaats van elk zestig à negentig jaar. Door het intensievere beheer wordt de extra stikstof afgevoerd. Het intensievere beheer brengt echter extra kosten met zich mee. Er is meer betaalde arbeid nodig en de verwijderde biomassa moet worden verwerkt. Als de depositie gaat dalen, dan zullen die kosten minder worden omdat er minder beheerd hoeft te worden. Met behulp van de modellen SMART2-SUMO en MOVE3 heb ik onderzocht of en hoeveel de beheerintensiteit verminderd zou kunnen worden en hoeveel geld dit de beheerder zou besparen (hoofdstuk 6). MOVE3 is een model vergelijkbaar met NTM3, maar in plaats van de natuurwaarde wordt door dit model de kans op het voorkomen van plantensoorten berekend op basis van Ellenberg-indicatorwaarden. Als uitgangspunt is het natuurdoeltypensysteem genomen. Per natuurdoeltype is een representatief aantal gebieden genomen, verspreid over Nederland. Vervolgens zijn de verschillende vormen van beheer evenredig met hun frequentie van toepassing toegekend aan de natuurdoeltypen, verspreid over heel Nederland. Met behulp van de modellen is de huidige natuurkwaliteit berekend voor de huidige beheerintensiteit. Vervolgens is voor een dalende depositie per gebied berekend welke van de vier doorgerekende beheerintensiteiten nodig is om minimaal dezelfde plantendiversiteit te behouden. De beheerkosten voor elk van de scenario's zijn geschat en voor het scenario met minimaal dezelfde biodiversiteit vergeleken met de huidige kosten. De modelberekeningen zijn niet uitgevoerd voor moerassen en vennen, omdat de modellen hiervoor niet geschikt zijn. De bossen zijn ook niet gemodelleerd, omdat het beheer nauwelijks of geen effect heeft op de stikstofhuishouding. Om toch een kostenschatting voor deze ecosystemen te kunnen maken is er gewerkt met expertkennis.

De resultaten laten zien dat bij een dalende stikstofdepositie inderdaad minder beheerkosten hoeven te worden gemaakt om de huidige botanische diversiteit te behouden. Voor een klein deel van de natuurdoeltypen wordt een lagere of gelijke biodiversiteit bereikt bij een dalende stikstofdepositie. Om de resultaten wat overzichtelijker te maken zijn de natuurdoeltypen geaggregeerd tot ecosysteemtypen. Volgens de modelberekeningen kan dan in totaal ongeveer € 42.000.000,- per jaar worden bespaard op het beheer van 2000 tot 2020, mits de depositie daalt volgens het hier gebruikte scenario. Jaarlijks wordt er naar schatting in Nederland in totaal tussen de 160.000.000,- en 190.000.000,- Euro aan natuurbeheer besteed. Absoluut gezien

kan het meeste worden bespaard op het beheer van graslanden (€ 28.000.000,-). Per hectare is de besparing het grootst voor rietland (299,- €/ha/j) en het laagst in bossen (5,- €/ha/j). Gemiddeld kan er 80 €/ha/j worden bespaard op het beheer als de depositie daalt en men dezelfde biodiversiteit blijft nastreven.

De modelketen SMART2-SUMO-NTM3 geeft de mogelijkheid om (internationale) beleidsdoelen te evalueren. In hoofdstuk 7 heb ik onderzocht of de doelstellingen van het Kyoto protocol te verenigen zijn met de biodiversiteitsdoelstellingen bij een veranderende stikstofdepositie. Voor een stikstofdepositie variërend van 5 kg N/ha (achtergronddepositie) tot 70 kg N/ha is de koolstofvastlegging en de plantenbiodiversiteit berekend. Dit is gedaan voor alle bossen in Nederland (koolstofvastlegging) en alle natuurgebieden (biodiversiteit). De koolstofvastlegging was hoger naarmate de depositie hoger was. Bij een lage stikstofdepositie zouden de Nederlandse bossen netto koolstof gaan uitstoten in plaats van vastleggen. Tegelijkertijd wordt door NTM voor de bossen weinig verandering in biodiversiteit gesimuleerd. Alleen bij de laagste depositie zou een klein deel van de bossen een relatief hoge botanische diversiteit kunnen krijgen. Echter voor heiden en graslanden worden bij een lagere depositie wel veel hogere biodiversiteitswaarden berekend. Om dit verder te onderzoeken heb ik een scenario gebruikt waarbij de depositie van gemiddeld 40 kg N/ha naar 10 kg N/ha per jaar zou dalen in 2020. Het resultaat is vergeleken met een constante depositie van 40 kg N/ha per jaar. Hieruit bleek dat een daling tot mogelijk 27% van de koolstofvastlegging bij een constante hoge depositie op zou kunnen treden. Ook voor het dalende depositiescenario is er nog weinig verbetering te verwachten van de botanische diversiteit in de bossen. Wel is er een enorme verbetering te zien in botanische diversiteit in heide en grasland. Aan het eind van de simulatie is de botanische diversiteit de waarde genaderd die gesimuleerd wordt bij een constant lage depositie (10 kg N/ha). Ik concludeer hieruit dat het erop lijkt dat de biodiversiteitsdoelstellingen gehaald kunnen worden voor graslanden en heiden, mits de stikstofdepositie daalt. Dit gaat echter ten koste van het koolstofvastleggende vermogen van de Nederlandse bossen, waardoor de doelstellingen uit het Kyoto protocol moeilijker kunnen worden gehaald.

Dankwoord



Dankwoord

Tis niet te geloven, maar het is gelukt! En dat dankzij de medewerking van velen. En voor degene die ik hierna ben vergeten te bedanken, toch bedankt!

Frank Berendse, jij stond aan de wieg van SUMO en wist elk artikel dat je kreeg voorgelegd weer van meerwaarde te voorzien, zelfs als alles al voorgekookt was door Han van Dobben en mij. Minstens zo interessant als de discussies over het proefschrift waren altijd weer de organisatorische en bestuurlijke perikelen van WUR. Han, voordat er zelfs maar sprake was van een proefschrift was jij er al bij betrokken. Veel discussies hebben we gevoerd over alle artikelen (en wat al niet meer), vaak ook inhoudelijk, maar vaker nog over spellingsregels. Want hoewel spellen tegenwoordig niet meer belangrijk lijkt viel er bij mij taalkundig steeds weer wat bij te schaven. Veel heb ik van je opgestoken.

Veel van het inhoudelijk onderzoek in dit proefschrift is gefinancierd door het Milieu en Natuur Planbureau, waarbij Dirk-Jan van der Hoek, Jaap Wiertz en Harm Houweling niet alleen voor de financiën en projectbegeleiding zorgden, maar ook inhoudelijk mee dachten.

Een belangrijk onderdeel van het proefschrift is gebaseerd op metingen die door velen in het veld zijn verricht. Aan deze mensen, die ik lang niet allemaal persoonlijk ken, ben ik veel dank verschuldigd. Meten is weten, hoewel dat in het modellengeweld gemakshalve wel eens wordt vergeten. Joop Schaminée, uit jouw bibliotheek zijn een groot aantal gegevens tevoorschijn getoverd.

De vele gegevens werden ingevoerd en gecontroleerd door Veronique Joosten, Joep Frissel en Ruut Wegman. Een zwaar karwei waar ik jullie zeer dankbaar voor ben. Pieter Slim, jij leidt al enige jaren als projectleider (of lijder?) dit project in goede banen, waardoor ik in de luwte kon werken aan de inhoud. Speciaal in de hoofdstukken twee en drie, maar ook in andere onderdelen is statistiek toegepast. Waar in het begin Cajo ter Braak de statistische kant voor zijn rekening nam (o.a. voor het model NTM), heeft later vooral Paul Goedhart significant bijgedragen aan de nog steeds doorgaande uitwerking van al die gegevens.

A major part of my ideas about the application and replacement of Ellenberg-indicator values originate from a visit to the group of Professor Philip Grime in Sheffield (UK). I enjoyed the discussions, as well as the scenery around Sheffield very much. Due to the research described in this thesis I had the opportunity to meet many people at symposia, workshops etc. Simon Smart thanks for your critical response on Chapter 2 in Journal of Vegetation Science. One thing led to another and now we are involved together with Chris Evens, Ed Rowe and Bridget Emmet, in plant species responses and modelling vegetation development for the UK. I enjoy working with you all very much. And Simon when are we going to participate together in an official

Dankwoord

long distance run? The paper about the Ellenberg-indicator values drew quite some attention and besides Simon other people reacted, which led to cooperation with Martin Diekmann, Jean Claude Gegout and José Miguel Olano. Your input was highly appreciated and hopefully the article will be ready this year. Ook Flip Witte reageerde en ook daaruit is een prettige samenwerking voortgevloeid.

Om de werking van procesmodellen te verbeteren is experimenteel werk onontbeerlijk, Adrie van der Werf, Tom Dueck en vooral Willem de Visser hebben mij veel bijgeleerd over het uitvoeren van experimenten. Jammer dat het onderzoek het proefschrift net niet gehaald heeft.

Aan de ontwikkeling van de modellen is en wordt gewerkt door verschillende mensen: Eric Schouwenberg, Janet Mol-Dijksyta, Hans Kros, Wim de Vries, Janien van der Gref en René Jochem. Jullie droegen bij en inspireerden wat leidde tot betere modellen. En Eric, kamergenoot, het is wel saai als je er eens een dagje niet bent.

Veel gezelligheid tijdens het werk komt voort uit het team (EMM tegenwoordig) en het 'andere' team EN. Koffiepauzes, lunches, wandellunches, teamuitjes en heidesessies zijn onmisbaar voor de uitstekende sfeer.

Alle collega's, vrienden en familie zeg ik: het is af. Eindelijk kan ik de vele vragen van jullie over wanneer is het zo ver, beantwoorden met een boekwerk. Veel plezier bij het lezen. Ik weet, ik heb wel eens gespeculeerd over promoveren in 2002, tegelijk met Christine. Het is een 'ietsje' later geworden. Anja en Fred, ik hoop dat we onze interessante discussies over de biologie nog lang voort kunnen zetten. Bijzonder speciale dank gaat uit aan Sandra en Janet die mijn paranimfen wilden zijn.

Christine, jij ging mij voor en leerde mij kritisch te kijken naar artikelen waarvan ik dacht dat ze al af waren. Ooit dachten we aan promoveren op dezelfde dag, het is voor mij wat later geworden en het zullen twee doctoren onder weer een nieuw dak worden, zonder stropdas, dat wel.

Groetjes

A handwritten signature in dark ink, consisting of a series of connected, slightly jagged lines that form a stylized, somewhat abstract shape.

Curriculum vitea



Curriculum vitae

De auteur van dit proefschrift Gerrit Willem Wieger Wamelink is geboren op 16 september 1966 te Winterswijk. Daar doorliep hij met goed gevolg achtereenvolgens kleuterschool de Zwanenpol, openbare lagere school O en de MAVO en HAVO aan de RSG Hamaland. Daarna ging hij een jaar lang op en neer naar de Hogere Laboratorium School te Hengelo (Overijssel), om vervolgens in Wageningen neer te strijken voor de studie botanisch laborant aan de Rijks Hogere Agrarische School Wageningen. Hij deed zijn stage bij RBL De Dorschkamp (nu Alterra) met onderzoek naar de vegetatieve vermenigvuldiging van eikenembryoos in weefselkweek en een afstudeervak bij het Stichting voor Plantenveredeling (SVP, nu Plant Research International; PRI) over de vermeerdering van het gras *Lolium perenne* met behulp van protoplasten cultuur. De studie werd daarna enige tijd onderbroken, waarin Wieger een klein half jaar bij de Stichting voor Bodemkartering (STIBOKA, nu Alterra) chemische analyses uitvoerde aan katteklei uit Borneo. Daarna mocht de vervangende diensttijd worden vervuld bij het Rijks Instituut voor Natuurbeheer (RIN, nu Alterra) aan het afrondende werk van het grote verzuringonderzoek (het scheiden van grassen en heide in gedroogd weefsel en het uitspoelen van wortels) en het inventariseren van korstmossen in het korstmossenmeetnetwerk in Nederland (op de fiets). Na het voortijdig beëindigen van de vervangende dienstplicht werd de studie voortgezet aan de Landbouwniversiteit Wageningen (LUW, nu Wageningen Universiteit; WU) van 1990 tot en met 1993, het eerste jaar gecombineerd met voortzetting van het werk voor het RIN. Als doorstromer plantenveredeling deed Wieger afstudeervakken bij de vakgroep plantenfysiologie aan de vegetatieve vermeerdering van tulpen en bij de vakgroep genetica aan de klonering van het late bloei gen van *Arabidopsis thaliana*.

Na het afstuderen ging Wieger vrijwilligerswerk doen bij het Instituut voor Bos- en Natuurbeheer (IBN, nu Alterra), waarna korte tijdelijke aanstellingen elkaar opvolgden. Bij de totstandkoming van Alterra mondden de contractjes uit in een vaste baan. In de IBN periode werd al de basis gelegd voor dit proefschrift met de start van het verzamelen van data. Het model NTM werd verbeterd en het successiemodel SUMO werd ontwikkeld (met de hulp van velen!). Daarnaast werkt hij al vanaf het prille begin aan de relatie plant-bodem, wat ook zijn weerslag heeft gevonden in dit proefschrift. Daarnaast werkt Wieger mee aan verschillende projecten als projectleider of projectmedewerker, wat ook blijkt uit de diversiteit aan rapporten en publicaties. Hij hoopt in de toekomst de ontwikkelde kennis en modellen verder uit te bouwen en ook in te zetten in het buitenland.

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