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HEATHSOL: sensitivity/uncertainty analysis and validation

A. de Koning[1] and A.H. Bakema

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[1] Agricultural University Wageningen
Department of soil science and plant nutrition

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National Institute of Public Health and the Environment. P.O. Box 1. 3720 BA Bilthoven. tel 030-2749111, fax 030-2742971.

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ABSTRACT

A sensitivity analysis and restricted uncertainty analysis and validation of a model describing competition between a heather and grass species (HEATHSOL), was carried out. The results of the sensitivity analysis show that the competition process is mostly influenced by parameters determining light and nutrient competition, mortality and minimum/maximum nitrogen content of the plant species. The uncertainty analysis was only carried out qualitatively. An evaluation was made of the parameters which may contribute substantially to the uncertainty of the model output. The most important are specific leaf area, root length, model initialisation and deposition. The validation shows that the model can describe the competition in a Calluna/Deschampsia and Calluna/Molinia vegetation satisfactorily.

SUMMARY

A sensitivity analysis and restricted uncertainty analysis of a model describing competition between a heather and grass species (HEATHSOL), was carried out. HEATHSOL simulates the development of a dry or wet type heathland vegetation as influenced by nitrogen deposition. The model focuses on the competition between a heather and a grass species for light and nutrients. The sensitivity of the competition process to variations in boundary conditions, model initialisation and model parameters was investigated using Monte Carlo simulation with Latin Hypercube Sampling in a preset range of the input parameter domain. The results of this analysis show that the model results are mostly influenced by specific leaf area, height coefficients, root lengths, mortality rates and minimum/maximum nitrogen contents of the species. These conclusions only apply for the used conditions. Specific leaf area and height coefficients of the plant species determine the light competition between the species and root length determines the nutrient competition between the species. In the statistical analysis the linear regression model could only be applied on the first 10 years of the simulation period. After this period the competition process lead to the practical disappearance of one of the species. The variation of the parameters causes the output of the model to be divided in two categories: the runs in which the grass species dominate and runs in which the heather species dominate the vegetation after several years. The subdivision of the output induces a corresponding subdivision of the input and by means of a statistical tool, Kolmogorov-Smirnov statistics, the importance of the parameters for the subdivision of the model output is measured.

The uncertainty analysis is needed to obtain information on the uncertainty in the predicted heathland development. Unfortunately the uncertainty analysis could only be carried out qualitively. There were hardly any data on the uncertainty of the sources. Therefore an evaluation was made (based on the results of the sensitivity analysis and expected uncertainty of the sources) of the parameters which may contribute substantially to the uncertainty of the model output. The most important are specific leaf area, root lengths, model initialisation and deposition. The uncertainty in the model output can be reduced by better assessing the uncertainty of these parameters. This however would call for extra experimental information.

For a calibration of the model the initial conditions that are highly uncertain and if necessary also the factors influencing the light competition and nutrient competition are the most obvious parameters to be used. The results of the validation of HEATHSOL show that with the adjustment of the initial biomass distribution, the competition between Calluna/Deschampsia and Calluna/Molinia can be described very well, when heatherbeetle plagues are included in the calculations. The competition between Erica/Molinia cannot be described satisfactory and adjustment of other parameters is required.

SAMENVATTING

Een gevoeligheidsanalyse en een beperkte onzekerheidsanalyse werden uitgevoerd van een model, dat de competitie tussen heide en gras soorten beschrijft (HEATHSOL). HEATHSOL beschrijft de ontwikkeling van een droog en nat type heide vegetatie zoals die wordt beïnvloed door stikstof depositie. Het model concentreert zich op de competitie tussen heide- en gras-soorten. De gevoeligheid van het competitieproces voor variaties in modelgrenzen, modelinitialisatie en modelparameters werd onderzocht, gebruik makend van Monte Carlo simulatie met 'Latin Hypercube Sampling' in een van te voren gedefinieerde parameterruimte. De resultaten van deze analyse laten zien dat de model uitkomsten het sterkst worden beïnvloed door specifiek bladoppervlak, hoogtecoëfficiënten, wortellengten, sterfte snelheden en minimum/maximum stikstof gehalten van de planten. Het specifiek bladoppervlak en de hoogtecoëfficiënt bepalen de lichtcompetitie tussen de planten, en de wortellengte bepaalt de nutrient competitie. Bij de statistische analyse bleek dat het lineaire regressiemodel alleen gebruikt kon worden voor de eerste tien jaar van de simulatieperiode. Na deze periode verdwijnt een van de twee soorten praktisch uit de vegetatie. De variatie van de parameters leidt tot het in twee delen uiteenvallen van de simulatie-runs: de runs waarin de heidesoorten overheersen en de runs waarin gras-soorten overheersen na enkele jaren. Deze tweedeling in de modelresultaten leidt tot een overeenkomende tweedeling in de invoer van het model en met behulp van een statistische techniek, Kolmogorov-Smirnov statistiek, kan de invloed van de parameters op deze tweedeling gemeten worden.

De onzekerheidsanalyse is nodig voor het verkrijgen van informatie over de onzekerheid in de voorspelde heidevegetatie-ontwikkeling. Helaas kon de onzekerheidsanalyse alleen kwalitatief uitgevoerd worden. Er waren te weinig gegevens over de onzekerheid in de parameters. Daarom is (op basis van de gevoeligheidsanalyse en de verwachtte onzekerheid in de bronnen) geschat welke bronnen substantieel bijdragen aan de totale onzekerheid van de modeluitkomsten. De belangrijkste zijn specifiek bladoppervlak, wortellengte, modelinitialisatie en depositie. De onzekerheid in de modelresultaten zou verkleind kunnen worden door het beter bepalen van de parameters maar dat zou extra experimenteel werk met zich meebrengen.

Voor een calibratie van HEATHSOL zijn de initiële condities (die erg onzeker zijn) en zonodig ook de factoren die de licht en nutrient competitie beïnvloeden de meest voordehandliggende parameters. De validatie van HEATHSOL laat zien dat met de aanpassing van de initiële biomassaverdeling, de competitie in Calluna/Deschampsia of Calluna/Molinia goed beschreven kan worden, wanneer heidekever-plagen meegenomen worden in de berekening. De competitie tussen Erica/Molinia kan niet goed beschreven worden en aanpassen van andere parameters is noodzakelijk.

1. INTRODUCTION

According to the 'wet milieubeheer', approximately every four years a study has to be made of the environmental problems in the Netherlands (Michiels, 1992). In 1988 the first of these 'National Environmental Outlooks' called 'Concern for tomorrow' was published (RIVM, 1988). This study gave an overall view of the environmental problems in the Netherlands, and evaluated the future developments analysing the effects of three environmental policy scenarios. For these studies a great number of models were used for evaluating the effects of policy scenarios. The models were not specially developed for this purpose and evaluating a policy scenario was very time consuming. It was therefore decided to create a set of models that would operate together as modules within one system specifically developed for evaluating policy scenarios. This model system was named EXPECT (EXPloring Environmental Consequences for Tomorrow) (Braat et.al. 1991) and aims at rapid evaluation of policy scenarios.

HEATHSOL is part of the EXPECT model system. HEATHSOL will be used to evaluate the impact of nitrogen deposition on heathland vegetation in the Netherlands. HEATHSOL was derived from two other models used to calculate the impact of nitrogen deposition on dry and wet type heathland vegetation (Calluna, NUCOM). These models were developed separately and were not compatible. Process formulations were different. Both models were combined to form HEATHSOL. The main objective of HEATHSOL is to describe the effects of nitrogen deposition on the species composition of a heathland vegetation (Bakema et.al.,1994). The model focuses on the competition for nutrients and light between a heather species (either Calluna vulgaris or Erica Tetralix) with a grass species (either Molinia caerulea or Deschampsia flexuosa). The model can be used to assess the effect of nitrogen deposition on the heathland vegetation. HEATHSOL became operational in march 1994. A sensitivity analysis or uncertainty analysis of the model had not been done. A sensitivity and uncertainty analysis can give valuable information on model behaviour and information for the calibration of the model. Sensitivity and uncertainty analysis is required for a correct calibration of a computer model, see Janssen & Heuberger 1992. It is one step in the model development cycle.

This study is part of the project: adaptation, calibration and validation of HEATHSOL for use in DAS (=Dutch Acidification Systems). The research was conducted from February 1995 till July 1995 for the project 408143 and 733001 and has been conducted on behalf and for the account of the Directorate-General for Environment, Directorate Strategic planning and Directorate Air.

The sensitivity analysis and uncertainty analysis was carried out with a software package called UNCSAM (= UNCertainty analysis by Monte carlo SAMpling techniques) developed at the RIVM by Janssen et.al. 1992, and a computer program GENSEN (= GENeralized SENsitivity analysis) recently developed at the RIVM by P.H.M. Janssen 1995. Both are specially developed for a concise analysis of computer models. The figures in this report where created with the graphical tool XY. This program has been developed to be coupled with simulation models and database programs. Input and output of the program is in ASCII-files which simplifies interfacing with the programs (Heerden & Tiktak, 1994).

The report starts with a description of how sensitivity and uncertainty analysis should be carried out on computer models. The statistical methods used in the sensitivity analysis of HEATHSOL are described in chapter 3. A description of the model HEATHSOL is given in chapter 4. First a (crude) sensitivity analysis for all the parameters in the model is made. Then a more refined analysis is made with a selection of the most sensitive parameters. In chapter 7 the parameters which contribute mostly to uncertainty of the model output, are identified. In Chapter 8 observed development of heathland vegetation is compared with model calculations. Finally the conclusions are given in chapter 9.

2. SENSITIVITY AND UNCERTAINTY ANALYSIS OF COMPUTERMODELS

2.1 Introduction

Computermodels are widely used for the assessment of the impact of human handling on the environment. These models should be reliable. Model analysis is needed to assess the reliability of a model. Model analysis will also give valuable insight in the behaviour of the model, crucial aspects of the model and limitations of the model. Assessment of the reliability of a model by model analysis usually consists of performing:

1 sensitivity analysis : The study of the influence of variations in model parameters, initial conditions etc. on the model outputs.
2 uncertainty analysis : the study of the uncertain aspects of a model, and their influence on the model outputs.

When applying sensitivity analysis the sensitivity of the model for variations of sources (i.e. modelparameters and initial values) will be examined. The probability of these variations is not looked at. This is the subject of investigation in an uncertainty analysis, where the results will be examined of the uncertainty in the sources on the model output. An uncertainty analysis will thus require more information about the parameters. A knowledge of the uncertainty of the parameters in the model is necessary. The uncertainty in the model output will depend on the sensitivity of a parameter. This is exemplified in the next table.

	not sensitive	sensitive
certain	-	?
uncertain	?	++

In which '-' denotes a low uncertainty contribution, '++' a high contribution and '?' a unknown (low/high) contribution.

The results of the sensitivity and uncertainty analysis will give information on parameters/sources which can be used for calibration of the model. Also experimental information can be attained more efficient. Parameters which need to be sampled with high accuracy are known a priori. Furthermore it can give information on the parts of the model which have to be adjusted or can be simplified. In the next section the strategy of a sensitivity or uncertainty analysis is given.

2.2 Strategy

Problem formulation

This stage should answer questions like: Why is sensitivity cq. uncertainty analysis needed?; What information is needed?; In which form should this information be reported?

Inventory of sensitivity or uncertainty 'sources'

Possible sources of sensitivity and uncertainty are:

(a) The model structure: Formulation of equations describing processes. Assumptions/simplified/neglected processes.
(b) The model inputs/external factors: It is not clear how the surroundings influence the system or process. Some factors are difficult to quantify (the weather).
(c) Boundary or initial conditions: Often little is known about initial conditions of model variables.
(d) Model parameters : The various coefficients characterizing the behaviour of the modelled processes. Exact values of these coefficients are often unknown.
(e) The computational scheme. Errors in data processing and communication. Rounding off and truncation of values. These are difficult to quantify but are usually minor.

Those sources are chosen that have partially (unknown) or varying values cq. factors that will/can be manipulated or controlled. In this study only sensitivity and uncertainty sources related to model parameters and inputs (b,c,d) will be considered.

Quantification of the sources.

As the number of sources is usually too great too handle at once, reduction of the sources is necessary. Also not all the sources can be quantified. A first screening will be necessary to preselect those sources that will be studied in detail. Quantification of those sources is then as follows:

(a) For sensitivity analysis specifying:
  - nominal values of sources
  - appropriate variations around values.
  large variations which cover a wide range in the parameter space (global analysis) or small variations covering the direct neighbourhood of the nominal value (local analysis).

Are we interested in the single variation of one parameter keeping other parameters at their nominal value or are we interested in the simultaneous variation of all the sources.

(b) uncertainty analysis will depend on:
- nature of the uncertainty
- information available

It is usually very difficult to quantify the uncertainty in the sources, and will at least require extensive literature studies or experimental work.
Two essentially different forms in which uncertainty shows up:
1 Uncertainty due to lack of knowledge or to lack of accuracy.
2 Uncertainty originating from natural variability cq heterogeneity.

Quantification of the uncertainty in the sources for HEATHSOL is also hampered by a lack of knowledge. The uncertainty analysis can only be carried out qualitatively.

Evaluation of the effects on model outputs.

(a) In a sensitivity analysis is evaluated, how the variations of the various sources around their nominal values affect the considered model outputs.
output:
- graphical; plotting model outputs for various values of the varying sources.
- computing sensitivity measures and reporting in tabular or graphical form.

Importance of various 'sources' is ranked in order to detect the most sensitive ones. Normalisation will often be necessary.

(b) In an uncertainty analysis one first evaluates the total influence of the uncertainties on the model outputs. This can be reported in several ways:
- the range of the model outputs
- the mean and the variance
- empirical distribution functions and histograms
- percentile values, e.g. 2.5, 50 (mean) and 97.5 percentile.

Information on the accuracy of the estimates of the parameters must be available .
One tries to discover which sources contribute substantially to the total uncertainty (total ranking).

2.3 Sensitivity and uncertainty analysis with UNCSAM

Sensitivity and uncertainty analysis of the mathematical model is performed with a software package called UNCSAM (= UNCertainty analysis by monte carlo SAMpling techniques). This software package was devolved at the RIVM by Janssen et.al. (1992) for performing sensitivity and uncertainty analyses in an appropriate and reliable way. UNCSAM uses a Monte Carlo method for sensitivity and uncertainty analysis.

Monte Carlo methods for sensitivity and uncertainty analysis rely on the fact that variations cq. uncertainties in the sources can usually be suitably described by specifying (simultaneous) probability distributions (mean, variance, distribution) and mutual correlations, which reflect these variations c.q. the probability (Janssen et. al., 1990). After specification of the distribution, random sampling is performed from these distributions (Monte Carlo sampling). The Monte Carlo sampling randomly generates model parameter values. These sampled values are subsequently used to simulate the model outputs. (Monte Carlo simulation). The results of the simulation are stored for further analysis. This further analysis consists of computing and showing basic statistical information (means variances percentiles), of assessing the accuracy of the determined quantities (confidence bounds) and performing regression and correlation analysis to obtain insight into the sensitivity and uncertainty contributions of the various 'sources' (see chapter 3). A disadvantage of the Monte Carlo approach is the large number of samples required.

In order to limit the computational load, specially for large models an efficient sampling technique is needed. A recently developed efficient sampling technique, called the Latin Hypercube Sampling technique (LHS), reduces the number of simulations. This technique uses a stratified way of sampling from the separate 'sources' on basis of a subdivision of the range of each source. The samples of each source are randomly paired to the sampled values of the second 'source, etc., which finally results in N combinations of p parameters. The occurrence of correlations between parameters is also easily incorporated with the LHS technique.

When using LHS, the parameter space is representatively sampled with only a few samples (i.e. N can be small). A choice of $N > 4/3$ p samples, where p is the number of parameters to be sampled, usually gives satisfactory results. $N = 4/3$ p could be too small when strong non-linear behaviour is expected. The number of samples to be taken should then be higher.

3. MEASURES FOR SENSITIVITY AND UNCERTAINTY ANALYSIS.

In this chapter the various statistics for quantifying the uncertainty or sensitivity of parameters/sources used in this study are given. For a complete reference of measures for sensitivity and uncertainty analysis see (Janssen et.al.,.1990).

3.1 Linear regression

Various statistics are employed to quantify the sensitivity and uncertainty contributions of the sources to the model outputs.

Part of the measures used in this study are deduced from the linear regression model. With linear regression analysis the relation between the computed value (y) and the various sources/parameters (x_1,...,x_p) can be represented by a linear model according to:

$$y = \hat{\beta}_0 + \hat{\beta}_1 x_1 + \ldots + \hat{\beta}_p x_p + \hat{e} \tag{3.1}$$

The original model (HEATHSOL) is replaced by a so called metamodel (linear regression model). The foregoing formulation is valid for one simulation run. When k simulation runs are performed the regression equation is given by:

$$y(k) = \hat{\beta}_0 + \hat{\beta}_1 x_1(k) + .. + \hat{\beta}_p x_p(k) + \hat{e}(k) \qquad k = 1,..,N \tag{3.2}$$

$$y(k) := \hat{y}(k) + \hat{e}(k) \qquad k = 1,\ldots,N \tag{3.3}$$

In which (β_1,...,β_p) denote the estimated regression coefficients and ê denotes the estimated regression residual. The regression coefficients are also called ordinary regression coefficients (ORC), and are a absolute measure of sensitivity.

The regression coefficients can be determined by minimizing the sum-of-squares according to:

$$\sum_{k=1}^{N}(y(k) - [\beta_0 + \sum_{i=1}^{p}\beta_i x_i(k)]^2) \tag{3.4}$$

The coefficient of determination (COD, also called R^2) of this regression is equal to:

$$R^2 := \frac{S_{\hat{y}}^2}{S_y^2} = 1 - \frac{S_{\hat{e}}^2}{S_y^2} \tag{3.5}$$

In which $S_{\hat{e}}$ is the standard deviation of the regression residual, and S_y is the standard deviation of the model outcome. The COD varies between 0 and 1. The COD measures the fraction of the variance in the model-outcome which is explained by the linear regression model. In fact the COD expresses the validity of the linear model representing the original model outcome y. When COD ≈ 1 the fit is good. When the COD is lower than 0.7 the linear regression model cannot be applied as a fair approximation of the model. The variance of the model outcome (S_y^2) is defined according to:

$$S_y^2 := \frac{1}{1-N} \sum_{k=1}^{N} (y(k) - \bar{y})^2 \tag{3.6}$$

The linear regression model has two disadvantages:

1 If y is also dependent on other quantities/parameters (z_1,..,z_h) and x is also strongly correlated with these quantities/parameters then regression analysis does not give the influence of x on y. The effects contributed by (z_1,..,z_h) are also included in the regression coefficients. z_1..z_h should be independent of x.

2 If the relation between x and y is strongly nonlinear, linear regression analysis is not a good measure for expressing the connection between x and y.

The first disadvantage can be overcome by applying partial or semi partial data regression. The second disadvantage can be overcome by using data transformation (for example regression on ranked data or second order regression)

3.2 Measures based on regression analysis

On the basis of the regression relations we can express the uncertainty in y (as expressed by its variance S_y^2) in terms of β_i, S_{x_i} and the correlation coefficients $r_{x_i x_j}$

$$S_y^2 = \sum_{i=1}^{p}\sum_{j=1}^{p} (\hat{\beta}_i S_{x_i})(\hat{\beta}_j S_{x_j}) + S_{\hat{e}}^2 \tag{3.7}$$

The summation on the right hand side of the equation expresses the total linear uncertainty contribution of the sources x_i. If x_i is uncorrelated with other sources ($r_{x_i x_j} = 0$ and $i \neq j$)

then $\beta_i Sx_i$ measures the linear uncertainty contribution of the sources x_i. The quantity $\beta_i Sx_i$ is a combination of the sensitivity and the uncertainty Sx_i in the 'source'.
The related dimensionless standardized quantity:

$$\hat{\beta}_i^s = \hat{\beta}_i \frac{S_{x_i}}{S_y} \tag{3.8}$$

is called the Standardized Regression Coefficient (SRC). It measures the fraction of the uncertainty in y which is contributed by x_i (In case $r_{x_i x_j} = 0$ and $i \neq j$). It will give only a valid impression of the contribution of source x_i if the sources show no substantial correlation and if the linear regression model is a fair approximation of the original model output (i.e. $R^2 \approx 1$). SRC is still considered a good measure when the $R^2 > 0.7$ (Janssen et.al., 1992) The SRC can be considered as a relative sensitivity measure, that measures the relative change Δ of y, relative to the standard deviation Sx_i, while other 'sources' remain constant:

$$\frac{\Delta y}{S_y} = SRC_i \frac{\Delta x_i}{S_{x_i}} \tag{3.9}$$

Another standardized quantity is called the Normalized Regression Coefficient (NRC). It is a relative sensitivity measure: It measures the (relative) change Δy of y, in terms of its average $\bar{y}$, if x_i changes (relatively) in terms of its average $\bar{x}_i$ while other 'sources' remain constant:

$$\frac{\Delta y}{\bar{y}} = NRC_i \frac{\Delta x_i}{\bar{x}_i} \tag{3.10}$$

This measure gives an impression of sensitivity. Interaction is not taken into account and application is only justified in case of a good linear approximation.

A sensitivity analysis does not aim at quantifying the uncertainties but the results can often easily be used to infer some conclusions about the uncertainties. During the sensitivity analysis one has computed the NRC's. If the standard deviation Sx_i expresses the actual variability of the source x_i, the SRC is related to the NRC as:

$$SRC_i = NRC_i \frac{CV_i}{CV_y} \tag{3.11}$$

where CV_i and CV_y denote the coefficients of variation for x_i and y respectively. This result shows that the relative uncertainty contribution, as measured by the SRC, can be expressed as the multiplication of the relative sensitivity contribution NRC, and the ratio between the relative uncertainty in the 'source' x_i and in the model output y. This establishes a simple link between sensitivity and uncertainty.

3.3 Measures based on correlation analysis

Correlation analysis consists of measuring the association between the parameter x_i and the model output y. The most simple measure is the Linear Correlation Coefficient r_{yx_i} (LCC). It measures the linear relationship between y and x_i. The linear correlation coefficient is defined as:

$$r_{xy} := \frac{\Sigma(x(k) - \bar{x})(y(k) - \bar{y})}{\sqrt{\Sigma(x(k) - \bar{x})^2} \cdot \sqrt{\Sigma(y(k) - \bar{y})^2}} \tag{3.12}$$

Values of the LCC lie between +1 and -1. A high value of r_{yx_i} indicates that y can be written as linear function of x_i. When LCC is approximately zero, x_i and y are not correlated. In case x_i is correlated to other parameters $z_1,..,z_h$, x_i also incorporates the effect of the other parameters on the model outcome y.

A way out is to use the Partial Correlation Coefficient (PCC), which is adjusted by correcting first y and x_i for all the effects of the other parameters.

$$PCC_i := r_{\tilde{y}_i,\tilde{x}_i} \tag{3.13}$$

In which x̃ and ỹ denote the corrected x_i and y. In this case y is also corrected for the influences of the correlated x_i. The uncertainty measure (PCC_i) is concerned with a different model output (i.e. $\tilde{y}_i$) for each different parameter $\tilde{x}_i$. This hampers a fair comparison between the various parameters (Janssen et.al., 1990). An alternative measure (SPC = Semi Partial Correlation coefficient) does not have this drawback. In this case only the parameter x_i is corrected, and the corrected quantity is correlated with the original model output y:

$$SPC_i := r_{y,\tilde{x}_i} \tag{3.14}$$

Also this measure may give wrong impression of the uncertainty contribution of x_i to y, specially when the correlation of x_i with $z_1,...,z_h$ is large (Janssen et.al., 1990).

A better measure of the uncertainty contributions of the various parameters was suggested by Janssen et. al., (1990). It is a combination of regression and correlation measures. It measures the fractional change ($\Delta Sy/Sy$) of the uncertainty (standard deviation) of y due to a fractional change ($\Delta Sx_i/Sx_i$) in the uncertainty in source x_i, taking the influence of the induced uncertainty change in the other correlated 'sources' into account:

$$\frac{\Delta S_y}{S_y} = PUC_i . \frac{\Delta S_{x_i}}{S_{x_i}} \tag{3.15}$$

The resulting quantity PUC_i is the so called Partial Uncertainty Contribution and is a combination of regression and correlation quantities:

$$PUC_i := \sum_{k=1}^{p} \hat{\beta}_i^{(s)} . r_{x_k y} . (r_{x_i x_k})^2 = \sum_{k=1}^{p} SRC_i . LCC_k . (r_{x_i x_k})^2 \tag{3.16}$$

If x_i is uncorrelated with x_j ($j \neq i$), PUC simplifies to:

$$PUC_i = SRC_i . LCC_i = \hat{\beta}_i^{(s)} \; . \; r_{y x_i} = \left(\hat{\beta}_i^{(s)}\right)^2 = (SRC_i)^2 \tag{3.17}$$

Due to this relationship the square root of the PUC is recommended as a measure of the uncertainty contribution (RTU = Root of Uncertainty):

$$RTU_i := \sqrt{|PUC_i|} \tag{3.18}$$

When the uncertainty sources are correlated, the linear regression coefficients do not exactly describe the cooresponding contibutions of uncertainty. But with adjusted measures this problem can be overcome (See above). When encountering strong non-linearities (i.e. COD < 0.7), the linear model also does not apply. Transformation of the data can be applied. It is very helpful to plot the obtained model output against the source x (scatter plot). There are two possibilities. Either there is no relation between the source x or an other relation (e.g. second order or higher) does apply. In the second case so called rank-transformation can be applied i.e. replacing the original values by their rankings, to obtain some information on the non-linear relationship.

The rank transformed data can be used for the so called rank regression. However due to the fact that variations and uncertainties in the ranked data have no clear and direct relation to the variations and uncertainties of the original data, it is difficult to interpret and use those measures for expressing the sensitivity c.q. uncertainty contributions. This method will not be used in this study.

3.4 Statistics of the Kolmogorov-Smirnov type

The statistics of this type are important in the sensitivity analysis of HEATHSOL. Because of its importance and because relatively little is said about this type of statistics in the manual of UNCSAM, it is explained in the next section.
Two types of test statistics will be discussed in detail.

Kolmogorov-Smirnov statistics are concerned with measuring the vertical distance between cumulative distribution functions either hypothesized or empirical. Statistics which are functions of the vertical distance between a hypothesized function and empirical distribution function are of the Kolmogorov type. Statistics which are functions of the vertical distance between two distribution functions are of the Smirnov type (Conover, 1971).

The application of Kolmogorov and Smirnov statistics is visualized in the following figure (figure 3.1)

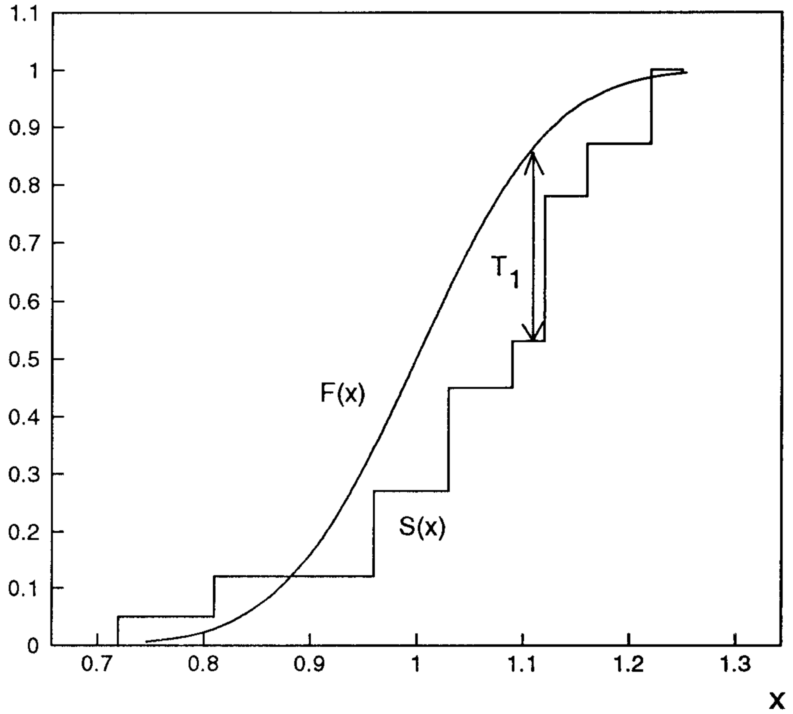

Figure 3.1 The hypothesized distribution function F(x) and the empirical distribution function S(x) and Kolmogorov's statistic T1

The simplest method to measure the discrepancy between the two distributions functions is the largest distance between the two graphs S(x) and F(x), measured in the vertical direction.

As will be explained later this type of statistic is also suitable for determining the sensitivity of the sources to the model output. Application of these statistics is however different (see section also section 5.5)

The Kolmogorov Goodness of Fit Test

The Kolmogorov test statistics can be used for examining if a random sample coincides with a specified hypothetical distribution function. It can also be used for calculating confidence bounds for empirical distribution functions (Conover, 1971). The test statistics are as follows:

The data consists of a random sample x_1, x_2,...x_n of size n associated with some unknown distribution function, denoted by F(x).

Assumptions: 1 The sample is a random sample
2 If the hypothesized distribution function, $F^*(x)$ in H_0 below, is continuous the test is exact. Otherwise the test is conservative.

Hypotheses: Let $F^*(x)$ be a completely specified distribution function.

A. Two sided test H_0: $F(x) = F^*(x)$ for all x from $-\infty$ to $+\infty$
H_1: $F(x) \neq F^*(x)$ for at least one value of x

B. One sided test H_0: $F(x) \geq F^*(x)$ for all x from $-\infty$ to $+\infty$
H_1: $F(x) < F^*(x)$ for at least one value of x

C. One sided test H_0: $F(x) \leq F^*(x)$ for all x from $-\infty$ to $+\infty$
H_1: $F(x) > F^*(x)$ for at least one value of x

Test statistics:

A. The test statistics T_1 consists of the greatest vertical distance (denoted by 'sup' supremum) between S(x) and $F^*(x)$:

$$T_1 = \sup_x |F^*(x) - S(x)| \tag{3.19}$$

B. The test statistics T^+_1 consists of the greatest vertical distance attained by $F^*(x)$ over S(x):

$$T_1^+ = \sup_x |F^*(x) - S(x)| \tag{3.20}$$

C. The test statistics T^-_1 consists of the greatest vertical distance attained by S(x) over $F^*(x)$:

$$T_1^- = \sup_x |S(x) - F^*(x)| \tag{3.21}$$

Decision rule: Reject H_0 at the level of significance α if the appropriate test statistics T , T^+ or T^- exceeds the 1-α quantile.

The Cramér-von Mises Two Sample Test

Another test statistic for determining whether the two distribution functions associated with two samples are identical or not is the Cramer von Mises two sample test. It considers not only the largest distance between the two empirical distribution functions but also considers n differences between the two functions.

The data consists of two independent random samples x_1, x_2,...x_n of size n and y_1, y_2,...y_m of size m, with unknown distribution functions F(x) and G(x) respectively.

Assumptions: 1 The samples are random samples, independent of each other.
2 The measurement scale is at least ordinal
3 The random variables are continuous. If the random variables are actually discrete the test is likely to be conservative.

Hypothesis: H_0: F(x) = G(x) for all x from $-\infty$ to $+\infty$
H_1: F(x) $\neq$ G(x) for at least one value of x.

Test statistics:
Let $S_1(x)$ and $S_2(x)$ be the empirical distribution functions of the two samples. The test statistics T_2 is defined as:

$$T_2 = \frac{mn}{(m+n)^2} \left\{ \sum_{i=1}^{n} [S_1(X_i)-S_2(X_i)]^2 + \sum_{j=1}^{m} [S_1(Y_j)-S_2(Y_j)]^2 \right\} \tag{3.22}$$

where the squared difference in the summation is computed at each x_i and at each y_j

Decision rule:
Reject H_0 at the approximate level α if T_2 exceeds the 1-α quantile.

Not only can statistics of the Kolmogorov-Smirnov type be used for quantifying differences between two (empirical) distribution functions but can also be used for determining confidence bounds for empirical distribution functions. It uses roughly spoken the reverse procedure of the above presented Kolmogorov Goodness of Fit test statistics. This procedure is used in UNCSAM for determining confidence bounds.

Use of the KS analysis in the sensitivity analysis:
Application of the KS analysis for sensitivity analysis can be done with UNCSAM. The sensitivity analysis of HEATHSOL was started with that, but a new computer program became available during the project. This program, GENSEN (=GENeralised SENsitivity) is specially developed for so called generalised sensitivity analysis. (Janssen, 1995). This analysis is concerned with model outputs in a more crude form than in a conventional analysis : the simulated model outputs are classified as 'acceptable' (behaviour) or 'non acceptable' (non-behaviour) instead of looking at their actual values or variations. The runs in which the heather species dominate the vegetation after several years is classified as acceptable and the runs in which the opposite is the case are classified as non acceptable. The subdivision of the output space induces a corresponding subdivision of the parameter space, and by means of statistical tools (KS-analysis, T-statistics, F-test) it is quantified whether individual parameters or parameter combinations show a different distribution in this dichotomy (Janssen, 1995).

GENSEN provides two kinds of analyses for evaluating the discrepancy/separation between the acceptable and non acceptable parameter sets:

1. A univariate analysis, which determines the discrepancy of the sets in the original (i.e. non transformed) parameter space. Typically the Kolmogorov-Smirnov statistic is preferred since it refers to the complete distribution, rather than to its mean or variance.

2. A multivariate analysis, which determines the discrepancy of the sets in the transformed parameter space by comparing the (marginal) cumulative distribution functions for both sets using the Kolmogorov-smirnov statistic. The transformation is applied for preventing that correlations obscure the determination of the impact of the parameters, and serves to make the (non) acceptable parameters uncorrelated.

The multivariate analysis was not applied because the transformations had an enormous influence on the analysis although correlations between the parameters were small ($<$ 0.20). Thereby we accept that the sensitivity/uncertainty of some parameters can be obscured by correlations .

The multivariate analysis is a rather heuristic method and the influence of correlations on the determined parameters is not clear. The univariate analysis is the same as the analysis which can be made with UNCSAM. However the analysis made with GENSEN provides some extra information (T-statistic, F-test).

The number of runs per selected group has to be greater than the number of parameters. This is true for the accepted and non accepted runs and the number of samples has to be greater than 17 otherwise the large sample approximation used is not valid.

It is unclear what the performance is of the non-parametric statistics as measure for the sensitivity and uncertainty contributions to the model output. It is a rather heuristic measure. Application does not require that $R^2 \approx 1$. The influence of correlations on this measure are unclear (Janssen et.al., 1990).

3.5 Significance of parameters

Several statistics are employed for determining the significance of the estimated regression coefficients. The level of significance α is the maximum probability of rejecting a true null hypothesis. The critical significance level is the smallest significance level at which the null hypothesis would be rejected for the given observation.

T-statistic can be used for assessing the significance of a parameter. The value of the t-statistic associated to the regression coefficient is indicative for testing the null-hypothesis $H_0 := 0$ against the alternative hypothesis
$H_1 \neq 0$ (i.e. testing the significance of the individual parameter β_i).
If $|t| > t_{N-(p+1)}(1- \frac{1}{2}\alpha)$, where $t_{N-(p+1)}(1-\frac{1}{2}\alpha)$ denotes the $100(1-\frac{1}{2}\alpha)$ percentile of the students-t distribution with N-(p+1) degrees of freedom, then the null-hypothesis is rejected at significance level α, i.e. the parameter is significant.

Roughly spoken, values of the t-statistic which are greater than 2 in absolute value indicate that the associated regression coefficients differs significantly from 0, at a significance level 0.95. Values which lie between -2 and 2 indicate insignificant coefficients /contributions (Janssen et.al., 1992).

Also Kolmogorov-Statistics can be used for determining the significance of a parameter. The values of the model output is partitioned into two disjunct parts. This induces a corresponding subdivision of the associated values of each parameter x_i. By quantifying for each parameter x_i the difference between these subdivided sets. one obtains an impression of the sensitive (important) parameters: x_i's with a large difference are considered to be important with respect to the chosen model output subdivision. Small values indicate that the distribution functions associated to the subdivision of the parameter space (e.g. parameter values leading to the 90 % lowest c.q. the 10 % highest function values; i.e. the separation index is 0.9) are significantly different (Janssen et.al., 1992).

The T-statistic tests only for differences between the mean of the parameter. KS statistic has the property of being consistent against all differences between the distribution functions and is regarded as more powerful for detecting differences (Conover, 1971).

The assumptions under which the results of the test statistic hold are not satisfied. Since we are applying regression on deterministic computer models, the estimation errors c.q. residuals do not have a random character, but a systematic one. This makes the use of the various test statistic somewhat debatable. (Janssen et.al., 1992)

3.6 Remarks

The choice for a certain method to calculate the sensitivity c.q. uncertainty contribution of the sources is important. All the presented measures have their own shortcomings and properties. It is not possible to select the best method. The various methods may even yield different results. It is thus important to apply more than one method. (Kros, 1990)

4. MODEL DESCRIPTION

4.1 Introduction

HEATHSOL is a mathematical model which simulates the dynamics of heather vegetation in the Netherlands, as determined by nutrient availability (Bakema et.al., 1994). It is a module within a greater set of modules which aims at rapidly evaluating the environmental consequences of policy scenarios (Braat et.al., 1991). This model was named EXPECT (= EXPloring Environmental Consequences for Tomorrow).

The object of the model HEATHSOL is to describe the effects of nitrogen deposition on heathland vegetation. The influence of management practices and heather beetle plagues on the vegetation is also included. The model focuses on the competition for light and nutrients between grasses and heather species (Bakema et.al., 1994). The competition between a heather species (either Erica tetralix or Calluna vulgaris) and a grass species (either Deschampsia flexuosa or Molinia caerulea) can be simulated. Other species can be incorporated in the model if the proper parameters are known.

The dominance of the heather species over the grass species is favoured by low nutrient availability. As a result of high nitrogen deposition and lack of management practices two thirds of the heathland vegetation is moderate to strongly dominated by grass species (Kootwijk et.al., 1994). It is the purpose to conserve or restore the heathland vegetation. This can be achieved by reduction of the nutrient availability by grazing, mowing or sod cutting. Moreover nitrogen deposition should be reduced. Sod cutting is by far the most efficient method of reducing the nutrient availability because all litter and plant biomass is removed.

HEATHSOL is a follow up of two previously developed heathland competition models: CALLUNA (Heil & Bobbink, 1990) describing the heathland competition for a dry type heathland and NUCOM 2 (Berendse, 1988) describing the heathland competition for a wet type heathland. CALLUNA was used in Environmental Outlook 2 for evaluating the effects of nitrogen deposition on dry heathland ecosystems. The parameter values of these two models, and also the value of the parameters in HEATHSOL have been based on previous experiments. The values of the parameters are given in appendix B. The uncertainty in the values (i.e. standard deviation, mean) is seldom known. Moreover some values were estimated. Specially the factors controlling light competition (height coefficient, patchiness, Specific Leaf Area) were not known. The lack of these data hampers an uncertainty analysis. In the next section a brief overview of the model is given. For the mathematical formulation of the model see appendix A.

4.2 Process description

Throughfall and canopy exchange

Wet and dry deposition of NO_x and NH_x are input for the model. Inputs are derived from the air transport model in EXPECT. Part of the nitrogen deposition is taken up by plants. The foliar uptake of NH_x and NO_x for the different plant species is different. The throughfall fluxes are added to nitrate and ammonium pools in soil layers.

Mineralization

Only the carbon and nitrogen cycles are described. The soil is divided in two layers. The first is the thin, organic layer and root zone. The second layer extends from the first layer down to the groundwater level. Only from the first layer can plant species extract nutrients. Nitrification and denitrification take place in both the first and second soil layer. Groundwaterlevels influence both nitrification and denitrification rates.

The litter compartments are divided in two classes, fresh litter which is one year old and the old litter. The mineralisation of the litter is treated separately for each plant part. The litter mineralization is calculated as a constant fraction of the total available amount. Fresh litter which is left after one year is added to the old litter. The resulting ammonium and nitrate, resulting from mineralisation and throughfall is available for uptake by the plants. If the plants do not take up all nitrogen, the remainder leaches to the groundwater.

Mortality

For all plant compartments, constant relative mortality rates have been specified. Each year the total mortality rate is calculated by multiplying the relative mortality rates with the total biomass present.

Redistribution

A fraction of the total amount of nitrogen present in the dying plant parts is reallocated and can be used for growth again.

Competition for nitrogen

The fraction of the total nitrogen taken up by the plant species is equivalent to the root length of the different species. Uptake of ammonium and nitrate takes place in the same ratio as their availability.

Competition for light

The potential growth rate is determined by the light intercepted. The potential growth rate is proportionate to the fraction of the total irradiation intercepted. The actual growth is determined by the nutrient availability. The fraction of the total irradiation intercepted is dependent on the total leaf area of the plant community and the differences in height between the plant species. Provision is made for both vegetation that are true mixtures of different species and for vegetation consisting of various patches of each species. When the potential growth has been calculated, the actual growth is calculated by an expression describing actual plant productivity as function of the nutrient supply rates.

Growth

Growth is defined as the yearly increase in biomass of the species and can be divided in increase in carbon and nitrogen content. Available carbon is distributed over the various plant parts according to a fixed distribution key. The growth is different in the various plant parts, which have different minimum and maximum nitrogen concentrations. The nitrogen is distributed to the various plant parts, according to a varying distribution key. The distribution key is dependent on the minimum and maximum nitrogen concentration in the plant parts and the available nitrogen.

Nitrification

Yearly a fixed proportion of ammonium is nitrified. A high groundwater level limits the nitrification process.

Denitrification

Part of the nitrate in the soil is denitrified. Low groundwater levels restrain the denitrification process.

Leaching

Remaining ammonium and nitrate fluxes leaches to the groundwater. The flow through the soil is a simple function of the waterflow through the soil.

Heather beetle outbreaks

Heather beetles (Lochmaea suturalis) affect Calluna. During a heather beetle outbreak plants die over large areas, because all leafs are eaten. There are no outbreaks in young Calluna stands (< 5 yr.). The chance of a heather beetle outbreak is once in the 15 to 20 years. The chance of a heather beetle outbreak is influenced by the food availability (leaf biomass) and food quality (nitrogen content) of the Calluna vegetation. There is a positive relationship between nitrogen content and heather beetle outbreaks. At very high nitrogen contents plants become toxic (increase of alkaloid content) for heather beetles. The heather beetle plagues are incorporated in the model as a stochastic process.

Management practices

Different types of management practices can be considered for heathland vegetations:
- grazing
- mowing + litter removal
- burning
- sod-cutting

The objective of management practices is to remove (part) of the nutrients from the heathland, thereby favouring the dominance of heather species over grass species. The interval of the management techniques is different. Also the management techniques differ in the efficiency of nutrient removal. Only sod-cutting has been incorporated in the model.

4.3 Model behaviour

As an example of model behaviour as it now exists the following simulations have been done (see figure 4.1). For more information about the model behaviour see Bakema et.al, 1994.

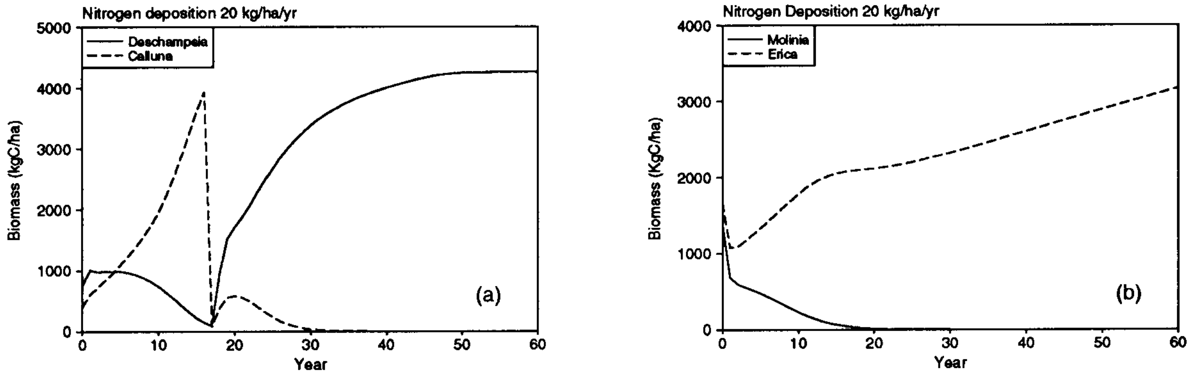

Figure 4.1 Two examples of the behaviour of HEATHSOL. Biomass Calluna and Deschampsia versus time (a) and Erica Molinia versus time (b). Both runs were made at a constant nitrogen deposition of 20 $kgha^{-1}yr^{-1}$.

The model was run for a Erica/Molinia vegetation and a Calluna/Deschampsia vegetation at a nitrogen deposition of 20 $kgha^{-1}yr^{-1}$. In the dry type heathland heather beetle plagues may occur. The biomass of the species is expressed as kgC/ha and includes underground biomass.

As can be seen in figure a and b the grass and heather species are both present in the heathland vegetation at the beginning of the simulation period. After some time one of the species, either grass or heather is replaced. The heathland vegetation becomes dominated by one species. This is always true at a constant deposition scenario. In a Calluna Deschampsia vegetation the effects of a heather beetle plague can be observed in Year 17. In this year a heather beetle plague occurs and the Calluna plants die completely. The Deschampsia plants are not affected and can develop without competition of the heather.

The model as it now exists behaves in a logical and plausible way, showing dominance of heather species when deposition is low, and dominance of grass species when deposition is high. Occurrence of heather beetle plagues in Calluna vegetation and changes in dominance after occurrence of heather beetle plagues both match field observations. (Bakema et.al., 1994).

5. A FIRST ANALYSIS OF SENSITIVE PARAMETERS IN HEATHSOL

5.1 Selected model output

As stated before the model aims at predicting the vegetation dynamics of a heathland vegetation over a period of about fifty years. It is therefore interesting to evaluate the influence of the parameters on the predicted dynamics of heathland vegetation. As a measure of the dynamics of heathland vegetation the total biomass of the grass and heather species in kgC/ha is used.

Other model outputs can be chosen for statistical analysis. An interesting one is the critical deposition of nitrogen on the heathland vegetation. One of the applications of the model could be to predict the maximum load of nitrogen (critical deposition) where the heathland vegetation is just dominated by the grass species. This model output is directly related to the predicted biomass of the grass and heather species. Parameters which influence the predicted biomass of the species will also influence the predicted critical load.

5.2 Parameter sampling

5.2.1 Method

In the ideal situation, the sensitivity of the model output for each parameter should be determined separately. However, evaluating all parameters (240) would take too much time. A method to reduce the number of parameters involved, is by lumping several parameters. Several parameters are replaced by one parameter (block parameter) which is used in the statistical analysis. The parameters are given the same variation as the block parameter. These lumped parameters are completely correlated. The plant species are composed of three to four plant compartments (Root, Culm, Leaf etc.) and each compartment has its own coefficients determining growth, senescence etc. All these coefficients for the compartments in one species are lumped giving one parameter which describes the behaviour of the plant species as a whole. This method will thus not give information on the most important parameters of a certain plant compartment but it gives the most important parameters affecting the plant as a whole.

This situation is exemplified by the mortality rate of the different plant parts. If the mortality rate of the root is increased the mortality rate of the leaf is also increased. The mortality rate of the whole plant is increased as one parameter. One lumped parameter (the carbon allocation fractions in one plant species) is organized in a different way. If the allocation fraction of the culm is increased also the allocation fraction of the leaf is increased. The allocation fraction of the root makes up for the rest, e.g. it is decreased. In chapter six the sensitivity for the individual parameters will be determined for the groups of parameters for which the model is most sensitive.

5.2.2 Implementation

This idea was implemented as follows. A Convert file was made in which the block parameters with their parameters are listed. In this file the variation which is given by UNCSAM to the block parameter is also listed. With help of a small computer program the Convert file is used for making the inputfiles of HEATHSOL. Sometimes only one parameter is given at a block parameter. This implies that the parameter was not lumped but for convenience it was described in this way.

It is important to notice that the formation of these block parameters leads to a worst case situation, where all related parameters fluctuate in the same direction. Normally when one parameter is underestimated, this will often be compensated by one of the other parameters that was overestimated. In this case both parameters will behave exactly the same which will give the greatest variability in model behaviour.

All initial conditions, boundary conditions and model parameters were varied. The values of the parameters were set to their default values. Deposition was set at the critical level, where changes in parameters can influence competition the most. All the parameters involved were given a normal distribution with a standard deviation 10% of the mean. No correlations were defined between the block parameters. The 10% variation parameters will influence the model output so; that as a result of the competition sometimes heather species will dominate the heathland vegetation and sometimes grass species. This will give the best information about the parameters influencing the competition between the heather and grass species, but it will make the sensitivity analysis more difficult, because of non-linearity.

Initial conditions are the amount of carbon and nitrogen in the initial biomass and in the litter layer. The amount of carbon and nitrogen in the litter layer were set to a value which is realistic for the amount remaining after sod cutting.

Examples of varied boundary conditions are the minimum and maximum nitrogen contents of the different plant parts. These are lumped under the block parameter ContNDes, ContNCal etc. This means that increasing ContNDes will both increase the minimum nitrogen content and the maximum N content of the plant parts.

The number of runs made for the sensitivity analysis is 5 x the number of varied (block)parameters. This was chosen because the model did not behave very linearly.

5.3 Selected scenario

Calculations were made for two heathland ecosystems; Wet type heathlands with Erica and Molinia species and dry type heathlands with Calluna and Deschampsia species. Furthermore the nitrogen deposition was set at two different values; At the critical nitrogen deposition 27 $kgha^{-1}yr^{-1}$ for Erica/Molinia and 24 $kgha^{-1}yr^{-1}$ for Calluna/Deschampsia) and at a somewhat lower value 20 $kgha^{-1}yr^{-1}$. These deposition levels correspond to the present, somewhat arbitrary, initial conditions, and should therefore not be interpreted as universally valid (see chapter 8).

No management practices were applied to the heathland ecosystem. In case of a Calluna/Deschampsia vegetation the outbreak of heather beetles can also be simulated. Outbreak of heather beetles plagues was not considered because application would require an enormous amount of computing time. As heather beetles are modelled as a stochastic process one run with the same input variables will be different from the second run with the same variables. A mean influence of the heather beetles has to be calculated. Numerous runs (100) have to be made to calculate the mean influence of the heather beetle outbreaks with a certain confidence (see Appendix C).

5.4 Linear regression analysis

5.4.1 Results

As a first impression of the model behaviour the mean biomass of the heather and grass species is given together with the 2.5 and 97.5 percentiles of the biomass for the critical deposition (Figure 5.1).

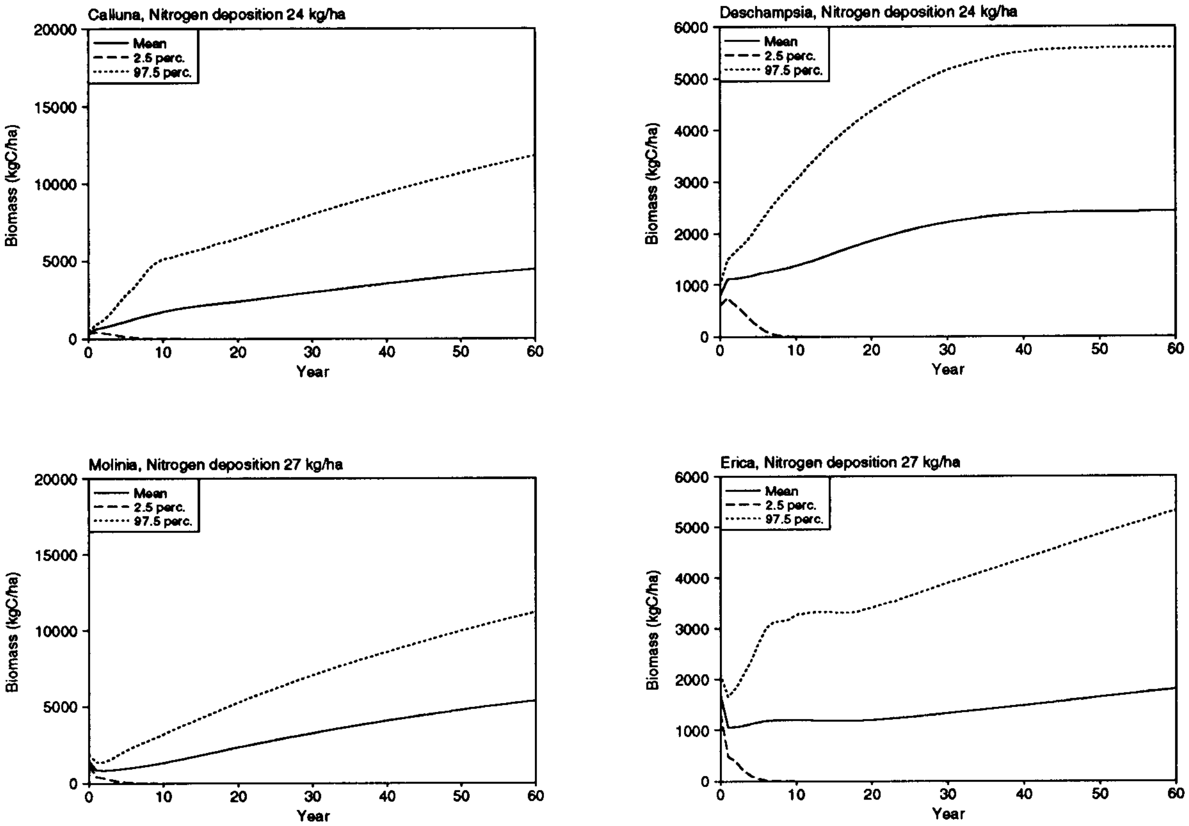

Figure 5.1. Biomass (KgC/ha) of Erica/Molinia and Calluna/Deschampsia at 24 kgha^{-1}yr^{-1} resp. 27 kgha^{-1}yr^{-1} nitrogen deposition. The Mean, the 2.5 and 97.5 percentiles are given.

It can be noticed in figure 5.1 that the variation in the predicted biomass is very large and that both biomass of the heather species and grass species can become zero after several years. This means that sometimes the heathland will be dominated by grass species and sometimes by the heather species after several years.

Further analysis of the results shows the effects of the competition between the grass and heather species. The grass and heather species are together present in the heathland vegetation for ca. 10 years. In these first 10 years the outcome of the competition is decided. This can clearly be seen in the histograms which show the biomass frequency distribution of Calluna over time for the Calluna/Deschampsia vegetation (Figure 5.2). The first year of the simulation period is the year 0.
The different runs fall in two categories: with Calluna dominating the heathland vegetation after several years and the Deschampsia dominating the heathland vegetation (Calluna biomass zero).

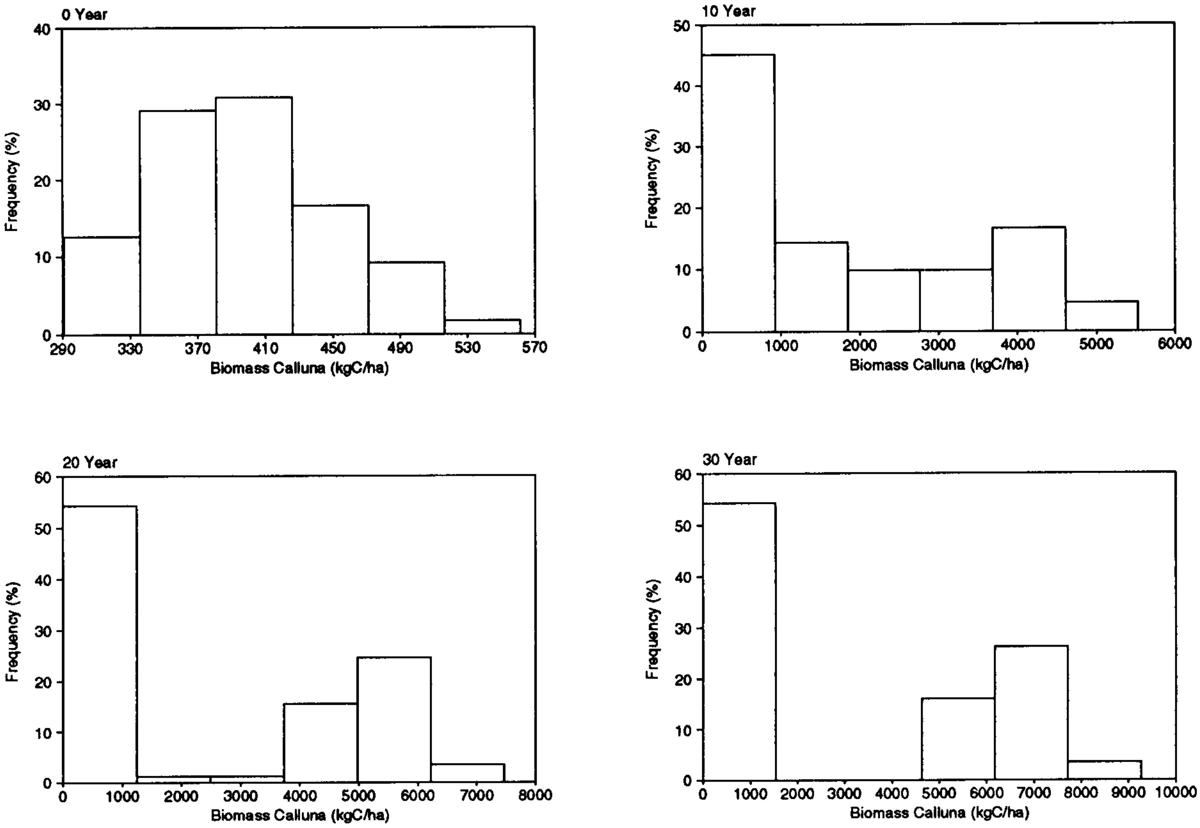

Figure 5.2 Frequency distribution of the biomass Calluna.(24 kgha^{-1}yr^{-1}). Because of the class-width the bar at the y-axis has a certain width but biomass in this class are all practically zero.

The observed frequency distribution in biomass shows that linear regression is not allowed here because the model does not behave in a linear way. Only the first 10 years is linear regression possible. This is also shown by the ordinary regression coefficient of the Erica/Molinia biomass and Calluna/Deschampsia biomass (Figure 5.3). It drops steadily to a value of about 0.7 after several years. Linear regression is not allowed at regression coefficients below 0.7 (Janssen et.al.,1992)

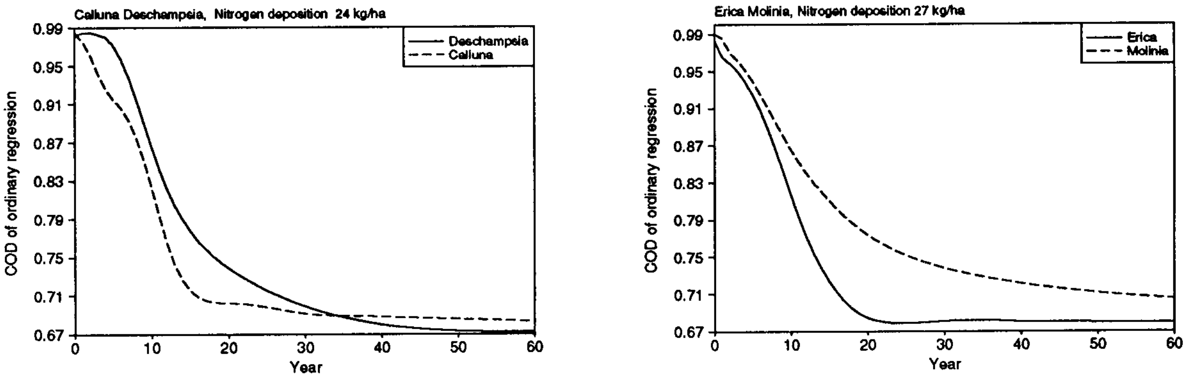

Figure 5.3 The COD (R^2) of ordinary regression for the Calluna\Deschampsia biomass and the Erica\Molinia biomass at 24 resp. 27 $kgha^{-1}yr^{-1}$ nitrogen deposition.

In the first ten years the result of the competition is determined. This means that the variation in the parameters influences the outcome of the competition during the first ten years. Thus the sensitivity of the outcome of the competition for variations in the parameters is determined during the first ten years. A sensitivity analysis for the first several years gives information on what parameters most strongly influence the competition process.

When applying linear regression on the model results of the first ten years of the simulation run the ranking of the most sensitive parameters changes over time
(see table 5.1)

Table 5.1. The five most sensitive block parameters influencing the biomass of the heather and grass species in the first ten years of the simulation period. Ranking according to NRC. The biomass is given in kgC/ha, The most sensitive blockparameter is given at the top of the list.

Selected model output	0 year		4 year		6 year		10 year	
biomass Calluna	CalVegC	0.91	SLACal	2.12	ContNDes	2.77	MortCal	-3.56
	FluxGrowCal	0.63	ContNDes	1.96	MortCal	-2.62	MortDes	3.21
	SLACal	0.62	FluxGrowCal	1.95	SLACal	2.60	ContNDes	3.14
	ContNCal	-0.22	MortCal	-1.82	MortDes	2.51	FluxGrowCal	3.01
	DesVegC	-0.22	MortDes	1.56	FluxGrowCal	2.44	SLACal	2.49
biomass Deschampsia	DesVegC	0.62	MortDes	-1.72	MortDes	-2.34	MortDes	-3.25
	ContNDes	-0.56	ContNDes	-1.69	ContNDes	-2.29	ContNDes	-2.99
	DesOLdLitN	0.46	RootLCal	-0.99	RootLCal	-1.41	MortCal	2.27
	FluxGrowDes	0.32	RootLDes	0.98	RootLDes	1.35	FluxGrowCal	-2.18
	RaNCDes	-0.32	SLACal	-0.83	SLACal	-1.27	RootLCal	-2.02
biomass Erica	EriVegC	0.87	MortEri	-2.37	MortEri	-3.14	MortEri	-3.98
	HthCoefMol	-0.33	HthCoefMol	-2.20	MortMol	2.52	MortMol	3.24
	HthCoefEri	0.30	HthCoefEri	1.98	HthCoefMol	-2.48	HthCoefEri	2.65
	MolVegC	-0.28	MortMol	1.83	HthCoefEri	2.33	HthCoefMol	-2.49
	FluxGrowEri	0.23	ContNMol	1.62	ContNMol	2.11	RootLMol	-2.42
biomass Molinia	MolVegC	0.78	MortMol	-2.56	MortMol	-3.22	MortMol	-3.88
	ContNMol	-0.48	ContNMol	-2.18	ContNMol	-2.54	MortEri	2.75
	MolOldLitN	0.39	HthCoefMol	1.60	MortEri	2.17	ContNMol	-2.71
	EriVegC	-0.29	RootLEri	-1.56	HthCoefMol	2.05	HthCoefMol	2.26
	RootLMol	0.26	RootLMol	1.56	RootLEri	-1.94	RootLEri	2.25

The NRC is chosen as measure of sensitivity. It measures the relative change Δy of y, in terms of average $\bar{y}$, if x_i changes relatively in terms of its average $\bar{x}_i$ while other sources remain constant. It can be used because there are no interactions between block parameters and $R^2 \approx 1$ (figure 5.3). So the linear model can be applied.

5.4.2 Discussion

Before drawing conclusions from this linear regression analysis the significance of the different sensitivity values has to be established. For this test the T-statistics is applied. According to the T-statistic at least the first 13 parameters are significant.

The block parameters which influence the biomass mostly in the first year of the simulation period are totally different from the ones after 10 years. This is not surprising because mortality does not influence the biomass much after one year. But as the simulation period is increased the mortality (rate) becomes more important.

The first year initial biomass expressed in kgC/ha (CalVegC, DesVegC, EriVegC and MolVegC) are most important for determining the predicted biomass (kgC/ha). After four years the initial biomass becomes unimportant for determining the biomass because parameters which influence the development of the vegetation are more important. Only in very slow growing species or at lower nitrogen levels initial biomass would longer be important.

There is an interesting difference between the two types of heathland vegetation The development of the Erica\Molinia vegetation is strongly influenced by the Height coefficients of the species as opposed to the Calluna\Deschampsia vegetation. The Height coefficient influences the light competition between the species if the vegetation is evenly distributed (see appendix A6; competition for light). The height coefficient becomes more important when the patchiness of the vegetation is decreased. Decreasing the patchiness of the vegetation means that the species are mixed more evenly. Increasing the patchiness means that the species are more separated. In that situation the height coefficient is less important for determining the development of the biomass. The patchiness in the Erica\Molinia vegetation is set at 10% in the Calluna\Deschampsia vegetation at 90% In the first case light competition is more important then in the last situation. Hence height coefficients are more important in Erica\Molinia vegetation. The big influence of the factors concerning light competition is unexpected. In reality in a newly developing vegetation the new seedlings are widely spaced with bare ground between them. Light competition would be of minor importance in that case.

Root length is another important parameter influencing biomass in the first ten years. The root length influences directly the competition for nutrients between the species. The remark made for the influence of the light competition can also be made here. In the first years of a developing vegetation, competition for nutrients will be minor because plants are widely spaced. A probable cause for this effect is that the Erica/Molinia vegetation is initialized with relatively high biomass, reflecting the situation several years after sodcutting.

The maximal growth rate (FluxGrowCal, FluxGrowDes and to a lesser extent FluxGrowEri) of the different plant species is also important for determining the predicted biomass of the species. The maximal growth rate becomes important for determining the growth rate of the heather and grass species when the nitrogen flux to the species divided by the minimum nitrogen content of the plant species is high compared with the potential growth rate (see appendix A7; growth). This situation is found in the Calluna, Deschampsia and to a lesser extent in the Erica species.

The last parameter which deserves attention is SLACal: the Specific Leaf Area of Calluna. As was stated, in the Calluna\Deschampsia vegetation the patchiness is greater then the patchiness in the Erica\Molinia vegetation. The Specific Leaf Area determines the light competition in a situation where the vegetation is patched. As the patchiness is increased the leaf area index becomes more important for determining the light competition between the heather- and grass species.

It can be concluded that a sensitivity analysis of the parameters yields interesting information about the most important processes determining the biomass in the first ten years.

To further analyze which parameters influence the final outcome of the competition most, the situation after more then ten years has to be taken into account. The strong non-linearity in this period prohibits the regression approach however.

There are several possible solutions for the problem of strong non-linearities:

1) Choosing a nitrogen deposition scenario which is far from the critical deposition. It must be located so far from the critical deposition that the variability of the parameters does not influence the outcome of the competition between the species. The main disadvantage of this approach is that the sensitivity analysis is not carried out at a scenario we are interested in.
2) Giving the parameters such a small variation (1% of the mean) that the variability of the parameters does not influence the outcome of the competition between the heather and the grass species. This approach will not give the most interesting model behaviour because factors influencing the result of the competition are not examined.
3) Selecting another model output, which behaves more linear and is also related to the purpose of the model. Possible candidate is the year in which the vegetation changed from grass-dominated to heather-dominated or vice versa. The problem with this model output is that sometimes the grass species are never replaced by the heather species. Then linear regression is also not possible.

   A second possibility is to use the critical deposition at which the heather species are just replaced by the grass species as output. A drawback of this solution is the amount of computing time involved in finding the critical deposition. For every sample of UNCSAM several runs have to be made to find the critical deposition which increases the computing time involved tremendously.
4) Applying different regression analyses. A method which can easily be used (because it is implemented in UNCSAM) is rank regression. A drawback of using rank regression is the difficulty of interpreting the sensitivity cq. uncertainty contributions of the ranked data, because they have no direct and clear relation with the original data (Janssen et.al. 1992).
5) A method which can be used is the so called Kolmogorov-Smirnov analysis:

5.5 Kolmogorov-Smirnov analysis

5.5.1 Introduction

Kolmogorov-Smirnov analysis is very suitable for the model behaviour as observed. In this case the model output is divided in two classes. One class in which grass species will finally dominate and one class where heather species will dominate. Each class is characterized by a different distribution of the parameters. This is exemplified by the next figure (figure 5.4a). In this figure biomass Molinia (model output y) is plotted as scatter graph against block parameter Mortality Molinia (source x_i). As can be seen the plotted points are divided into two distinct classes. One class in which biomass molinia is zero and one class in which the biomass is not zero.

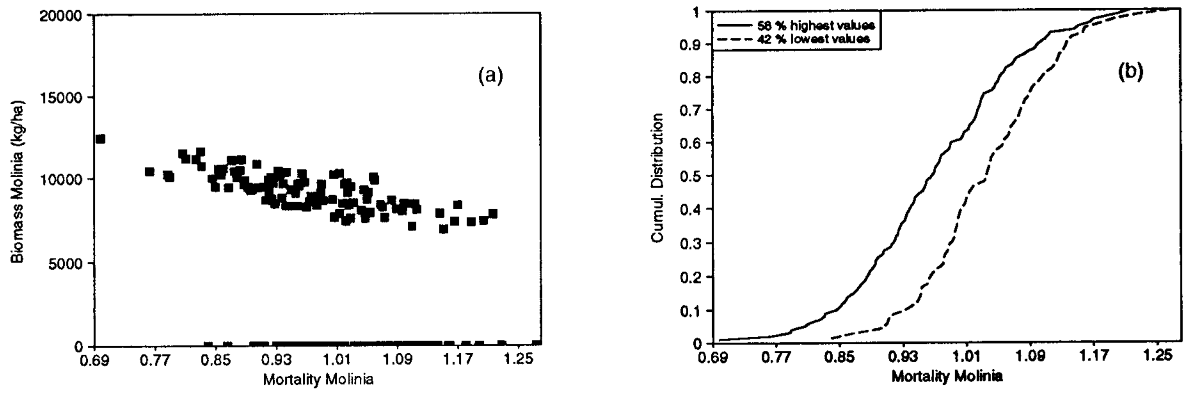

Figure 5.4. Scatterplot of model output Biomass Molinia as function of block parameter Mortality Molinia (a). The model output is divided into two classes. Each class has its own associated parameter distribution. These empirical distribution functions of the parameter Mortality Molinia is given (b). The class belonging to the 42 % lowest values are the 73 runs in which Biomass Molinia is practically zero. Total number of runs made is 175.

Every class has its own distribution of the parameter x_i (figure 5.4b). When the two classes with their associated distribution curves of the parameter strongly differ, the sensitivity of the class-division for this parameter is high. The division of the classes is given by the separation index of the KS analysis. It gives the percentage of the model outputs which is located in the lowest class i.e. the class in which biomass Molinia is zero. The separation index can be found by plotting the frequency distribution of the biomass at a year in which the competition between the species is already decided i.e. after 10 years or more.

5.5.2 Results

In table 5.2 the ten most sensitive parameters according to the KS analysis are given. Both a Erica/Molinia vegetation and Calluna/Deschampsia vegetation are given. The parameters are given which are significant according to the value of the 80 % significance level.

Table 5.2. Most sensitive parameters influencing the outcome of the competition according to Kolmogorov-Smirnov analysis. Calculations were made at 24 $kgha^{-1}yr^{-1}$ nitrogen deposition for Calluna\Deschampsia vegetation and 27 $kgha^{-1}yr^{-1}$ for Erica\Molinia vegetation

Calluna\Deschampsia		Erica\Molinia	
Parameter	SMIR	Parameter	SMIR
ContNDes	0.33	MortMol	0.34
RootLCal	0.32	MortEri	0.29
FluxGrowCal	0.32	ContNMol	0.27
MortDes	0.31	HthCoefEri	0.25
MortCal	0.26	RootLMol	0.24
SLACal	0.24	HthCoefMol	0.23
SLADes	0.24	RootLEri	0.23
FrAlCal	0.20	FluxGrowEri	0.22
RootLDes	0.19	ContNEri	0.21
DesOldLitC	0.19	SLAMol	0.20
RMinDesOld	0.19	MolVegC	0.18
		SLAEri	0.18
		FrAlEri	0.17

In case of a Kolmogorov-Smirnov analysis the results of the analysis is the same with regard to biomass Grass and biomass Heather. This is not surprising because the analysis is concerned with the outcome of the competition between the species and not with the biomass of the species. In figure 5.5 the five most sensitive parameters are given as function of time.

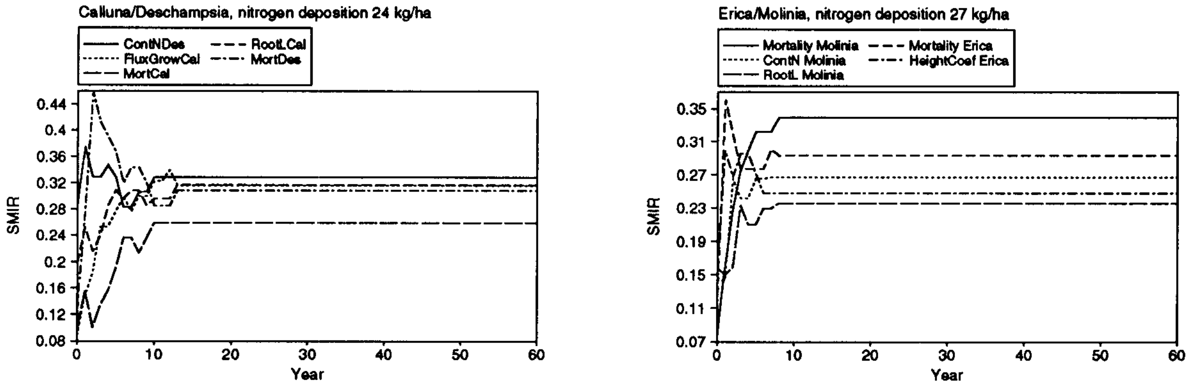

Figure 5.5 The five most sensitive parameters according to the KS analysis for Calluna/Deschampsia and Erica/Molinia. The value of the SMIR for a parameter is plotted as function of time

5.5.3 Discussion

The results of the KS analysis do not change with time after 10 to 15 years. After that time, the result of the competition is known. The KS analysis can thus be limited to one year for example after thirty years.

The most important parameters according to the KS analysis do not differ much with the results obtained from a linear regression analysis. The ranking is almost the same. The ten most sensitive block-parameters do not differ much for the two types of heathland vegetation. Seven parameters are found in the ten most important parameters of both vegetation types.

The mortality of the species (MortMol, Mortcal, MortDes, MortEri) is important for determining the result of the competition between the heather and grass species. This was already noticed in the linear regression analysis.

The minimum and maximum nitrogen content (ContNDes,ContNMol,ContNEri) are also sensitive parameters. The nitrogen content of the grass species is more sensitive than the nitrogen content of the heather species. The nitrogen content of the Calluna species (ContNCal) is not very sensitive.

The maximal growth rate of the heather species (FluxGrowcal, FluxGrowEri) are also of importance as opposed to the maximal growth rate of the grass species. This can be explained by the fact that at the critical deposition level the heather species have a high nitrogen influx divided by the average minimum nitrogen content of the heather species compared with the potential growth rate. Therefore the biomass of the heather species is more determined by maximal growth rate than by nitrogen availability.

Furthermore the factors determining the competition between the heather and grass species are of importance. In a Erica/Molinia vegetation the height coefficients are important and in the Calluna/Deschampsia vegetation the Specific Leaf areas are important for the competition for light. As explained in section 5.2.4 this is the result of the difference in the patchiness in the heathland ecosystems.

5.6 Variation in nitrogen deposition

Until now the nitrogen deposition was fixed at a certain amount. This is in accordance with the idea of evaluating deposition scenario's (or policy scenario's). However the nitrogen deposition on a heathland vegetation will be highly variable; variable on a time scale and spatial scale. It is therefore interesting to quantify the sensitivity of the model output for variations in the deposition. The objective is to examine if the sensitivity for the deposition is higher/lower for other sources. As we want to quantify the sensitivity of the deposition with regard to the other parameters all the parameters have to be taken into account (total 36, including deposition).

The mean of the deposition was set at the critical deposition. The deposition was given a normal distribution with standard deviation 10% of the mean. All other (block) parameters were given the same distribution as in the former section.

As before a linear regression analysis was made for the first ten years of the simulation period. A Kolmogorov-Smirnov analysis was made for the end result of the competition of the heathland species.

5.6.1 Linear regression analysis

The results of the linear regression analysis including a variable deposition are shown below.

Table 5.3. The five most sensitive block parameters influencing the biomass of the heather and grass species in the first ten years of the simulation period. Ranking according to NRC. The most sensitive block parameter is given at the top of the list.

Selected model output	0 year		4 year		6 year		10 year	
biomass Calluna	CalVegC	0.90	FluxGrowCal	2.12	MortCal	-3.01	MortCal	-3.80
	SLACal	0.65	SLACal	2.08	SLACal	2.84	FluxGrowCal	3.46
	FluxGrowCal	0.63	MortCal	-2.08	MortCal	2.70	ContNDes	3.09
	DesVegC	-0.20	ContNDes	1.84	ContNDes	2.62	SLACal	3.00
	ContNCal	-0.19	RootLCal	1.47	RootLCal	2.16	MortDes	2.68
biomass Deschampsia	DesVegC	0.62	ContNDes	-1.70	ContNDes	-2.32	MortDes	-3.19
	ContNDes	-0.55	MortDes	-1.67	MortDes	-2.30	ContNDes	-3.14
	DesOldLitN	0.47	RootLCal	-1.07	RootLCal	-1.54	FluxGrowCal	-2.31
	DesOLdLitC	-0.32	RootLDes	1.04	RootLDes	1.50	MortCal	2.27
	RaNCDes	-0.32	Deposition	0.87	SLACal	-1.45	SLACal	-2.27
biomass Erica	EriVegC	0.88	MortEri	-2.35	MortEri	-2.95	MortEri	-3.47
	HthCoefMol	-0.37	HthCoefMol	-2.25	MortMol	2.65	MortMol	3.23
	HthCoefEri	0.29	MortMol	1.93	HthCoefMol	-2.60	ContNMol	3.09
	MolVegC	-0.25	ContNMol	1.86	ContNMol	2.49	HthCoefMol	-2.80
	SLAEri	0.22	HthCoefEri	1.81	HthCoefEri	2.07	HthCoefEri	2.18
biomass Molinia	MolVegC	0.78	MortMol	-2.66	MortMol	-3.25	MortMol	-3.73
	ContNMol	-0.50	ContNMol	-2.47	ContNMol	-3.06	ContNMol	-3.67
	MolOldLitN	0.40	HthCoefMol	1.84	HthCoefMol	2.39	HthCoefMol	2.69
	EriVegC	-0.30	RootLEri	-1.51	RootLEri	-1.90	RootLEri	-2.26
	Deposition	0.30	RootLMol	1.39	MortEri	1.87	MortEri	2.23

Linear regression for these years is allowed because R^2 is above 0.8 (Figure 5.6). No correlations were defined between parameters. According to the T-statitics at least the first 15 parameters are significant in the given years.

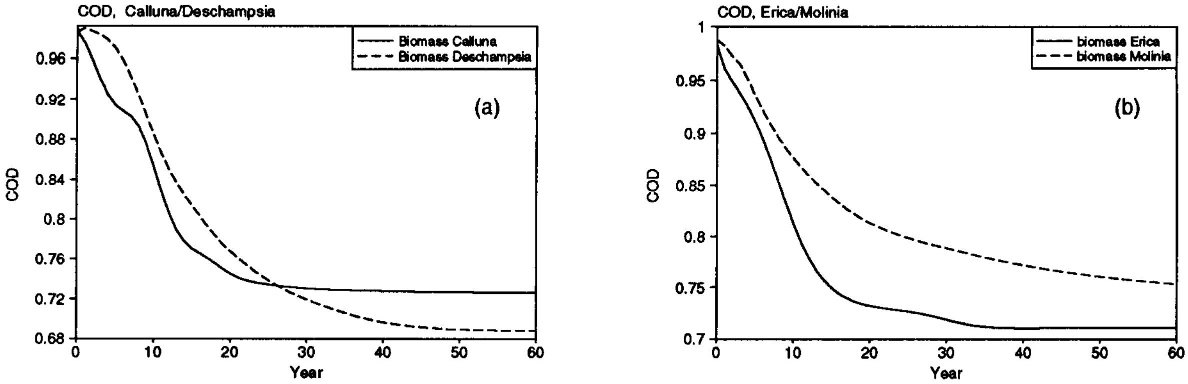

Figure 5.6 Coefficient of ordinary regression, variable deposition Calluna/Deschampsia vegetation (a) and Erica Molinia vegetation (b).

The result of the linear regression analysis is not very different from the linear regression analysis made without a variable deposition for a Erica/Molinia vegetation.

5.6.2 Kolmogorov-Smirnov analysis

The results of the KS analysis are give in table 5.4 and table 5.5. The results of the KS analysis with and without variable deposition are given.

Table 5.4. The most sensitive (block) parameters with and without a variable deposition. Calluna/Deschampsia vegetation. Deposition fixed at 24 $kgha^{-1}yr^{-1}$ or varied around 24 $kgha^{-1}yr^{-1}$ normal distribution, st. dev 10% of the mean. Critical value for the 80% significance level: 0.1598 (variable deposition), 0.1624 (fixed deposition)

fixed deposition			variable deposition		
block-parameter	SMIR	Sign.	block-parameter	SMIR	Sign.
ContNDes	0.33	$0.17\ 10^{-3}$	SLACal	0.31	$0.41\ 10^{-3}$
RootLCal	0.32	$0.32\ 10^{-3}$	ContNDes	0.30	$0.72\ 10^{-3}$
FluxGrowCal	0.32	$0.33\ 10^{-3}$	MortCal	0.28	$0.19\ 10^{-2}$
MortDes	0.31	$0.53\ 10^{-3}$	RootLCal	0.27	$0.26\ 10^{-2}$
MortCal	0.26	$0.58\ 10^{-2}$	MortDes	0.27	$0.30\ 10^{-2}$
SLACal	0.24	$0.11\ 10^{-1}$	Deposition	0.23	$0.15\ 10^{-1}$
SLADes	0.24	$0.13\ 10^{-1}$	FluxGrowCal	0.23	$0.18\ 10^{-1}$
FrAlCal	0.20	$0.63\ 10^{-1}$	RootLDes	0.22	$0.15\ 10^{-1}$
RootLDes	0.19	$0.78\ 10^{-1}$	SLADes	0.21	$0.40\ 10^{-1}$
DesOLdLitC	0.19	$0.78\ 10^{-1}$	FrAlCal	0.20	$0.50\ 10^{-1}$
RMinDesOld	0.19	$0.88\ 10^{-1}$	ThrFallCal	0.18	0.104

Table 5.5. The most sensitive (block) parameters with and without a variable deposition. Erica Molinia vegetation. Deposition fixed at 27 $kgha^{-1}yr^{-1}$ or varied around 27 $kgha^{-1}yr^{-1}$, normal distribution, st. dev. 10% of the mean. Critical value for the 80% significance level: 0.1612 (variable deposition), 0.1640 (fixed deposition)

fixed deposition			variable deposition		
block-Parameter	SMIR	Sign.	block-Parameter	SMIR	Sign.
MortMol	0.34	$0.11\ 10^{-3}$	MortMol	0.42	$0.46\ 10^{-6}$
MortEri	0.29	$0.14\ 10^{-3}$	ContNMol	0.36	$0.16\ 10^{-6}$
ContNMol	0.27	$0.46\ 10^{-2}$	HthCoefMol	0.28	$0.19\ 10^{-2}$
HthCoefEri	0.25	$0.11\ 10^{-1}$	MortEri	0.27	$0.31\ 10^{-2}$
RootLMol	0.24	$0.18\ 10^{-1}$	RootLMol	0.27	$0.31\ 10^{-2}$
HthCoefMol	0.23	$0.20\ 10^{-1}$	RootLEri	0.26	$0.56\ 10^{-2}$
RootLEri	0.23	$0.26\ 10^{-1}$	HthCoefEri	0.24	$0.12\ 10^{-1}$
FluxGrowEri	0.22	$0.37\ 10^{-1}$	FluxGrowEri	0.17	0.14
ContNEri	0.21	$0.50\ 10^{-1}$	MolVegN	0.17	0.15
SLAMol	0.20	$0.66\ 10^{-1}$	FrAlMol	0.17	0.16
MolVegC	0.18	0.12			
SLAEri	0.18	0.13			
FrAlEri	0.17	0.15			

In a Erica Molinia vegetation the only difference between the sensitivity analysis with a fixed and variable deposition is the replacement of the parameter MolvegN by ContNEri in the ten most important parameters. In a Calluna/Deschampsia vegetation the block parameter DesOLdLitC is replaced by the parameter Deposition. The rest of the ten most important parameters change little.

5.6.3 Influence of deposition

Adding one extra parameter in the analysis influences the results of the univariate KS analysis strongly. A different ranking is made of the parameter sensitivity. It could be expected that the evaluation of one extra parameter would not greatly influence the ranking of the other parameters. This effect is caused by the occurrence of (random and low < 0.25) correlations between parameters. The sensitivity of parameters can be obscured by these correlations in a univariate analysis. The different ranking made when adding one extra parameter is the result of the random changes in correlations between the parameters when adding one extra parameter. When applying a multivariate analysis the result of the KS analysis will be corrected for correlations between parameters. A multivariate analysis will therefore not be influenced by adding one extra parameter (Appendix F).

The results of this analysis show that the result of the competition is not very sensitive for changes in the deposition when it is varied in the same proportions as the other parameters. However we now know the sensitivity of the model for the deposition but we don't know the uncertainty in the nitrogen deposition. We do know however that in contrast with the other parameters, deposition in reality can easily vary between 50% and 200% of the value used in this analysis (15-50 $kgha^{-1}yr^{-1}$). The influence of deposition will therefore still be very high.

The sensitivity of a Calluna/Deschampsia vegetation for deposition is somewhat greater than for a Erica/Molinia vegetation. The total effect of the species characteristics and vegetation must be responsible for this.

It also can be seen that small changes in the parameters involved in the analysis will not influence the result of the KS analysis. The already mentioned sensitive parameters are still the most important.

5.7 Conclusion

Linear regression is possible for the first ten years of the simulation period. The biomass of the species can be taken as model output. A different approach is needed for the model output after more then ten year. A Kolmogorov-Smirnov analysis can be applied. The result of the competition is taken as model output. Linear regression analysis is not conclusive about the most sensitive block parameters because these change in course of time. Still a linear regression analysis is important for explaining model behaviour.

The most important sources determining the model output are concerned with the mortality rate of the species, the coefficients determining the (light)-competition between the species and to a lesser extent the factors concerning growth of the species. The most important sources are given in table 5.6. according to the critical 99 % significant level. The number of parameters given in table 5.6 are thus more than given in table 5.2. The higher critical level will give more certainty that all sensitive parameters are included in the further analysis of the separate parameters (chapter 6).

Table 5.6 The most sensitive (block)-parameters which influence the result of the competition mostly at the critical deposition. They are valid for the scenario of calculation.

Calluna/Deschampsia	Erica/Molinia
ContNDes	MortMol
RootLCal	MortEri
FluxGrowCal	ContNMol
MortDes	HthCoefEri
MortCal	RootLMol
SLACal	HthCoefMol
SLADes	RootLEri
FrALCal	FluxGrowEri
RootLDes	ContNEri
DesOLdLitC	SLAMol
RMinDesOld	MolVegC
ReDisCal	SLAEri
	FrAlEri
	RMinEri

The now determined ranking of most sensitive sources is only valid under the scenario of calculation. Changing the scenario i.e. other deposition scenario, initial conditions or other mean values of parameters etc. can have effect on the determined sensitivity of the parameters. With the now determined most important sources a further sensitivity analysis was made in which the separate parameters are varied. The results are presented in chapter 6.

6. SENSITIVITY ANALYSIS OF SEPARATE PARAMETERS

6.1 Introduction

In chapter five the (block)-parameters which were most sensitive were established. In this chapter a sensitivity analysis is made with the separate parameters which belonged to the most sensitive block parameters. Mostly this means that we are not looking at the variation of parameters for a plant species as a whole but at the plant parts. The heather species are composed of three compartments (Leaf, Culm, Root) and the grass species are composed of four compartments (Leaf, Branch, Flower, Root).

When a block-parameter is sensitive, the sensitivity of all the parameters lumped in this block can be evenly distributed over the parameters An other possibility is that one parameter in the block is very sensitive and the others not. As the analysis is mostly the same as applied in chapter 5, the analysis will be discussed shortly.

6.2 Parameter sampling

The (block)-parameters mentioned in table 5.6 were used for the sensitivity analysis of the separate parameters. Only one parameter mentioned in table 5.6 was not used in the separate analysis. This was the allocation fraction. An analysis of the separate four allocation fractions of the four plant compartments was not possible. The total of all the allocation fractions must be one, otherwise more nitrogen would be distributed than available. This can be done by varying the above ground allocation fractions and adjusting the value of the root allocation fraction. This cannot be done with UNCSAM because the variability of the root allocation fraction is then not taken into account in the statistical analysis.

A correlation had to be defined between the minimum and maximum nitrogen concentrations of a plant compartment to avoid a smaller maximum nitrogen concentration than minimum nitrogen concentration. The correlation coefficient was set at 0.99. (totally correlated) The occurrence of correlation between parameters makes interpretation of the regression analysis more difficult. When high correlation coefficients occur in the regression analysis the NRC is not a good measure for comparing the sensitivity of the individual parameters. But with the knowledge of the correlations it can still be interpreted. When applying the NRC as measure it has to be kept in mind that the minimum and maximum nitrogen concentrations of a plant compartment are correlated and an interpretation of the separate minimum or maximum nitrogen concentration of a plant compartment is not possible. It is better to speak of the nitrogen concentration of a compartment. A measure which can be applied when correlations exist between parameters was suggested by Janssen et.al. 1990. This is the RTU (=Root of Total Uncertainty). When high correlations coefficients exist between parameters it is still not conclusive and more sensitivity measures have to be evaluated before a conclusion can be made.

The parameters were given a normal distribution with a st.dev. 10 % of the mean. It is expected that the model behaviour is almost equal with the former sensitivity analysis (chapt 5) because all the significant parameters are varied accordingly.

Calculations were made for Calluna/Deschampsia vegetation and a Erica/Molinia vegetation at 24 $kgha^{-1}yr^{-1}$ and 27 $kgha^{-1}yr^{-1}$ respectively. Also calculations were made in which deposition was not a scenario but treated as parameter. The nitrogen deposition was varied around 24 $kgha^{-1}yr^{-1}$ for a Calluna/Deschampsia vegetation and 27 $kgha^{-1}yr^{-1}$ for an Erica/Molinia vegetation. The deposition was also given a standard deviation 10 % of the mean.

6.3 Results and discussion

In a Calluna/Deschampsia vegetation and an Erica/Molinia vegetation the variability of the parameters did result in a variable outcome of the competition at this deposition level. Linear regression was possible for the first ten years of the simulation period, because COD > 0.7 (Figure 6.1).

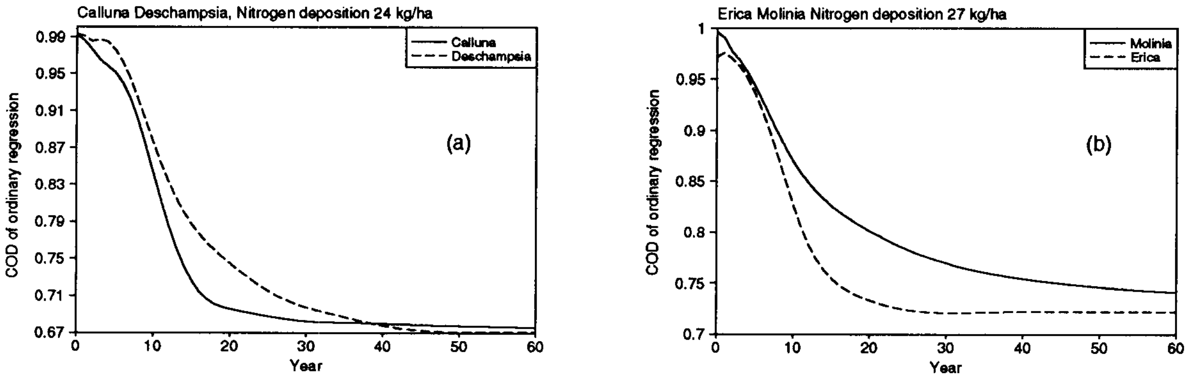

Figure 6.1 COD of ordinary regression Calluna/Deschampsia vegetation (a) and Erica/Molinia (b) vegetation at nitrogen deposition fixed at 24 $kgha^{-1}yr^{-1}$ and 27 $kgha^{-1}yr^{-1}$ respectively.

6.3.1 Linear regression analysis

First we will present the results of the linear regression analysis. For this analysis the right measure for expressing the sensitivity of the parameters should be established. As an example the linear regression results for Calluna/Deschampsia in year 10 are presented. (table 6.1) The NRC, RTU and LCC measures are given. The five most sensitive parameters are given. It can be seen that the ranking of the most sensitive measures according to NRC, RTU and LCC is equal.

Table 6.1 Results of linear regression analysis of the Calluna/Deschampsia vegetation in year 10 of the simulation period. Biomass Deschampsia as model output. The NRC, RTU and LCC are given as measures of the sensitivity of the parameters. Deposition included as parameter. Significance according to T-statistic for LCC sensitivity measure.

parameter	NRC	parameter	RTU	parameter	LCC	Signif.(LCC)
MortDesLeaf	-2.75	MortDesLeaf	0.42	MortDesLeaf	-0.43	-5.01
CNDesRootMax	-2.47	CNDesLeafMin	0.35	CNDesLeafMin	-0.36	-4.08
FluxGrowCal	-2.16	CNDesLeafMax	0.34	CNDesLeafMax	-0.36	-4.05
RootLCal	-2.12	FluxGrowCal	0.32	FluxGrowCal	-0.32	-3.56
CNDesLeafMin	-2.07	RootLCal	0.32	RootLCal	-0.31	-3.53

It can be seen that the ranking of the parameters according to RTU and LCC is equal. For uncorrelated parameters the LCC, SPC and SRC are equal (Janssen et.l.,1990). As we know that the maximal nitrogen concentration in the plant compartment is correlated with the minimum nitrogen concentration, the ranking according to NRC is equal to the ranking according to LCC and RTU. Because simple correlations exist between a few parameters, one sensitivity measure will be enough for interpreting the sensitivity contributions of the parameters. The sensitivity measure chosen is the RTU.

In table 6.2 the results of the linear regression analysis is shown. The analysis is made for the first 10 years of the simulation period. Deposition is included as parameter. RTU is used as sensitivity measure. According to the T-statistic all the parameters are significantly influencing the model output.

Table 6.2 Result of the linear regression analysis for the Calluna/Deschampsia vegetation and Erica/Molinia vegetation at 24 kgha^{-1}yr^{-1} and 27 kgha^{-1}yr^{-1} nitrogen deposition respectively. Deposition included as parameter. Sensitivity measure RTU.

Selected model output	0 Year		4 Year		6 Year		10 Year	
biomass	FluxGrowCal	0.68	FluxGrowCal	0.44	FluxGrowcal	0.41	FluxGrowcal	0.39
Calluna	SLACal	0.66	SLACal	0.41	SLACal	0.37	CNDeslEafMin	0.34
	Deposition	0.16	CNDesLeafMin	0.35	CNDesLeafMin	0.36	SLACal	0.33
	DesOldLitRoot	0.14	CNDesLeafMax	0.34	CNDesLeafMax	0.34	CNDesLeafMax	0.33
	RootLCal	0.12	RootLDes	0.32	RootLDes	0.33	RootLDes	0.32
biomass	CNDesLeafMin	0.52	CNDesleafMin	0.46	CNDesLeafMin	0.43	CNDesLeafMin	0.40
Deschampsia	CNDesLeafMax	0.51	CNDesleafMax	0.45	CNDesLeafMax	0.43	CNDesLeafMax	0.40
	Deposition	0.43	MortDesLeaf	0.41	MortDesLeaf	0.41	MortDesLeaf	0.39
	DesOldLitRoot	0.43	RootLCal	0.37	RootLCal	0.37	RootLCal	0.34
	SLADes	0.33	RootLDes	0.36	RootLDes	0.36	RootLDis	0.33
biomass	HthCoefMol	0.52	HthcoefMol	0.47	HthCoefMol	0.42	HthCoefEri	0.37
Erica	HthCoefEri	0.45	HthCoefEri	0.42	HthCoefEri	0.40	HthcoefMol	0.33
	FluxGrowEri	0.36	RootLEri	0.25	RootLMol	0.27	MortMolLeaf	0.30
	MolLeafC	0.35	FluxGrowEri	0.24	RootLEri	0.26	RootLMol	0.30
	SLAEri	0.29	RootLMol	0.24	MortMolLeaf	0.26	RootLEri	0.26
biomass	MolRootC	0.62	HthCoefEri	0.36	HthCoefEri	0.38	HthCoefEri	0.38
Molinia	Deposition	0.37	HthCoefMol	0.34	HthCoefMol	0.34	HthCoefMol	0.31
	CNMolRootMin	0.35	RootLEri	0.32	RootLMol	0.30	RootLEri	0.31
	CNMolRootMax	0.34	RootLMol	0.31	RootLEri	0.30	MortMolLeaf	0.29
	MolLeafC	0.32	CNMolRootMin	0.30	MortMolRoot	0.27	RootLEri	0.28

It is interesting to notice that deposition shows up in the first years of the simulation period. After ten years it ranks much lower and is sometimes not even significant. (table 6.3) when varied in the same relative way as the other parameters. In reality deposition has changed enormously over the last decades and various regions. In real situations it therefore remains a very determinant factor for the outcome of the competition between heather and grass species.

Table 6.3 Linear regression analysis for Calluna/Deschampsia and Erica/Molinia with variable deposition. Sensitivity of model output biomass species for parameter deposition in simulation year 0 and 10. Significance according to T-statistics.

model output	year 0			year 10		
	ranking	RTU	signif.	ranking	RTU	signif.
biomass Erica	9	0.14	9.81	24	0.05	-1.23
biomass Molinia	2	0.37	59.18	8	0.22	6.57
biomass Calluna	3	0.16	12.86	15	0.07	-1.78
biomass Deschampsia	3	0.43	47.46	12	0.16	5.37

The importance of the parameters determining the light competition is clearly visible. In a Calluna/Deschampsia vegetation these are the Specific Leaf Area of Calluna and Deschampsia and in the Erica/Molinia vegetation the height coefficients of Erica and Molinia and to a lesser extent the Specific Leaf Area of Erica.

The Root length biomass ratio for all the species is strongly influencing the predicted biomass.

However it must be remembered that the linear regression analysis is carried out with the parameters which were most important according to the Kolmogorov-Smirnov analysis (Section 5.5). These consists of the parameters which have the greatest impact on the outcome of the competition. A parameter which is likely to be very important in the first few years of the simulation period is the initial biomass amount of the heather and grass species. This is not included in the analysis.

6.3.2 Kolmogorov-Smirnov analysis

In table 6.4 the results of the KS analysis are given for the Calluna/Deschampsia vegetation. All the parameters which are significant (80 % level) are given. Both the analysis with and without a variable deposition is given.

Table 6.4 The most sensitive parameters according to the 80 % significance level with and without a variable deposition. Calluna/Deschampsia vegetation, Nitrogen deposition fixed at 24 kgha^{-1}yr^{-1} or varied around 24 kgha^{-1}yr^{-1} normal distribution st.dev. 10% of the mean. Critical value at 80% significance level: 0.1857 (fixed deposition), 0.1987 (variable deposition)

fixed deposition			variable deposition		
parameter	SMIR	Signif.	parameter	SMIR	Signif.
SLADes	0.44	0.67 10^{-5}	CNDesLeafMin	0.34	0.23 10^{-2}
SLACal	0.42	0.21 10^{-4}	SLACal	0.32	0.60 10^{-2}
RootLDes	0.27	0.15 10^{-1}	CNDesLeafMax	0.31	0.68 10^{-2}
CNDesLeafMin	0.26	0.23 10^{-1}	RootLDes	0.30	0.12 10^{-1}
CNDesLeafMax	0.26	0.25 10^{-1}	MortDesLeaf	0.29	0.16 10^{-1}
RootLCal	0.22	0.73 10^{-1}	FluxGrowCal	0.29	0.17 10^{-1}
CNDesRootMax	0.20	0.13	RootLCal	0.24	0.65 10^{-1}
RDiscalLeaf	0.20	0.15	CNDesRootMin	0.22	0.13
			MortCalBranch	0.21	0.15
			MortCalLeaf	0.21	0.15
			CNDesRootMax	0.20	0.19

In table 6.5 the results of the KS analysis are given for the Erica/Molinia vegetation. All the parameters which are significant (80 % level) are given. Both the analysis with and without a variable deposition is given.

Table 6.5 The most sensitive parameters according to 80% significance level with and without a variable deposition. Erica/Molinia vegetation, Nitrogen deposition fixed at 27 $kgha^{-1}yr^{-1}$ or varied around 27 $kgha^{-1}yr^{-1}$ normal distribution, st.dev. 10% of the mean. Critical value at 80% significance level: 0.1667 (fixed deposition), 0.1655 (variable deposition)

fixed deposition			variable deposition		
parameter	SMIR	Sign.	parameter	SMIR	Sign.
HthCoefMol	0.42	0.80 10^{-6}	MortMolLeaf	0.34	0.98 10^{-4}
RootLMol	0.34	0.14 10^{-3}	HthCoefEri	0.33	0.28 10^{-3}
RootLEri	0.33	0.28 10^{-3}	RootLEri	0.32	0.49 10^{-3}
FluxGrowEri	0.29	0.16 10^{-2}	RootLMol	0.31	0.75 10^{-3}
MortEriLeaf	0.25	0.11 10^{-1}	MortMolRoot	0.24	0.16 10^{-1}
SlaMol	0.25	0.12 10^{-1}	HthCoefMol	0.23	0.23 10^{-1}
HthCoefEri	0.25	0.14 10^{-1}	CNMolRootMax	0.22	0.36 10^{-1}
MortMolRoot	0.24	0.18 10^{-1}	MortEriRoot	0.21	0.43 10^{-1}
MortMolLeaf	0.23	0.30 10^{-1}	CNMolRootMin	0.21	0.53 10^{-1}
SLAEri	0.20	0.81 10^{-1}	FluxGrowEri	0.21	0.54 10^{-1}
CNEriFlMin	0.20	0.85 10^{-1}	MortEriLeaf	0.20	0.78 10^{-1}
MolLeafC	0.19	0.11	CNEriRootMin	0.19	0.97 10^{-1}
MortEriRoot	0.19	0.11	CNMolLeafMin	0.18	0.12
CNEriRootMin	0.19	0.11			

This univariate analysis is strongly influenced by adding the parameter deposition. This is caused by the same process as discussed in section 5.6.3 (see also appendix F).

We will compare the Kolmogorov-Smirnov analysis for the separate parameters (table 6.4 and 6.5) and for the analysis made with the block parameters (table 5.4 and 5.6) for the variable deposition. The parameters which have a significant influence on model output according to the 80% significance level will be included. The importance of the block parameter mortality in the Erica/Molinia vegetation was caused by the importance of the Root and Leaf of Erica and Molinia. The mortality rate of the culm, branch and flowers was less important. In a Calluna/Deschampsia importance of parameter mortality rate was caused by the mortality rate of the Calluna leaf and branch and Deschampsia leaf.

The importance of the block parameter ContNEri, ContNMol and ContNDes was caused by the importance of the nitrogen contents of the roots of grass and heather species. Parameters which were important as block parameter but were not significant when its separate parameters are analyzed are : MolVegC and ThrFallCall. The separate parameters are both not significant.

In a Erica/Molinia vegetation the Specific Leaf Area of Erica and Molinia are both not significantly influencing the model output in the separate analysis of the parameters. This is also true for the SLADes.

6.4 Conclusion

Light competition coefficients are very sensitive (under the selected scenario). Also specific root length is an important parameter determining competition between the species. However this parameter was introduced in the model to be able to accomodate for strong differences in effective rooting depth. At present this parameter has the same arbitrary value for all species, and therefore it does not influence the model output. Furthermore the minimum and maximum nitrogen concentrations of some plant parts are significantly influencing the outcome of the competition.
The model is not very sensitive for a variable deposition but in reality the range in deposition is tremendous.

It should be remembered that the sensitivity of the parameters is determined in a specific range of model coefficients, boundaries and initial conditions (local analysis). Severely changing these could have an important effect on the sensitivity of the parameters.

7. UNCERTAINTY ANALYSIS

7.1 Introduction

An uncertainty analysis is meant to obtain two kinds of information:

a) The influence of total uncertainty on obtained model output, i.e. the reliability of the model predictions.

b) Identify major sources of uncertainty. This information is most useful for the further development of the model; calibration, validation or even adjustment of the model for a better description of the experimental data.

Unfortunately an uncertainty analysis can only be carried out when information is available on uncertainty in the 'sources'. Detailed information on mean, type of distribution, variance and correlation between parameters should be available. For HEATHSOL this information of the uncertainty of the sources is seldom available.

Ideally the parameters which have to be considered in the uncertainty analysis are at least those who are significantly influencing the model output (Table 6.5). For a complete uncertainty analysis this is not enough because parameters which are not very sensitive may be very uncertain and thereby contribute to the total uncertainty in the model output.

A quantitative assessment of the total uncertainty of obtained model prediction is thus not possible. Only a qualitative assessment is possible. In the next section the sources of uncertainty which will have a great contribution to the uncertainty in the model output are mentioned. The influence of heather beetle plagues on Calluna was not considered in this analysis. However it must be realized that the occurrence of heather beetle outbreaks will have an enormous influence on the development of the vegetation.

7.2 Important sources of uncertainty

Deposition

Although the sensitivity of the parameter deposition was not very great, it may contribute substantially to the uncertainty in the model output because of its great variability. Specially in the first several years of the vegetation development it has a moderate influence on model predictions. Of course the main aim of the HEATHSOL model is to predict the development of a heathland vegetation, given a certain deposition level. In other words, the sensitivity of the model output for deposition is a basic property of the model. When deposition is not precisely known (as will almost always be the case), this will be an important source of uncertainty in the model output.

Competition

As could be observed in the sensitivity analysis the factors influencing the nutrient and light competition between the heather and grass species were very sensitive. Furthermore the very sensitive parameter specific leaf area for the various species was estimated. Unfortunately we cannot quantify the uncertainty accurately.

Other parameters which were very sensitive were the root lengths of the species. The root lengths were all set to the same value. Specific root length was never measured for heathland ecosystems. So also this parameter will contribute substantially to the uncertainty in the model predictions.

Model initialisation

Previous calculations already showed the importance of the model initialisation after sodcutting for the model output. Two things are very uncertain in the model initialisation: The initial distribution of the biomass over the heather and the grass species and the initial amount nitrogen present in the soil litter.

The quantification of the initial nitrogen pool is difficult. This amount is dependent on the amount of material removed during sod cutting. This amount will thus be highly variable on a spatial scale depending on the thoroughness of sod cutting. The uncertainty in the initial nitrogen pool may contribute substantially to the obtained model output although the sensitivity of this parameter was not very great. The uncertainty in the initial distribution of the biomass can be reduced by using the actual grassification of the heathland vegetation.

Mortality

In the sensitivity analysis the mortality rates of some of the plant parts was of importance. Specially the mortality rate of the Root and Leaf were important. The uncertainty in the mortality rates of the different plant parts cannot be quantified. But the uncertainty in mortality rates of the MoliniaLeaf, MoliniaRoot and DeschampsiaLeaf will be very small because Molinia and Deschampsia are annual grasses which die completely at the end of the growing season. The uncertainty in the mortality rate of EricaLeaf, EricaRoot, CallunaLeaf and CallunaBranch will be higher. The mortality rate will fluctuate through the years and the determination of the root mortality rate will be difficult to measure.

7.3 Conclusion

The deposition, factors determining light- and nutrient-competition and model initialisation are the major sources of uncertainty in the model.

8. COMPARING MODEL CALCULATIONS WITH FIELD OBSERVATIONS

8.1 Introduction

In this chapter the model as it presently exists with the model coefficients described in Appendix B will be compared with field observations. It will give an impression of the reliability of the model as it now exists. If model predictions deviate from observed, the model has to be calibrated. The first parameters which should be adjusted are initial nitrogen content of the litter layer and the initial biomass amount of the species. If adjustment of the initial conditions does not give a satisfactory description of the field observations other parameters have to be adjusted. Calibration of other parameters (for instance height coefficients) have not been done in this study because of the limited time available and the lack of appropriate field data.

The experimental data are taken from a paper written by F. Berendse, 1990. That paper describes a correlative study comparing the plant biomass, the soil organic matter and annual nitrogen mineralisation in heathland plots where secondary succession had been in progress for different periods. Five series of plots were selected in three heathland areas in the Netherlands. The Dwingeloose heide in the northern part (two series), the Hoge Veluwe in the central part (two series) and the Strabrechtse heide in the southern part (one series). Two main criteria were used in selecting plots. The year in which turf removal had taken place had to be known and the environmental conditions (Soil profile, groundwater table) in the plots within one series had to be similar (table 8.1). In one plot the exact year of sod cutting could not be established with certainty (Hoge Veluwe II). The data of this plot were discarded. Plots were not mown, grazed or burned during the period between turf removal and the experiments except in the plots in the Dwingeloose heide II series, where during measurement a grazing experiment was started. The data on the mineralisation rates from these plots were discarded. It is not mentioned if heather beetle plagues or severe frost occurred during the secondary succession in the Calluna and Erica vegetation. Both events may have influenced the development of the vegetation. Not only the model predictions are uncertain but also the data which have to be simulated.

Several experimental data have been determined and can be used for comparison with the model. The data which were determined are amounts of organic matter in the soil, above and below ground biomass and annual nitrogen mineralisation. For a complete description of the experimental methods used and environmental conditions in the five series of plots is referred to F. Berendse, 1990. The above and below ground biomass measured is used for validation of the model.

Table 8.1 Listing of the five series of plots, the year in which the turf layer was removed, and the measured above ground biomass percentages of the present plant species (F. Berendse, 1990). DW: Dwingeloose heide; HV: Hoge Veluwe; Str: Strabrechtse heide

Series	Year	Biomass percentages
Dw I	1982	Erica(40%), Calluna(30%), Molinia(30%)
	1979	Erica(22%), Calluna(63%), Molinia(15%)
	1976	Erica(47%), Calluna(42%), Molinia(11%)
	1935*	Molinia(99.99%), Erica(0.01%)
Dw II	1954	Erica(100%)
	c. 1935*	Molinia(100%)
HV I	1982	Calluna(100%)
	1976	Calluna(100%)
	1971	Calluna(100%)
	1954	Calluna(100%)
HV II	1983	Bare ground with a few Erica and Calluna Seedlings
	1980	Erica(79%), Calluna(12%), Molinia(9%)
	1977	Erica(68%), Calluna(12%), Molinia(2%)
	unknown	Erica, Calluna (plant biomass not measured)
	c. 1935*	Molinia(100%)
Str	1981	Calluna(100%)
	1978	Calluna(100%)
	1975	Calluna(100%)
	1972	Calluna(100%)
	1968	Calluna(100%)
	1966	Calluna(100%)
	1954	Calluna(97%), Deschampsia(3%)
	c. 1935*	Molinia(100%)

* The plots sodcutted in 1935 or c. 1935 are assumed to be fifty years old in 1984.

In each plot above and below ground biomass was measured. The above ground biomass was harvested in September 1984 (end of growing season). Additional root samples were taken from the 0-10 cm and the 10-30 cm layers. The results of these analyses are presented in figure 8.1 During the first twenty years after the turf removal there was an almost linear increase in the total above ground biomass. Thereafter the above-ground biomass in plots dominated by dwarf shrubs did not increase beyond about 1300 gm^{-2}. The above ground biomass in molinia plots was always much lower (about 400 gm^{-2}) because of the phenology of this perennial grass species, which dies off completely at the end of the growing season. The maximum living root biomass is also reached after about thirty years. The mean root biomass at that time is about 800 gm^{-2}. Root biomass decreased to about 500 gm^{-2} when plots became dominated by Molinia.

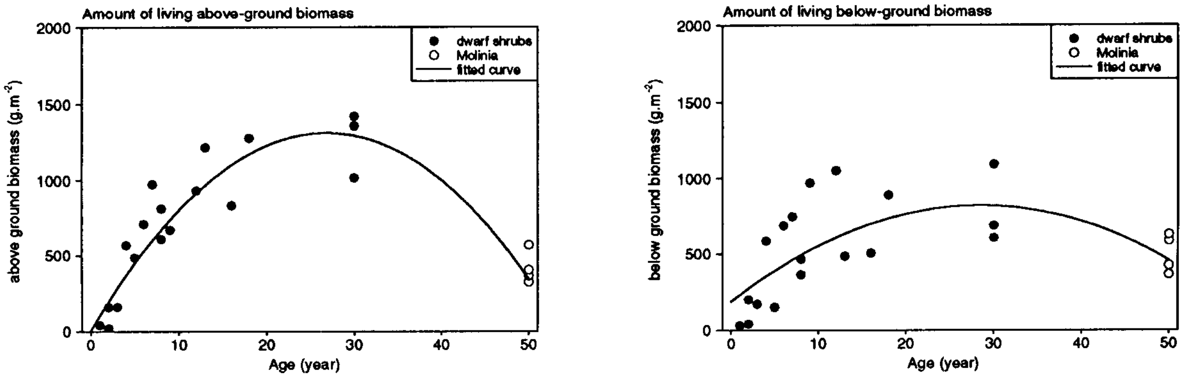

Fig 8.1 The measured amount of living above ground biomass (AB) and the measured amount of living below ground biomass (BB) in five series of plots in heathland areas in the Netherlands vs. the number of years since turf removal (T). The equation of the fitted curves are: $AB=8.86+97.11T-1.81T^2$ ($P<0.0001$), $BB=188.30+44.35T-0.78T^2$ ($P<0.025$), (•) plots dominated by dwarf shrubs; (o) plots dominated by Molinia caerulea (Berendse, 1990)

8.2 Method of model calculations

As a first test of the reliability of the model the biomass percentages at the end of the year 1984 will be simulated with HEATHSOL.

It is necessary for a fair comparison of the model and gathered experimental data to calculate the development of the heathland vegetation with a realistic nitrogen deposition during the simulation time. The historical nitrogen deposition on the various heathland plots has not been measured. As an estimation of the historical deposition on the heathland plots, the deposition data from DAS are used. These deposition data are calculated from estimated (historical) emission data for so called acidification area's from 1950 onwards (Boer, K.F. de, 1992). The deposition of nitrogen was corrected for the differences in land use. The deposition on heathlands was used. The heathland plots are located in three acidification area's (table 8.2).

Table 8.2 The scenario of calculation for the five series of plots. The acidification area according DAS in which the plots are located is given and the heather and grass species are given.

series	acidification area	vegetation
Hoge Veluwe I	6	Calluna/Deschampsia
Hoge veluwe II	6	Erica/Molinia
Dwingeloose heide I	3	Erica/Molinia
Dwingeloose heide II	3	Erica/Molinia
Strabrechtse heide	18	Calluna/Molinia

In figure 8.2 the total nitrogen deposition in (kgha^{-1}yr^{-1}) is given. As can be seen the nitrogen deposition increased steadily during this period.

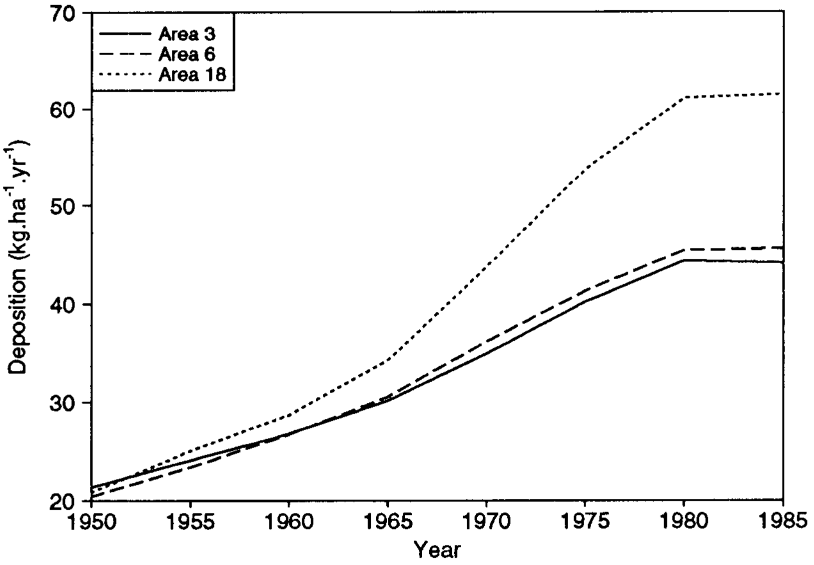

Fig. 8.2 Total nitrogen deposition (kgha^{-1}yr^{-1}) in the three acidification area's on heathlands according to DAS.

For calculations from 1935 onwards the deposition in 1950 is also used for the years 1935 to 1950. Probably the nitrogen deposition is overestimated from 1935 to 1950, but it can be used as a first estimation of the nitrogen deposition at that time.

The simulation of the development of the series of plots is hampered by a limitation of the model; only one heather species (either Calluna or Erica) can be combined with one grass species (either Deschampsia or Molinia). The plots at the Dwingeloose heide I show that one grass species (Molinia) can occur together with two heather species (Erica and Calluna). The choice of the species used in the simulation depends on the vegetation now present and the height of the ground water table. The chosen species for simulation of the various plots are listed in table 8.2.

8.3 Model initialisation

The results of the validation of HEATHSOL using the arbitrary initialisation of the sensitivity analysis and not considering heather beetle plagues, would not reflect the measurements as could be expected.

In this analysis of the reliability of HEATHSOL initial nitrogen content and initial biomass distribution are adapted to the experimental data gathered by F.Berendse. According to the measurements done by F.Berendse, in the first few years of the heathland succession few grass species were present (table 8.1). The fitted curves for the above and below ground biomass distribution are used to predict the initial heather biomass. Although this does not guarantee a complete agreement between model initialisation and the experimental initial conditions a more exact model initialisation can not be made with the data available. The above ground initial grass biomass is set at 1% of the above ground heather biomass. For below ground biomass the same ratio would lead to rather high root biomass values for the heather species. According to figure 8.1 the total below ground initial biomass is very low however. Therefore initial root biomass for the heather species was set at the same low value as used for the grass species. The relative nitrogen content is equal to the former defined relative nitrogen content of the initial biomass. The initial biomass amount thus calculated is given in table 8.3

Table 8.3 Initial biomass distribution for the heather and grass species.

Species compartment			biomass (kg.ha^{-1})	Species compartment			biomass (kg.ha^{-1})
Molinia	Leaf	N	0.012	Calluna	Leaf	N	0.51
		C	0.44			C	22.15
	Culm	N	0		Branch	N	0.22
		C	0			C	22.15
	Root	N	0.19		Flower	N	0
		C	9.41			C	0
					Root	N	0.094
						C	9.41
Deschampsia	Leaf	N	0.016	Erica	Leaf	N	0.1
		C	0.44			C	5.28
	Culm	N	0		Branch	N	0.78
		C	0			C	39.02
	Root	N	0.21		Flower	N	0
		C	9.41			C	0
					Root	N	0.188
						C	9.41

Vegetation specific factors are not considered. The estimated above and below ground biomass was fitted on the results of the biomass measurements of several vegetation types. An initial biomass estimated from this regression curve is thus the average for several vegetation types. The carbon content of the heather and grass species is set at 0.5gC/gDW. The initial biomass distribution according table 8.4, the initial nitrogen content of the litter layer was set at 168 kgha^{-1}.

8.4 Results and discussion

For the Strabrechtse heide (Calluna Molinia vegetation) and the Hoge Veluwe I (Calluna Deschampsia vegetation) the occurrence of heather beetle plagues was included in the calculations. The average of 100 runs have been calculated and the results are given in table 8.4.

Table 8.4 Predicted aboveground biomass percentages for five series of plots. DW: Dwingeloose heide; HV; Hoge Veluwe; Str: Strabrechtse heide.

series	Year of sodcutting	Years since sod cutting	biomass heather percentages (%)
DW I	1982	2	Erica(60%)
	1979	5	Erica(53%)
	1976	8	Erica(41%)
	1935	50	Erica(100%)
DW II	1954	30	Erica(100%)
	c. 1935	50	Erica(100%)
HV I	1982	2	Calluna(97%)
	1976	8	Calluna(93%)
	1971	13	Calluna(87%)
	1954	30	Calluna(85%)
HV II	1983	1	Erica(80%)
	1980	4	Erica(54%)
	1977	7	Erica(43%)
	c. 1935	50	Erica(100%)
Str	1981	3	Calluna(93%)
	1978	6	Calluna(96%)
	1975	9	Calluna(94%)
	1972	12	Calluna(90%)
	1968	16	Calluna(79%)
	1966	18	Calluna(80%)
	1954	30	Calluna(83%)
	c. 1935	50	Calluna(62%)

The results of the competition between Calluna and the grass species agree reasonably well with the measurements (Strabrechtse heide and Hoge Veluwe I). Calculations for the Strabrechtse heide show only dominance of the grass species (expressed as total biomass) when sodcutting had occurred 50 years ago. The occurrence of heather beetle plagues is the trigger which changes the vegetation structure. It must be remembered that the figures are composed of the average of 100 runs. The dominance of grass over heather species due to heather beetle plagues can only take place when a large amount of nitrogen has been collected in the litter layer. A high nitrogen deposition is not a direct cause of grassification of heathland vegetation, but increases the nitrogen accumulation rate. If the heather canopy is not opened by frost or heather beetle plagues they are not replaced in reality by grass species when nitrogen availability is as high as 200 $kgha^{-1}yr^{-1}$ (Aerts, 1993). This is also the prediction of the model.

The results of the calculations of the model for the Erica/Molinia vegetation (Hoge Veluwe II, Dwingeloose heide) are not in agreement with the observed biomass development. For instance the results of the calculations made for the Dwingeloose heide. when sodcutting occurred in 1935 the heather species dominate the vegetation because of the low nitrogen input at that time. The heather species are not replaced by grass species in later years. When sodcutting occurs in 1976 the model predicts the dominance of grass species in 1984. At the high nitrogen input at that time the heather species are replaced by the grass species. In reality the grass species dominate the vegetation in 1984 when sodcutting occurred in 1935 and the heather species dominate the vegetation in 1984 when sodcutting occurred in later years. This conclusion applies also for the calculations of Hoge Veluwe II.

A comparison of the predicted biomass with the derived biomass development curves (figure 8.3) can be made. The simulated development of the biomass is almost always lower than measured. Especially the growth of the root is much slower than measured.

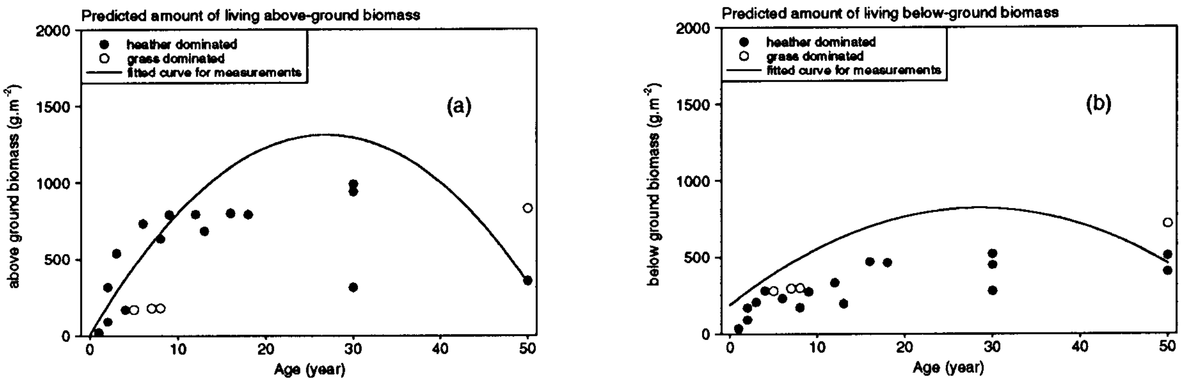

Fig 8.3 The predicted amount of living above ground biomass (a) and the predicted amount of living below ground biomass (b) in five series of heathland areas in the Netherlands vs. the year since turf removal (T). The fitted curves are derived from measured values (fig 8.1). For explanation of the scenario of calculation, is referred to the text. (•) plots dominated by dwarf shrubs, (○) plots dominated by Molinia according model calculations. Dominance of grass species is derived from the total biomass of the species.

8.5 Conclusion

The model describes the outcome of the competition for a Calluna/Deschampsia or Calluna/Molinia reasonably well. The change of vegetation from heather dominated to grass dominated is triggered in the model by the occurrence of heather beetle plagues. When heather beetle plagues are not considered in the model calculations, the heather species are not replaced by the grass species. This is in good agreement with the field observations were the heather species are not replaced by grass species even at a nitrogen availability of 250 $kgha^{-1}yr^{-1}$ if the Calluna canopy remains closed (Heil & Aerts, 1993).

The calculated competition in a Erica/Molinia vegetation is not in agreement with field observations. The development of the grass species is favoured too much and probably the factors determining the competition between the species should be calibrated further. It can be concluded that the model at present is not suited for application to humid heathlands, where Erica is the dominating heather species. However, the model can be used to predict the competition between Calluna and grass species, as influenced by nitrogen deposition. The dry heathlands where these species occur comprise roughly 90-95% of the totally occurring heathlands in the Netherlands.

9. CONCLUSIONS

The sensitivity analysis showed the importance of parameters influencing the outcome of the competition between heather and grass species. The most important parameters are the specific leaf area, height coefficients, root lengths and the minimum/maximum nitrogen content of some plant parts. The results of this analysis should be interpreted carefully because determined sensitivities are dependent on the scenario of calculation. Although the relative sensitivity for deposition is relatively low, observed fluctuations in nitrogen deposition are several times larger then the estimated uncertainty in model parameters making nitrogen deposition one of the more critical model inputs.

The uncertainty analysis was carried out qualitatively. No data were available on the uncertainty in model coefficients, initial conditions and boundary conditions. Thus the uncertainty contribution of the sources to the model output cannot be quantified. A guess was made (based on the results of the sensitivity analysis and expected uncertainty of the sources) of the parameters which may contribute substantially to the uncertainty of the model output. In order of decreasing uncertainty contribution the deposition, the specific leaf area, root lengths and model initialisation have probably the greatest contribution to the total uncertainty of the model output. The uncertainty in the model output cannot be quantified exactly. The competition within a Calluna/Deschampsia or Calluna/Molinia vegetation is described satisfactory by the model, when heather beetle plagues are included in the calculations. For the Erica/Molinia vegetation the competition between the species is not yet described satisfactory by the model. Further calibration of the model for this type of vegetation will be necessary.

The reliability of the model can be increased if measured initial conditions are used for the model simulation. This last option is already available from the HEIMON data (Kootwijk et. al., 1994) and implemented in the EXPECT model system. However many naturally occurring stochastic events (mortality of complete heather bushes, frost damage, variability within vegetation, variability in time) are not included in the model. Only heather beetle plagues in the Calluna/Deschampsia vegetation are taken into account. One of the consequences is that in the model, once heather species dominate the vegetation, the grass species cannot take over, at least not in a the Erica/Molinia vegetation. In reality, due to the stochastic nature of events even a closed heather canopy can gradually become dominated by grass. The comparison of model calculations show also the importance of the initial biomass and to a lesser extent the initial nitrogen amount.

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APPENDIX A: PROCESS FORMULATIONS HEATHSOL

In this appendix the process formulations of HEATHSOL are presented. The processes are dealt with in the same order as they are executed in the program. The time step of the program is one year and the spatial scale is one hectare.

A.1 Troughfall and canopy exchange.

Deposition is calculated as the sum of dry and wet deposition, which are input data for the model. The fraction canopy exchange is calculated as:

$$E_i = \sum_{j=1}^{n} E_{ij}$$

$$E_{ij} = \frac{B_j}{Bc_j} Em_{ij}$$

where

E_i : canopy exchange fraction of compound i (-)
E_{ij} : canopy exchange fraction of compound i by species j (-)
Em_{ij} : maximum compound exchange fraction of compound i by species j (-)
B_j : biomass of species j (kg C.ha^{-1})
Bc_j : biomass of species j where the canopy is closed (kg C.ha^{-1})

$$T_i = D_i(1-E_i)$$

where

T_i : throughfall of compound i (NH_x or NO_x) (kg N.ha^{-1}.yr^{-1})
D_i : deposition of compound i (kg N. ha^{-1}.yr^{-1})

A2 Mineralization

Mineralization is calculated separately for each litter compartment, both fresh and old litter, resulting in a C and organic N flux.

The carbon flux is calculated as:

$$C_{xj} = B_{xj} R_{xj}$$

where

C_{xj} : carbon flux of compartment x of species j (kg C.ha^{-1}.yr^{-1})
B_{xj} : biomass of compartment x of species j (kg C.ha^{-1})
R_{xj} : mineralisation rate of compartment x of species j (yr^{-1})

The nitrogen flux is calculated as:

$$N_{xj} = (NC_{xj} - NCcrit_{xj})R_{xj}\frac{B_{xj}}{1-RF}$$

where
N_{xj} : flux N of compartment x of species j (kg N.ha^{-1}.yr^{-1})
NC_{xj} : nitrogen carbon ratio of compartment x of species j (kg N (kg C)$^{-1}$)
$NC_{crit\,xj}$: critical NC ratio of compartment x of species j (yr^{-1})
R_{xj} : mineralisation rate of compartment x of species j (yr^{-1})
B_{xj} : biomass of compartment x of species j (kg C.ha^{-1})
RF : respiration factor

A3 Mortality

$$M_{xj} = B_{xj}MR_{xj}$$

where
M_{xj} : mortality rate of compartment x of species j (kg C.ha^{-1}.yr^{-1})
B_{xj} : biomass of the compartment x of species j (kg C.ha^{-1})
MR_{xj} : relative mortality rate of the compartment x of species j (yr^{-1})

The corresponding nitrogen flux is calculated as:

$$MN_{xj} = NC_{xj}M_{xj}$$

where
MN_{xj} : nitrogen flux in dying tissue (kg N.ha^{-1}.yr^{-1})
NC_{xj} : nitrogen carbon ratio of the compartment (kg N.(kg C)$^{-1}$)

A4 Redistribution

$$R_j = \sum_{x=1}^{n} MN_{xj}Rf_{xj}$$

where
R_j : total redistribution in species j (kg N.ha^{-1}.yr^{-1})

Rf_{xj} : fraction redistribution in compartment x of species j (-)

A5 Competition for nitrogen

$$A_j = E_j + R_j + S_j$$

where

A_j : nitrogen available for growth of species j (kg $N.ha^{-1}.yr^{-1}$)

S_j : nitrogen available from soil:

$$S_j = S\frac{L_jB_j}{\Sigma L_jB_j}$$

where

S : total nitrogen available from soil

L_j : specific root length for species j (m.(kg $C.ha^{-1})^{-1}$)

A6 Competition for light

The fraction intercepted light is calculated for each species as:

$$F_j = Fs_j + Fm_j$$

where

F_j : fraction of incident light intercepted by species j (-)

Fs_j : fraction intercepted in single species vegetation (-)

Fm_j : fraction intercepted in mixed species vegetation (-)

$$Fs_j = S\frac{LAI_j}{\Sigma LAI_j}(1 - e^{-\Sigma kLAI_j})$$

where

S : fraction of vegetation that is single species (-)

LAI_j : leaf area index of species j (-)

k : extinction coefficient (-)

The first term ($LAI_j/\Sigma LAI_j$) gives the fraction of the single species vegetation that is formed by this species. The second term ($1-\exp(\Sigma-k_j\ ALI_j)$) gives the fraction of light intercepted according to Beer's law.

$$Fm_j = (1-S)(U_j + L_j)$$

where

U_j : fraction intercepted light in upper layer of mixed vegetation (-)

L_j : fraction intercepted light in lower layer of mixed vegetation (-)

The upper layer is defined as the layer where only the tallest species occur, while the lower layer where both species occur. The leaf area index of the tallest species in the upper layer is calculated as:

$$LAIU = \frac{(H_{tall} - H^d_{short})}{H^d_{tall}} LAI_{tall}$$

where

H : height of species (m)

while LAIU = 0 for the shorter species.

Leaf area in the lower layer is calculated for both species as:

$$LAIL = LAI - LAIU$$

Fraction light interception by both species in both layers is now calculated as:

$$U_j = 1 - e^{-k\,LAIU_j}$$

$$L_j = \frac{LAIL_j}{\Sigma LAIL_j}(1 - e^{\Sigma -k\,LAIL_j})$$

where

$LAIU_j$: leaf area index of species j in upper layer (-)

$LAIL_j$: leaf area index of species j in lower layer (-)

A7 Growth

From the fraction intercepted light, potential growth is calculated:

$$Gpot_j = F_j\,Gmax_j$$

where

$Gpot_j$: potential growth rate of species j ($kgC.ha^{-1}.yr^{-1}$)

$Gmax_j$: maximum growth rate of species j in monoculture ($kgC.ha^{-1}.yr^{-1}$)

Actual growth rate is then calculated on based on nitrogen availability:

$$Gact_j = Gpot_j(1 - e^{\frac{-A_j}{n_j Gpot_j}})$$

where

Gact$_j$: actual growth rate of species j (kg C.ha^{-1}.yr^{-1})

n$_j$: minimum average content of species j (-)

Carbon growth for each plant is then calculated as:

$$Gact_{xj} = f_{xj} Gact_j$$

where

f$_{xj}$: fraction carbon distributed to part x of species j (-)

A$_j$: total available flux of N for species j (kg N.ha^{-1}.yr^{-1})

Nitrogen growth is calculated as:

$$N_{SJ} = G_{xj}\left(NCmin_{xj} + (NCmax_{xj} - NCmin_{xj})\,\frac{A - Nmin_j}{\mathrm{Nmax}_j - Nmin_j}\right),\quad forA_j \leq Nmax_j$$

$$N_{xj} = G_{xj} NCmax_{xj}\,,\qquad for A_j > Nmax_j$$

where

Nmin$_j$: minimum flux of N to species j (kg N.ha^{-1}.yr^{-1})

NCmin$_{xj}$: minimum nitrogen / carbon ratio of that compartment (-)

Nmax$_j$: maximum flux of N to species j (kg N.ha^{-1}.yr^{-1})

NCmax$_{xj}$: maximum nitrogen / carbon ratio of that compartment (-)

A8 Nitrification

In the mineral soil layers nitrification and denitrification takes place
The nitrate flux is calculated as:

$$NO_3 = NH_4 soil NF$$

$$NF = 0.25 \ , \qquad for\ GW < 0.45$$

$$NF = 10\log(2\ GW) \ , \qquad for\ 0.45 < GW < 2.5$$

$$NF = 1 \ , \qquad for\ GW > 2.5$$

where
NO_3 : nitrate flux (kg $N.ha^{-1}.yr^{-1}$)
NH_4 : soil ammonium mass in the soil solution(kg $N.ha^{-1}$)
NF : nitrification factor (yr^{-1})
GW : groundwater level (m)

A9 Denitrification

The nitrogen flux is calculated as:

$$N = NO_3 soil\, DF$$

with:

$$DF = \frac{1}{1 + e^{(6GW - 0.9)}}$$

where
N : nitrogen flux which is lost (kg $N.ha^{-1}.yr^{-1}$)
NO_3 : soil nitrate mass in the soil solution (kg $N.ha^{-1}.yr^{-1}$)
DF : denitrification fraction (-)
GW_u : upper groundwater level (m)

A10 Leaching

First a temporary concentration is calculated:

$$C_{NO_3,l} = 10^{-4} M_{NO_3,l}(m_l^{-1} t_l^{-1} + i^{-1})$$

where

$C_{NO3,l}$: concentration of nitrate in layer 1 (kg N.m^{-3})
$M_{NO3,l}$: total mass of nitrate in layer 1 (kg N.ha^{-1})
m_l : moisture content of layer 1 (-)
t_l : thickness of layer 1 (m)
10^{-4} : conversion factor from hectares to m^2
i : net infiltration (m)

Next leaching is calculated:

$$L_{NO_3,l} = 10^4 C_{NO_3,l}\, i$$

where

$L_{NO3,l}$: leaching of nitrate from layer l (kg N.ha^{-1})
10^4 : conversion factor from m^2 to hectare

APPENDIX B: THE INPUTFILE OF HEATHSOL

The input file of HEATHSOL (heather.ini file) is the text file in which all the model boundaries, initial values and coefficients are written. This file is read by HEATHSOL into the program before calculations are made. The values of the parameters as given are the mean values where the calculations are made with.

```
[heathland]
[Molinia]
{
  [Leaf]
    N = 7.35
    C = 262.5
  [Culm]
    N = 0.0
    C = 0.0
  [Root]
    N = 10.5
    C = 500.
}
[Deschampsia]
{
  [Leaf]
    N = 1.65
    C = 44.5
  [Culm]
    N = 0
    C = 0
  [Root]
    N = .96
    C = 43.0
}
[Calluna]
{
  [Leaf]
    N = .53
    C = 23.0
  [Branch]
    N = .23
    C = 23.0
  [Flower]
    N = 0.0
    C = 0.0
  [Root]
    N = .185
    C = 18.5
```

```
}
[Erica]
{
  [Leaf]
    N = 1.67
    C = 83.5
  [Branch]
    N = 12.35
    C = 617.5
  [Flower]
    N = 0.13
    C = 6.5
  [Root]
    N = 6.64
    C = 332
}
[MoliniaOldLitter]
{
  [Leaf]
    N = 0
    C = 0
  [Culm]
    N = 0
    C = 0
  [Root]
    N = 84
    C = 2800
}
[DeschampsiaOldLitter]
{
  [Leaf]
    N = 0
    C = 0
  [Culm]
    N = 0
    C = 0
  [Root]
    N = 84
    C = 2800
}
[CallunaOldLitter]
{
  [Leaf]
    N = 0
    C = 0
  [Branch]
    N = 0
    C = 0
```

```
  [Flower]
    N = 0
    C = 0
  [Root]
    N = 84
    C = 2800
}
[EricaOldLitter]
{
  [Leaf]
    N = 0
    C = 0
  [Branch]
    N = 0
    C = 0
  [Flower]
    N = 0
    C = 0
  [Root]
    N = 84
    C = 2800
}
[throughfall]
CanopyExchangeCallunaNH4 = 0.38
CanopyExchangeEricaNH4 = 0.35
CanopyExchangeMoliniaNH4 = 0.19
CanopyExchangeDeschampsiaNH4 = 0.16
CanopyExchangeCallunaNO3 = 0.28
CanopyExchangeEricaNO3 = 0.25
CanopyExchangeMoliniaNO3 = 0.1
CanopyExchangeDeschampsiaNO3 = 0.0
[mortality]
RateMortMoliniaLeaf = 1.0
RateMortMoliniaCulm = 1.0
RateMortMoliniaRoot = 1.0
RateMortCallunaLeaf = 0.86
RateMortCallunaBranch = 0.41
RateMortCallunaFlower = 1.0
RateMortCallunaRoot = 0.64
RateMortDeschampsiaLeaf = 1.0
RateMortDeschampsiaCulm = 1.0
RateMortDeschampsiaRoot = 0.96
RateMortEricaLeaf = 0.71
RateMortEricaBranch = 0.53
RateMortEricaFlower = 1.0
RateMortEricaRoot = 0.92
[Redistribution]
FracRedisMoliniaLeaf = 0.0
```

```
FracRedisMoliniaCulm = 0.0
FracRedisMoliniaRoot = 0.0
FracRedisCallunaLeaf = 0.17
FracRedisCallunaBranch = 0.0
FracRedisCallunaFlower = 0.0
FracRedisCallunaRoot = 0.0
FracRedisDeschampsiaLeaf = 0.0
FracRedisDeschampsiaCulm = 0.0
FracRedisDeschampsiaRoot = 0.0
FracRedisEricaLeaf = 0.36
FracRedisEricaBranch = 0.0
FracRedisEricaFlower = 0.0
FracRedisEricaRoot = 0.0
[Competition]
HeightDisMolinia = 2.
HeightDisDeschampsia = 1.5
HeightDisCalluna = 1.5
HeightDisErica = 1.75
HeightCoefMolinia = .5
HeightCoefDeschampsia = .5
HeightCoefCalluna = .45
HeightCoefErica = .45
RootLengthMolinia = 0.1
RootLengthDeschampsia = 0.1
RootLengthCalluna = 0.1
RootLengthErica = 0.1
SLAMolinia = .010
SLADeschampsia = .0075
SLACalluna = .0025
SLAErica = .005
PatchinessEricaMolinia = 0.1
PatchinessEricaDeschampsia = 0.0
PatchinessCallunaMolinia = 0.5
PatchinessCallunaDeschampsia = 0.9
ExtCoeff = 1.
[Growth]
METHOD = 3
FluxGrowMolinia_max = 14000
FluxGrowCalluna_max= 7800
FluxGrowDeschampsia_max= 4500
FluxGrowErica_max= 7400
ContNMoliniaLeaf_min = 0.0276
ContNMoliniaCulm_min = 0.0124
ContNMoliniaRoot_min = 0.0208
ContNCallunaLeaf_min = 0.0206
ContNCallunaBranch_min = 0.0098
ContNCallunaFlower_min = 0.172
ContNCallunaRoot_min = 0.0198
```

```
ContNDeschampsiaLeaf_min = 0.0246
ContNDeschampsiaCulm_min = 0.018
ContNDeschampsiaRoot_min = 0.0176
ContNEricaLeaf_min = 0.018
ContNEricaBranch_min = 0.008
ContNEricaFlower_min = 0.0156
ContNEricaRoot_min = 0.0218
ContNMoliniaLeaf_max = 0.0644
ContNMoliniaCulm_max =0.0158
ContNMoliniaRoot_max = 0.0416
ContNCallunaLeaf_max = 0.0506
ContNCallunaBranch_max = 0.0184
ContNCallunaFlower_max = 0.0284
ContNCallunaRoot_max = 0.0264
ContNDeschampsiaLeaf_max = 0.0692
ContNDeschampsiaCulm_max = 0.0322
ContNDeschampsiaRoot_max = 0.0416
ContNEricaLeaf_max = 0.0416
ContNEricaBranch_max = 0.0166
ContNEricaFlower_max = 0.029
ContNEricaRoot_max = 0.034
FracAllocMoliniaLeaf = 0.35
FracAllocMoliniaCulm = 0.00
FracAllocMoliniaRoot = 0.65
FracAllocCallunaLeaf = 0.36
FracAllocCallunaBranch = 0.40
FracAllocCallunaFlower = 0.02
FracAllocCallunaRoot = 0.22
FracAllocDeschampsiaLeaf = 0.66
FracAllocDeschampsiaCulm = 0.0
FracAllocDeschampsiaRoot = 0.34
FracAllocEricaLeaf = 0.12
FracAllocEricaBranch = 0.15
FracAllocEricaFlower = 0.06
FracAllocEricaRoot = 0.67
[Mineralization]
RateMinMoliniaLeaf = 0.2675
RateMinMoliniaCulm = 0.15
RateMinMoliniaRoot = 0.3325
RateMinCallunaLeaf = 0.22
RateMinCallunaBranch = 0.19
RateMinCallunaFlower = 0.22
RateMinCallunaRoot = 0.14
RateMinMoliniaLeaf_old =  0.2675
RateMinMoliniaCulm_old = 0.15
RateMinMoliniaRoot_old =0.3325
RateMinCallunaLeaf_old = 0.22
RateMinCallunaBranch_old = 0.19
```

```
RateMinCallunaFlower_old = 0.22
RateMinCallunaRoot_old = 0.14
RateMinDeschampsiaLeaf = 0.50
RateMinDeschampsiaCulm = 0.235
RateMinDeschampsiaRoot = 0.32
RateMinEricaLeaf = 0.155
RateMinEricaBranch = 0.13
RateMinEricaFlower = 0.155
RateMinEricaRoot = 0.04
RateMinDeschampsiaLeaf_old = 0.50
RateMinDeschampsiaCulm_old = 0.235
RateMinDeschampsiaRoot_old = 0.32
RateMinEricaLeaf_old = 0.155
RateMinEricaBranch_old = 0.13
RateMinEricaFlower_old = 0.155
RateMinEricaRoot_old = 0.04
RatioNCMoliniaLeaf = 0.0294
RatioNCMoliniaCulm = 0.0294
RatioNCMoliniaRoot = 0.0179
RatioNCCallunaLeaf = 0.0426
RatioNCCallunaBranch = 0.0235
RatioNCCallunaFlower = 0.0426
RatioNCCallunaRoot = 0.02
RatioNCMoliniaLeaf_old = 0.0294
RatioNCMoliniaCulm_old = 0.0294
RatioNCMoliniaRoot_old = 0.0179
RatioNCCallunaLeaf_old = 0.0426
RatioNCCallunaBranch_old = 0.0235
RatioNCCallunaFlower_old = 0.0426
RatioNCCallunaRoot_old = 0.02
RatioNCDeschampsiaLeaf = 0.0351
RatioNCDeschampsiaCulm = 0.0351
RatioNCDeschampsiaRoot = 0.02
RatioNCEricaLeaf = 0.0256
RatioNCEricaBranch = 0.0256
RatioNCEricaFlower = 0.0256
RatioNCEricaRoot = 0.018
RatioNCDeschampsiaLeaf_old = 0.0351
RatioNCDeschampsiaCulm_old = 0.0351
RatioNCDeschampsiaRoot_old = 0.02
RatioNCEricaLeaf_old = 0.0256
RatioNCEricaBranch_old = 0.0256
RatioNCEricaFlower_old = 0.0256
RatioNCEricaRoot_old = 0.018
GW_step = 7.0
FracEff = 0.2
FracNit_max = 1.0
[Events]
```

```
SodCuttingYear0 = 0
SodCuttingYear1 = 0
SodCuttingYear2 = 0
SodCuttingYear3 = 0
SodCuttingYear4 = 0
SodCuttingYear5 = 0
SodCuttingYear6 = 0
SodCuttingYear7 = 0
SodCuttingYear8 = 0
SodCuttingYear9 = 0
chance = 0.06
c = .0002
c0 =  23.75
c1 = -54.292
c2 =  41.111
c3 = -9.722
CallunaSusceptibility = 1
EricaSusceptibility = 0
[Soil]
N = 0
NO3 = 0
NH4 = 0
```

APPENDIX C: MEAN INFLUENCE OF HEATHER BEETLE PLAGUES

In this appendix the feasibility of including heather beetles (Lochmaea suturalis) in the sensitivity analysis is examined. Heather beetle plagues only affect the Calluna species. During an outbreak, the Calluna plants die almost completely over large areas. Outbreaks of heather beetle only occur under certain conditions of food quality and micro climatological conditions.

As the outbreak of heather beetle is modelled as a stochastic process, one simulation is not enough for assessment of the influence of heather beetles on the heathland vegetation. The number of runs to be made is examined by running the model 10 times with the number of runs and calculating 10 times the mean of the output. If a large variation exists between the 10 multiple runs the number of runs made is not sufficient. Ideally no variations between the 10 runs should be observed but this can not be attained practically.

The mean influence of heather beetles can be assessed rather accurately if 100 runs are made with the same initial conditions (figure C1). A number of 50 runs is not enough because a large variation is still observed in the calculated mean of the biomass Calluna. calculations were made at nitrogen deposition of 20 kgha^{-1}.

Due to the large number of runs that would be needed (x in the regular sensitivity analysis times 100 =....), it is decided to discard the influence of heather beetle plagues in the sensitivity analysis.

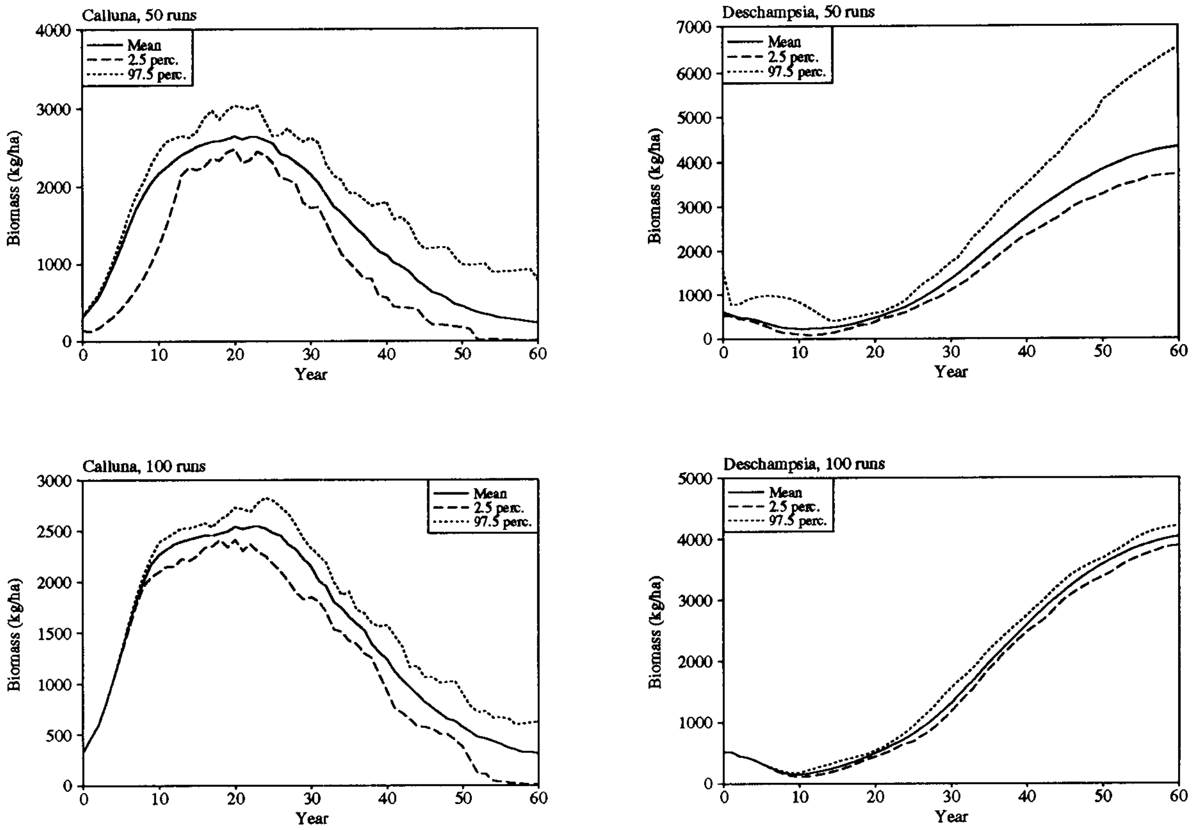


Figure C1. Average influence of heather beetle plagues on the development of Calluna. The mean 2.5 percentile and 97.5 percentile are given. The mean and percentiles are calculated for 50 and 100 runs. Nitrogen deposition 20 kgha^{-1}.

APPENDIX D: LIST OF SYMBOLS AND ABBREVIATIONS

Abbreviations used to denote (block) parameters

C : Carbon Content
Cal : Calluna
CN : Content Nitrogen
Des : Deschampsia
Eri : Erica
Fl : Flower
FluxGrow : FluxGrow Maximum
HthCoef : HeigthCoefficient
Max : Maximum
Min : Minimum
Mol : Molinia
OldLitN : Nitrogen Content OldLitter
Patch : Patchiness
RaNC : Ratio Nitrogen/Carbon
RDis : Fraction Redistribution
RootL : RootLength
SLA : Specific Leaf Area
ThrFall : ThroughFall
Veg : Initial plant biomass

Abbreviations

COD : Coefficient Of Determination
CV : Coefficient of Variation
DAS : Dutch Acidification Systems
EXPECT : EXPloring Environmental Consequences for Tomorrow
GENSEN : GENeralized SENsitivity
KS : Kolmogorov-Smirnov
HEIMON : HEIde MONitoring
LCC : Linear Correlation Coefficient
LHS : Latin Hypercube Sampling

NRC : Normalized Regression Coefficient
ORC : Ordinary Regression Coefficient
PCC : Partial Correlation Coefficient
PUC : Partial Uncertainty Contribution
RTU : Root of Total Uncertainty
SPC : Semi Partial Correlation coefficient
SRC : Standardized Regression Coefficient
UNCSAM : UNCertainty analysis by monte carlo SAMpling

Symbols used in describing statistics

$\tilde{x}$: x corrected for correlations
$\bar{x}$: average x
$\hat{e}$: estimated regression residue
$\tilde{y}$: y corrected for correlations
$\bar{y}$: average y
$\hat{y}$: estimated model output
$\beta_1..\beta_p$: estimated regression coefficients
e : regression residue
r : correlation coefficient
S_x : Variance x
S_y : Variance y
$x_1..x_p$: parameters 1..p
y : model output
$z_1..z_h$: parameter 1..h correlated with parameter x

Symbols used in describing process formulations HEATHSOL

A_j : total available flux of N for species j ($kg.ha^{-1}.yr^{-1}$)
A_j : nitrogen available for growth of species j ($kg.ha^{-1}.yr^{-1}$)
Bc_j : biomass of species j where the canopy is closed ($kgC.ha^{-1}$)
B_j : biomass of species j ($kgC.ha^{-1}$)
B_{xj} : biomass of compartment x ($kgC.ha^{-1}$)
$C_{NO3,1}$: concentration of nitrate in layer 1 ($kg.m^{-3}$)
DF : denitrification factor (-)
D_i : deposition of compound i ($kg.ha^{-1}.yr^{-1}$)
E_i : canopy exchange fraction of compound i (-)
E_{ij} : canopy exchange fraction of compound i by species j (-)

Em_{ij} : maximum compound exchange fraction of compound i by species j (-)
F_j : fraction of incident light intercepted by species j (-)
Fm_j : fraction intercepted in mixed species vegetation (-)
Fs_j : fraction intercepted in single species situation (-)
f_{xj} : fraction carbon distributed to part x of species j (-)
$Gact_j$: actual growth rate of species j (kgC.ha^{-1}.yr^{-1})
$Gmax_j$: maximum growth rate of species j in monoculture (kgC.ha^{-1}.yr^{-1})
$Gpot_j$: potential growth rate of species j (kgC.ha^{-1}.yr^{-1})
GW : groundwater level (m)
GW_u : upper groundwater level (m)
H : height of species (m)
i : net infiltration (m)
k : extinction coefficient (-)
LAI_j : leaf area index of species j (-)
$LAIL_j$: leaf area index of species j in lower layer (-)
$LAIU_j$: leaf area index of species j in upper layer (-)
L_j : specific root length for species j (m.(kgC.ha^{-1})$^{-1}$)
L_j : fraction intercepted light in lower layer of mixed vegetation (-)
m_1 : moisture content of layer 1 (-)
$Mmax_j$: maximum flux of N to species j (kg.ha^{-1}.yr^{-1})
$M_{NO3,1}$: total mass of nitrate in layer 1 (kg.m^{-3})
MN_{xj} : nitrogen flux in dying tissue (kg.ha^{-1}yr^{-1})
MR_{xj} : relative mortality rate of the compartment x of species j (yr^{-1})
M_{xj} : mortality rate of compartment x of species j (kgC.ha^{-1}.yr^{-1})
N : nitrogen flux which is lost (kg.ha^{-1}.yr^{-1})
$NC_{crit,xj}$: critical NC ratio of compartment x of species j (yr^{-1})
$NCmax_j$: maximum nitrogen/carbon ratio of that compartment (-)
$NCmin_j$: minimum nitrogen/carbon ratio of that compartment (-)
NC_{xj} : nitrogen carbon ratio of compartment x of species j (kg.(kgC)$^{-1}$)
NF : nitrification factor (yr^{-1})
NH_4 : soil ammonium mass in the soil solution (kg.ha^{-1})
n_j : minimum average content of species j (-)
$Nmin_j$: minimumflux of N to species j (kg.ha^{-1}.yr^{-1})
NO_3 : nitrate flux (kg.ha^{-1}.yr^{-1})
N_{xj} : flux N of compartment x of species j (kgha^{-1}yr^{-1})
RF : respiration factor (-)
RF_{xj} : fraction redistribution in compartment x of species j (-)
R_j : total redistribution in species j (kg.ha^{-1}.yr^{-1})
R_{xj} : mineralisation rate of compartment x of species j (yr^{-1})
S : fraction of the vegetation that is single species (-)

S_j : total nitrogen available from the soil

t_1 : thickness of layer 1 (m)

T_i : throughfall of compound i ($kg.ha^{-1}.yr^{-1}$)

U_j : fraction intercepted light in upper layer of mixed vegetation (-)

X_{xj} : carbon flux of compartment x of species j ($kgC.ha^{-1}.yr^{-1}$)

APPENDIX E: RESULTS VALIDATION HEATHSOL

First in table E.1 the predicted biomass values for the five series of plots in 1984 are given. The biomass development for the five series of plots is depicted in the figures.

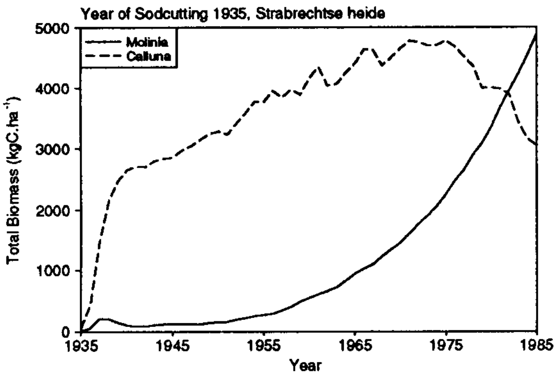
Table E.1 Predicted biomass for five series of plots in the year 1984. DW: Dwingeloose heide; HV: Hoge Veluwe; Str: Strabrechtse heide; AB: above ground; BB: below ground (root). The biomass in the year 1984 is given. The biomass percentage is calculated from the above ground biomass.

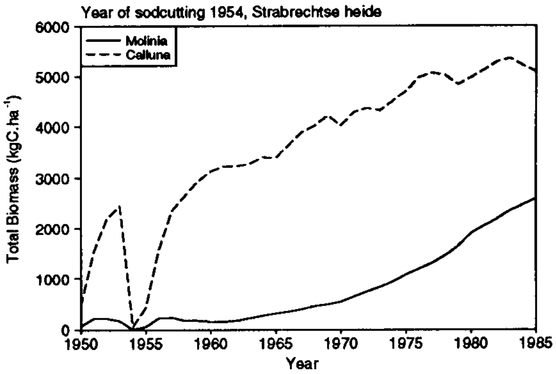
Series	Year	Age (year)	grass (kgC.ha^{-1})			heather (kgC.ha^{-1})			biomass distribution % grass	total	
			total	above ground	below ground	total	above ground	below ground		AB (g/m2)	BB (g/m2)
Dw I	1982	2	518	181	337	783	275	508	39.7	91	17
	1979	5	1136	398	737	1090	448	643	47.0	169	276
	1976	8	1518	531	987	869	370	499	59.0	180	397
	1935[*]	50	0	0	0	4274	1758	2516	0	352	503
Dw II	1954	30	3	1	2	3789	1557	2231	0	312	447
	c. 1935[*]	50	0	0	0	4274	1758	2516	0	352	503
HV I	1982	2	79	52	27	1950	1522	428	3.3	315	91
	1976	8	347	227	120	3666	2932	734	7.2	632	171
	1971	13	684	445	239	3704	2961	743	13.1	681	196
	1954	30	1087	708	379	4988	3989	999	15.1	939	276
HV II	1983	1	61	21	40	213	83	130	20.2	21	34
	1980	4	1106	387	719	1129	451	678	46.2	168	279
	1977	7	1446	506	940	911	386	525	56.7	178	293
	c. 1935[*]	50	0	0	0	4325	1778	2547	0	356	509
Str	1981	3	505	177	328	3215	2514	701	6.6	538	206
	1978	6	371	130	241	4427	3518	909	3.6	730	230
	1975	9	656	230	426	4645	3711	934	5.8	788	272
	1972	12	1192	417	775	4418	3538	880	10.5	791	331
	1968	16	2413	844	1569	3926	3143	783	21.2	797	470
	1966	18	2353	823	1530	3900	3121	779	20.9	789	462
	1954	30	2462	861	1601	5087	4082	1005	17.4	989	521
	c. 1935[*]	50	4551	1593	2958	3159	2543	616	38.5	827	715

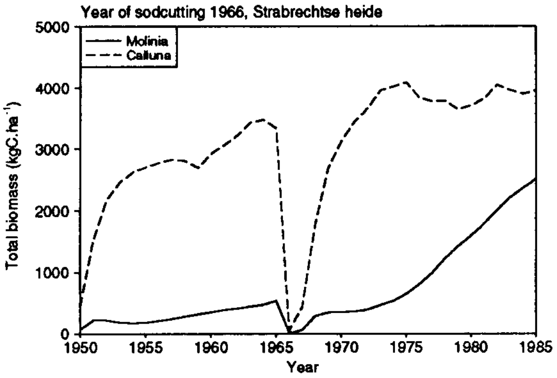
[*] The plots sod cutted in 1935 or c. 1935 are all assumed to be fifty years old.

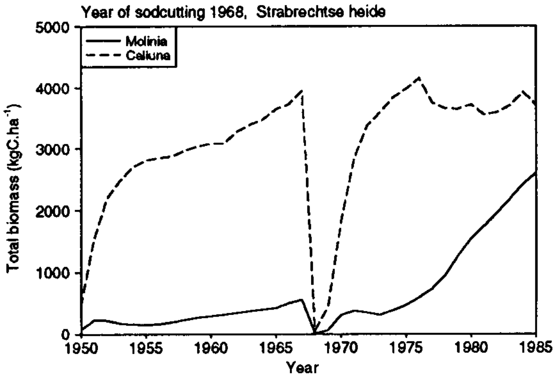
Strabrechtse heide

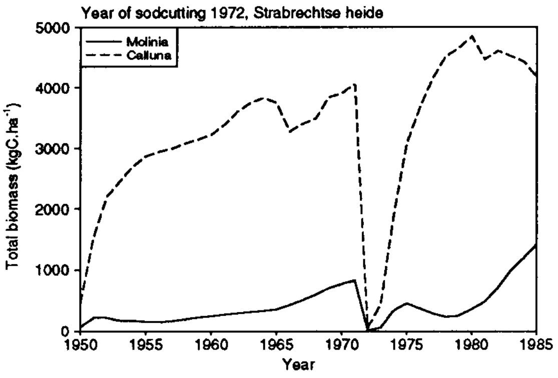
Conditions: Calluna/Molinia vegetation, Initial nitrogen amount: 168 $kgha^{-1}$. Initial biomass distribution: 15% grass, Effect of heatherbeetle plagues included, The average of 100 runs is given.

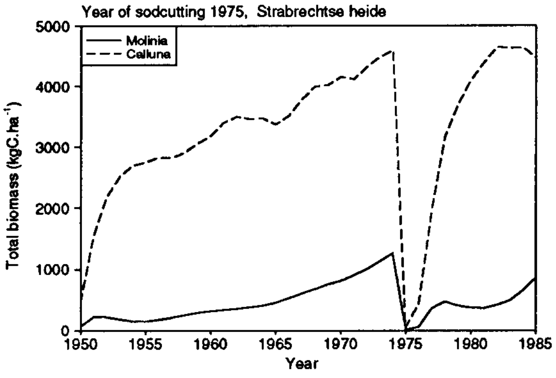


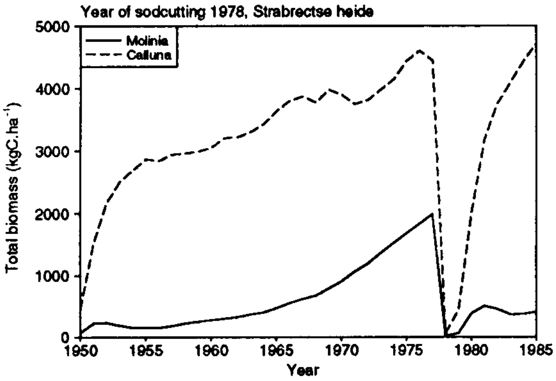


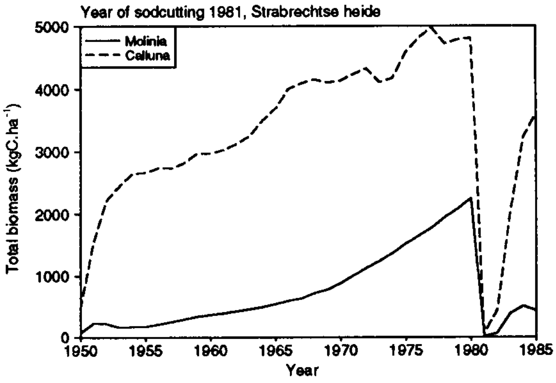






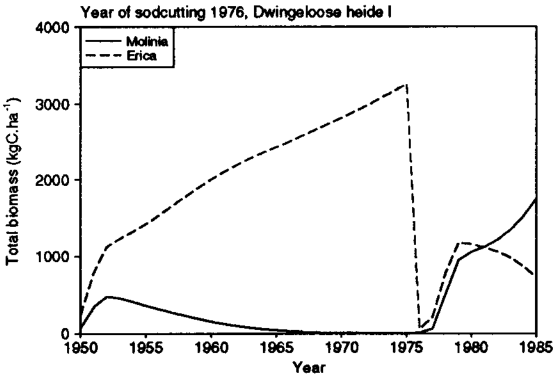


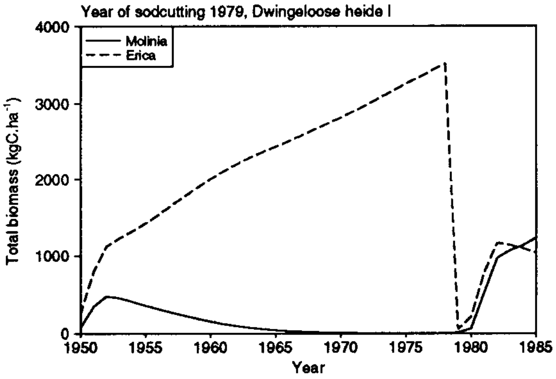

Year of sodcutting 1978, Strabrectse heide

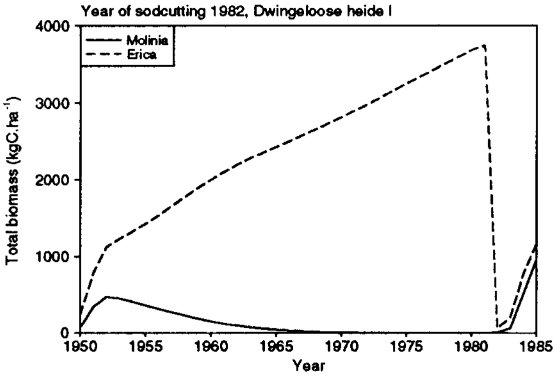

Year of sodcutting 1981, Strabrechtse heide

Dwingeloose heide I

Conditions: Erica/Molinia vegetation, Initial nitrogen amount: 168 kgha^{-1}, Initial biomass distribution: 15% grass.

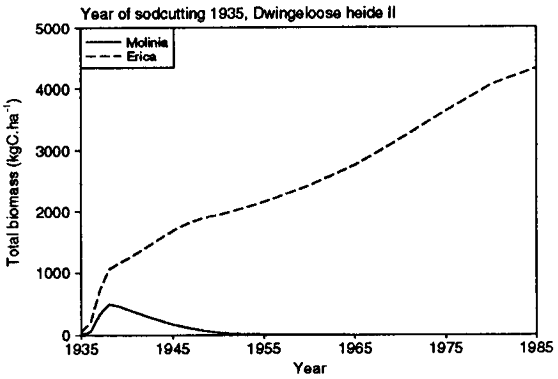

Year of sodcutting 1976, Dwingeloose heide I

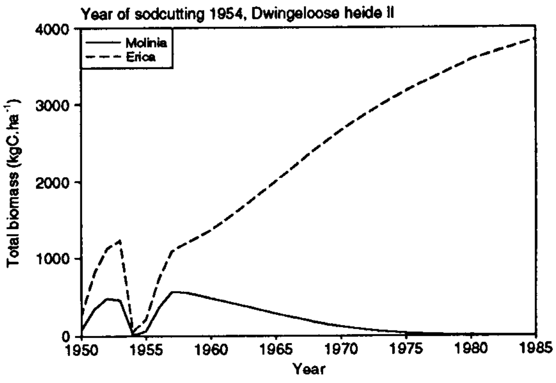

Year of sodcutting 1979, Dwingeloose heide I


Year of sodcutting 1982, Dwingeloose heide I

Dwingeloose heide II

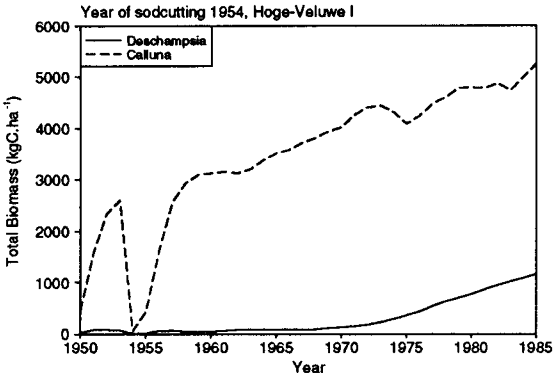
Conditions: Erica/Molinia vegetation, Initial nitrogen amount: 168 kgha^{-1}, Initial biomass distribution: 15% grass.

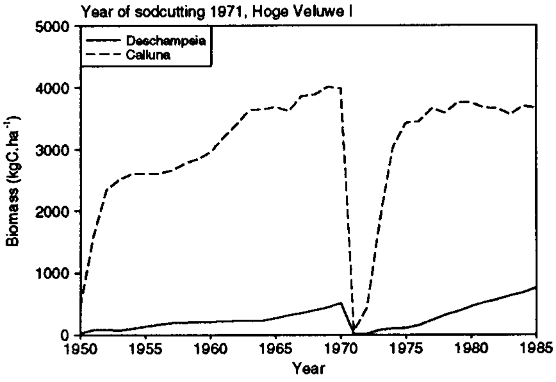


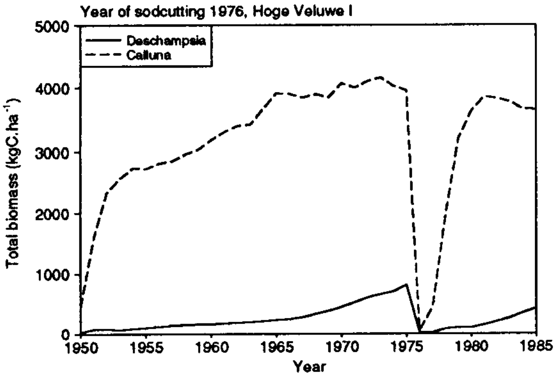


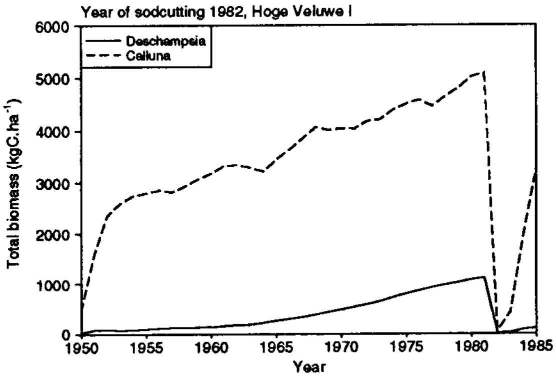
Hoge Veluwe I

Conditions: Calluna/Deschampsia vegetation, Initial nitrogen amount: 168 kgha^{-1}, Initial biomass distribution: 15% grass, Effect of heatherbeetle plagues included, The average of 100 runs is given.



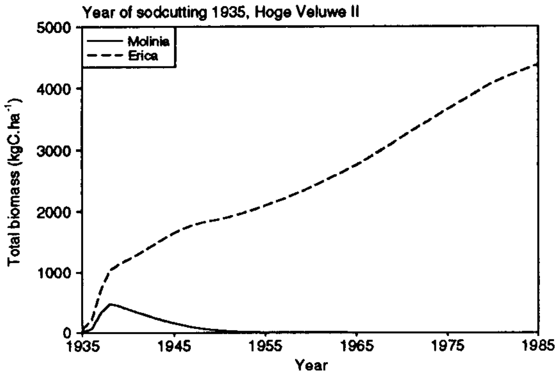


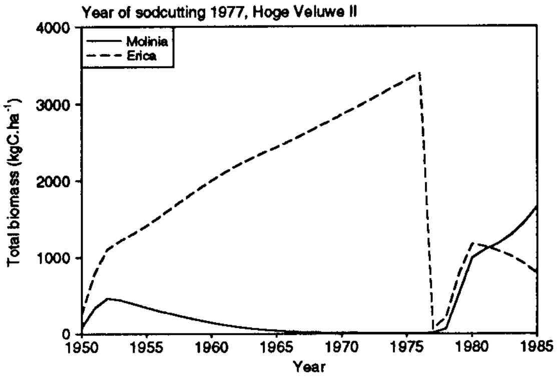


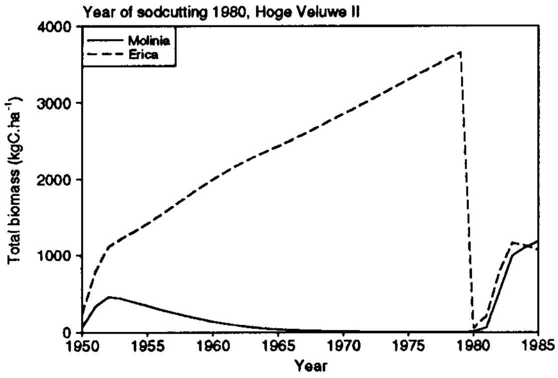


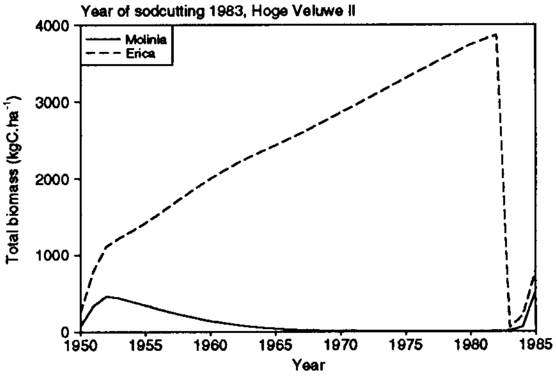
Hoge Veluwe II

Conditions: Erica/Molinia vegetation, Initial nitrogen amount: 168 $kgha^{-1}$, Initial biomass distribution: 15% grass.









APPENDIX F: INFLUENCE OF CORRELATIONS ON KOLMOGOROV-SMIRNOV ANALYSIS.

In this appendix the result of the univariate KS analysis and multivariate KS analysis are compared for the sensitivity analysis made in section 6.3.2. In that analysis the sensitivity of separate parameters for a Calluna/Deschampsia vegetation at a fixed nitrogen deposition and a variable deposition is made. The results of both analyses differed considerably although only one extra parameter (deposition) was added (see table F1). In the univariate analysis the importance of the parameters can be obscured by correlations between the parameters. It is therefore advised to apply a transformation of the parameters to make the parameters uncorrelated. In the multivariate analysis the KS analysis is made based on these transformed parameters. The resulting surrogate sensitivities are rather heuristic quantities and should therefore interpreted carefully. Low correlations have a significant influence on the multivariate analysis and where therefore not used in the sensitivity analysis. But the multivariate analysis is not influenced by altered correlations between the parameters. This can be seen in the KS analysis of the separate parameters for the situation with a fixed and variable deposition. The univariate analysis is greatly influenced by the addition of one parameter but the multivariate analysis not (table F1 and F2).

Table F1 The results of the univariate KS analysis for Calluna/Deschampsia vegetation. Nitrogen deposition fixed at 24 $kgha^{-1}yr^{-1}$ or varied around 24 $kgha^{-1}yr^{-1}$. Critical value at 80% significance level : 0.1857 (fixed deposition), 0.1987 (variable deposition)

fixed deposition			variable deposition		
parameter	SMIR	Signif.	parameter	SMIR	Signif.
SLADes	0.44	$0.67\ 10^{-5}$	CNDesLeafMin	0.34	$0.23\ 10^{-2}$
SLACal	0.42	$0.21\ 10^{-4}$	SLACal	0.32	$0.60\ 10^{-2}$
RootLDes	0.27	$0.15\ 10^{-1}$	CNDesLeafMax	0.31	$0.68\ 10^{-2}$
CNDesLeafMin	0.26	$0.23\ 10^{-1}$	RootLDes	0.30	$0.12\ 10^{-1}$
CNDesLeafMax	0.26	$0.25\ 10^{-1}$	MortDesLeaf	0.29	$0.16\ 10^{-1}$
RootLCal	0.22	$0.73\ 10^{-1}$	FluxGrowCal	0.29	$0.17\ 10^{-1}$
CNDesRootMax	0.20	0.13	RootLCal	0.24	$0.65\ 10^{-1}$
RDisCalLeaf	0.20	0.15	CNDesRootMin	0.22	0.13
			MortCalBranch	0.21	0.15
			MortCalLeaf	0.21	0.15
			CNDesRootMax	0.20	0.19

For the multivariate analysis a different measure is used for expressing the sensitivity of the parameters. Based on the KS statistics for the transformed parameters a so called absolute surrogate sensitivity index is calculated. Application of this measure enables a fair comparison between generalised sensitivity analyses where the number of acceptable and non acceptable parameters is different. For further comments of this measure see Janssen, 1995.

Table F2 The results of the multivariate KS analysis for Calluna/Deschampsia vegetation. Nitrogen deposition fixed at 24 $kgha^{-1}yr^{-1}$ or varied around 24 $kgha^{-1}yr^{-1}$. The so called absolute surrogate sensitivity is given for the first eleven parameters.

fixed deposition		variable deposition	
parameter	Absolute surrog. sens.	parameter	Absolute surrog. sens.
SLACal	$0.91\ 10^{+1}$	SLACal	$0.99\ 10^{+1}$
SLADes	$0.37\ 10^{+1}$	SLADes	$0.45\ 10^{+1}$
CNDesCulmMin	$0.18\ 10^{+1}$	CNDesCulmMin	$0.20\ 10^{+1}$
CNDesLeafMin	$0.12\ 10^{+1}$	CNDesRootMin	$0.16\ 10^{+1}$
CNDesRootMin	$0.12\ 10^{+1}$	CNDesLeafMin	$0.12\ 10^{+1}$
CNDesCulmMax	$0.11\ 10^{+1}$	CNDesCulmMax	$0.11\ 10^{+1}$
CNDesRootMax	0.64	CNDesRootMax	0.77
CNDesLeafMax	0.43	CNDesLeafMax	0.47
RootLCal	0.41	RootLDes	0.40
RootLDes	0.38	RootLCal	0.36
RDisCalLeaf	0.19	RDisCalLeaf	0.20

As can be observed in table F2 the multivariate analysis made is almost similar when one extra parameter is evaluated. Even the value of the absolute surrogate sensitivity is nearly the same.