

NATIONAL INSTITUTE OF PUBLIC HEALTH & ENVIRONMENTAL PROTECTION
BILTHOVEN, THE NETHERLANDS

Report nr: 259102009

**HEATHSOL:
a heathland competition model**

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March, 1994

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This study has been conducted on behalf of and for the account of the Directorate-General for Environment, Directorate Strategic Planning and Directorate Air, as part of the projects 259102 and 733001

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SUMMARY

This report describes the model HEATHSOL. HEATHSOL has been developed to simulate the competition for nitrogen and light between grass and heather species occurring in natural heathlands in the Netherlands. The model aims at predicting the biomass of both grass and heather species as influenced by both nitrate and ammonium deposition, and will be used for evaluating the effects of different deposition scenarios on the species composition of heathland communities.

Simulations can be carried out with a community consisting of one of the grass species Molinia caerulea and Deschampsia flexuosa and one of the heather species Erica tetralix and Calluna vulgaris.

Sod-cutting can be simulated at user-specified times as a management practice. When Calluna vulgaris is simulated, stochastically simulated heather beetle plagues can be included.

SAMENVATTING

Dit rapport beschrijft het model HEATHSOL. HEATHSOL is ontwikkeld om de concurrentie om stikstof en licht tussen gras- en heidesoorten in natuurlijke Nederlandse heidevegetaties te beschrijven. Het model kan gebruikt worden om de biomassa van gras- en heidesoorten te voorspellen zoals die beïnvloed wordt door nitraat- en ammoniumdepositie. Het model is bedoeld om het effect van verschillende depositiescenario's op de soortensamenstelling van heidevegetaties te evalueren.

Simulaties kunnen worden uitgevoerd met een vegetatie bestaande uit een van de grassoorten Molinia caerulea en Deschampsia flexuosa en een van de heidesoorten Erica tetralix en Calluna vulgaris.

Plaggen van de heide kan worden uitgevoerd op door de gebruiker gespecificeerde tijden. Wanneer Calluna vulgaris deel uitmaakt van de gesimuleerde vegetatie kan het optreden van heidekeverplagen stochastisch worden gesimuleerd.

1 INTRODUCTION

This report describes a model to simulate the dynamics of heather vegetation in the Netherlands, as determined by nutrient availability and management practices.

The model is the result of a joint effort by the authors to combine existing models and expand these to more species, using data from earlier experiments.

1.1 Background

In 1988 the first 'National Environmental Outlook' for the Netherlands was published (RIVM, 1988), called 'Concern for Tomorrow'. This study gave an overall view of the present environmental problems in the Netherlands, and the future developments were evaluated by analyzing the environmental effects of three policy scenarios. The study received much attention both nationally and internationally. Its results were used by the Dutch government in preparing the first 'National Environmental Policy Plan' (VROM, 1989). This plan was later updated after a change of government (VROM, 1990).

The second and third 'National Environmental Outlook' (RIVM, 1991 and 1993) evaluated the future environmental impact of the policy changes that had been implemented at the time.

For these studies a great number of environmental impact models were used, while often one model would generate part of the input for another model. Special attention was needed to ensure proper data transfer between models that were not developed to be linked together. Moreover, the detailed process models could often only be operated by those who developed them, and some took hours or days to simulate twenty years. Evaluating a policy scenario in this way was obviously very time consuming. This severely restricted the number of scenarios that could be evaluated for their environmental impacts. Also, the effect of small changes in scenarios could not be evaluated easily. For this reason it was decided to create a set of models that would operate together as modules within one model system. This model system was named EXPECT (EXPLoring Environmental Consequences for Tomorrow). EXPECT aims at rapid evaluation of policy scenarios.

The heathsol model is part of the EXPECT model and will be used to evaluate the impact of nitrogen deposition on heathland vegetation in the Netherlands.

1.2 Objectives

The main objective of the model is to describe the effects of the deposition of acidifying and eutrophying substances on the species composition of a heathland vegetation. 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 structure is suitable to describe competition between other species as well, when the proper parameters for those species are known. Process formulations are based on the earlier model NUCOM2 by Berendse (1988) which describes the dynamics of communities with Erica tetralix and Molinia caerulea, and the

model CALLUNA (Heil, 1990), describing communities with Calluna vulgaris and Deschampsia flexuosa and the occurrence of heather beetle plagues. The model includes some of the process formulations of these models, several more general formulations to describe competition (Berendse, 1994), while other formulations were developed specifically for this model. The soil module is partly based on NUCOM2 and partly on the RESAM model (de Vries et. al., 1988), while the parameter values used have been derived from both published and unpublished experimental results. The model was implemented in the C++ programming language to fit within the EXPECT framework (Braat et al., 1991, Bakema et al., 1994).

1.3 Structure of the report

In chapter 2 a general overview is given of the newly developed model. In chapters 3 to 8 the processes included in the model are described in more detail, together with their respective theoretical backgrounds, while chapter 10 shows some typical examples of simulation results. In chapter 11 the expected future developments of the model are briefly discussed. References to the literature are listed in appendix A, and in appendix B a summary of the process formulations is given.

2 MODEL OVERVIEW

The model simulates growth processes of the vegetation and uses a timestep of one year. The spatial scale is one hectare.

In the model, the plants have been divided in compartments. For *Calluna* and *Erica* four compartments are distinguished (leaves, flowers, branches and roots) and for *Molinia* and *Deschampsia* three (leaves, culms and roots).

For each of these compartments, biomass (expressed as kg carbon/hectare) and amount of nitrogen is calculated based on yearly growth rates. Nitrogen concentration in the biomass can change from year to year, depending on nitrogen availability, but remains within specified limits.

Growth rates in the model are dependent on light and nitrogen availability for the whole plant, and are affected by photosynthetic capacity and maximum absolute growth rate. Total available nitrogen is the sum of deposited nitrogen and nitrogen released by mineralization.

The two species compete for the total available nitrogen and light. The outcome of this competition determines the amount of C and N available for the growth of each plant species. The available C is divided over the plant parts using a constant allocation factor. The available N is distributed over the various compartments using an allocation factor that depends on the present nitrogen content of each plant compartment.

Senescence of the plants is simulated by dying of plant compartments. This mortality is assumed to take place at a constant compartment-specific relative mortality rate. Part of the nitrogen from dying plant compartments can be reallocated and used for growth. The unused nitrogen is added to the soil litter pool. Senescence of whole plants due to old age has not yet been included in the model.

Mineralization of the litter is simulated in the soil model. The litter from each plant compartment is treated separately. The resulting nitrogen in the form of ammonium and nitrate is available for uptake by the plants. If not all nitrogen is taken up by the plants, the remainder leaches to the mineral soil layer. In the mineral soil layer nitrification, denitrification and leaching to the groundwater are taking place.

In the model, provisions have been made for external influences on the vegetation. Heather beetle plagues may occur, which decimate the living biomass of *Calluna*, or sods can be cut as a management action. In sod cutting all living biomass and part of the soil litter is removed (including most of the systems nitrogen pool), thereby hampering the prolific growth of the grass species.

The model was implemented in the C++ programming language, using an object-oriented modeling approach. For this purpose a collection of C++ classes has been prepared (Bakema et al., 1993). With these classes, compartments containing various chemicals, can easily be linked together, and processes specific for each compartment can be added. The model can be used both under UNIX and DOS operating systems.

3 COMPETITION

3.1 Competition for soil nutrients

We shall first consider competition for soil nutrients between different plant species that are completely identical in their ability to absorb nutrients from the soil. In this case, the amount of the limiting resource (i.e. nitrogen) available from the soil to each plant population (S_j) is assumed to be proportional to the fraction that the species contributes to the total biomass of all species:

$$S_j = \frac{B_j}{\sum B_k} N \quad (1)$$

where N is the resource supply rate (through mineralization and atmospheric deposition), B_j represents the biomass of species i and $\sum B_k$ is the summed biomass of both species. If the two populations are not identical, but have e.g. different specific root lengths (root length per unit root weight) or different ratios of active root surface to root weight, the biomass of each species should be replaced by a function $f_j(B_j)$ that converts the biomass of each species into its root length, root surface or any other variable that determines the fraction of available nutrients that it can absorb. Lacking more specific data, the most simple function is used, namely a linear relationship i.e. $f_j(B_j) = \alpha_j B_j$, where α_j measures the root length/biomass ratio. The partitioning of the resource between such species is given by:

$$S_j = \frac{\alpha_j B_j}{\sum \alpha_k B_k} N \quad (2)$$

Nitrogen is also available to the plants via redistribution of nitrogen from dying plant parts (R_j , see chapter 4) and canopy exchange (E_j , see chapter 5). Total available nitrogen for each species (A_j) is therefore given by:

$$A_j = S_j + R_j + E_j \quad (3)$$

Whether all available nitrogen can actually be used by the plant depends on its growth rate and its minimum and maximum nitrogen concentration (see chapter 4). The growth rate is determined both by its ability to compete for light and by the availability of nutrients (see next sections).

3.2 Competition for light

When soil fertility is sufficiently high, plant growth is completely regulated by the amount of irradiation that can be captured (assuming that no other resources have a growth reducing effect). In such environments the vegetation is able to realize its potential productivity. The maximum growth rate (G_{max} ; $g\ C.m^{-2}.yr^{-1}$) of each species is defined as its productivity in monoculture at optimum nutrient supply, when its canopy has closed and light interception is complete. Such conditions only apply when disturbance is not too frequent. In mixtures of two or more species, each species can realize a fraction of its maximum growth rate (measured as growth per unit ground area). This fraction is

proportional to the fraction of the total irradiation that it can intercept. When the competing plant species are equally tall and are identical in all other respects except for the ratio of leaf area to total biomass (β), the biomass of each species in equation (1) should be multiplied by β , so that it is converted to its leaf area. The amount of energy captured by a species is then proportional to the share of that species in the total leaf area of the plant community. The potential growth (G_{pot}) of species i is then given by:

$$G_{pot_j} = \frac{\beta_j B_j}{\sum \beta_k B_k} G_{max_j} \quad (4)$$

In the above equation we assume that plants are of equal height and that the canopy is closed. In heathlands, as in most vegetations, large differences in height can develop between plant species. Such differences influence the amount of irradiation that can be intercepted by the competing species. To develop a model that can simulate the competition for light between plants with different heights, we need to include an expression that describes the relation between plant biomass (B) and plant height (H). Analysis of the results of a fertilization experiment with Erica tetralix, Calluna vulgaris and Molinia caerulea (Aerts et al., 1990) showed that the following expression yields a reasonable fit:

$$H = B^c \quad (5)$$

For Molinia the exponent c was estimated to be about 0.5; for Erica and Calluna 0.45 yielded the best fit. With expression (5) the model can calculate the height of a species on the basis of plant biomass in a monoculture. When two species are present, the same relation is used, but for B the total biomass of the two species is used.

Subsequently, light interception should be calculated in the various leaf layers. In a model of two competing species a minimum number of two layers should be distinguished: one layer in which both species are present and one layer in which only the taller species can intercept the irradiation. Before the light interception by each species can be calculated, the amount of leaf biomass or leaf area in each separate layer needs to be calculated first. For a species with a rectangular leaf area distribution a fraction h/H_j of its biomass is present below height h . For a vertical leaf area distribution with the shape of an isosceles triangle, this fraction is described by h/H_j^2 , and if the vertical distribution is cone-shaped the fraction equals h/H_j^3 . In the model we use a generalization of this formula, where the fraction of the biomass that is present below height h is calculated as h/H_j^d , where d is called the distribution coefficient. The biomass that is present in the upper layer can then be calculated as:

$$Ba_j = \frac{(H_j - H_k)^d}{H_j^d} B_j \quad (6)$$

and the biomass in the lower layer by:

$$Bb_j = B_j - Ba_j \quad (7)$$

where H_j H_k represent the height of the taller and the lower species respectively, and d is called the distribution coefficient. The appropriate values were estimated to be 2.0 for Molinia caerulea, 1.75 for Erica tetralix, and 1.5 for both Deschampsia flexuosa and Calluna vulgaris. The distribution coefficient d is a simple but quite appropriate parameter that describes the plant architecture in a way that is relevant to our modeling approach. An

assumption still to be tested is that d is not dependent on the plant height H_j .

The final step is calculation of the light absorption by each species. Here we can not assume that the irradiation is intercepted completely, so that we must apply the Law of Lambert-Beer for exponential extinction (Monsi & Saeki, 1953). The interception by species i in the upper layer (Ia_j) is calculated by:

$$Ia_j = (1 - e^{-k\beta B a_j}) I \quad (8)$$

and the interception in the lower layer by species i (Ib_j) is calculated by:

$$Ib_j = \frac{\beta_j B b_j}{\sum \beta_k B b_k} (1 - e^{-\sum k\beta_k B b_k}) (I - Ia_j) \quad (9)$$

where k represents the extinction coefficient and β the leaf area/biomass ratio.

I represents the photosynthetic active irradiation. In environments where plant production is completely energy regulated, the growth of species i in mixture is given by:

$$Gpot_j = \frac{Ia_j + Ib_j}{I} Gmax_j \quad (10)$$

assuming that the maximum growth rate $Gmax$ is achieved when $((Ia_j + Ib_j)/I)$ approaches unity.

In the model, provision is made both for vegetations that are true mixtures of different species, in which case the above formulations are used to simulate light competition, and for vegetations consisting of various patches of each species. For the latter the most simple situation is used, in which leaf area of both species together is homogeneously distributed over the ground area. In this case the ratio between the amount of intercepted light for both species is linearly related to the ratio between their leaf area indices:

$$I_j = \frac{\beta_j B_j}{\sum \beta_k B_k} (1 - e^{-\sum k\beta_k B_k}) I \quad (11)$$

It is also possible to specify any mixture of these two vegetation types. For Calluna and Deschampsia vegetations a default value of 10% mixed and 90% single-species vegetation is used, while for Erica and Molinia 90% mixed and 10% single species is used as the default value.

3.3 Competition at increasing nutrient supply

The approach presented in the preceding two sections enables us to simulate the effects of competition in extremely nutrient-poor and in very nutrient-rich environments. However, we need to calculate the outcome of competition at a whole range of nutrient supply rates. In order to achieve this purpose we have to find an expression that describes actual plant productivity ($Gact$) depending upon the nutrient supply rate (N). Such an expression should satisfy two requirements:

$$\lim_{A \rightarrow 0} Gact = \frac{A}{n} \quad (\text{only nutrients limiting}) \quad (12)$$

$$\lim_{A \rightarrow \infty} Gact = Gpot \quad (\text{only light limiting}) \quad (13)$$

where n stands for the minimum nitrogen content of the growing tissue, and therefore A/n stands for the upper limit on growth rate based on nitrogen availability alone, when the plants are growing with minimum nitrogen content. Three simple expressions that satisfy these requirements are:

$$Gact = \min \left(\frac{A}{n}, Gpot \right) \quad (14)$$

$$Gact = \frac{\frac{A}{n}}{\frac{A}{n} + Gpot} Gpot \quad (15)$$

$$Gact = Gpot \left(1 - e^{-\frac{A}{n Gpot}} \right) \quad (16)$$

In the model the use of expression (16) is implemented as standard procedure, whereas the use of expressions (14) and (15) is optional. In expression (14) the nitrogen concentration in the growing tissues does not change with increasing nitrogen supply until the potential growth rate $Gpot$ has been reached. With a further increase in nitrogen supply the nitrogen concentration in the growing tissues increases linearly up to its maximum. In expressions (15) and (16) the nitrogen concentration in the plants increases with increasing nitrogen availability over the whole range of nitrogen supplies, until the maximum nitrogen concentration is reached. In figure 3.1 and 3.2 the differences in growth rate and nitrogen content of the growing tissue are illustrated, resulting from the use of equation 14, 15 and 16.

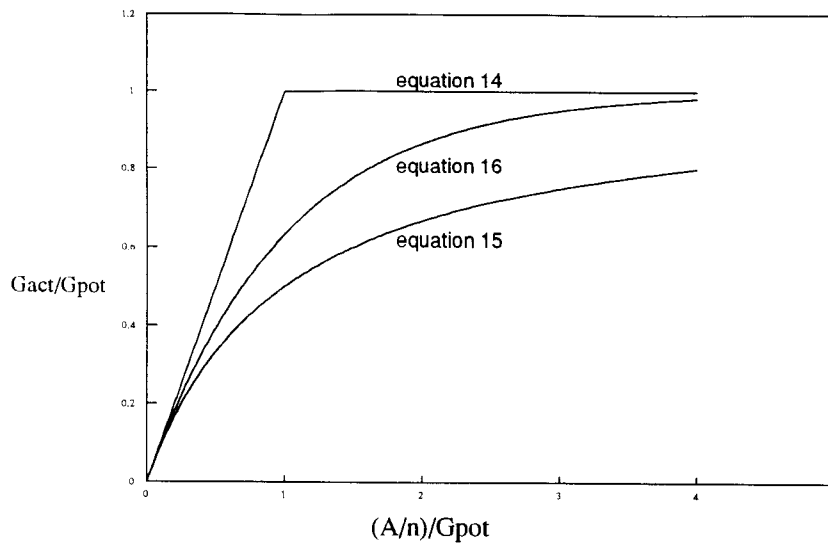


Figure 3.1

The relation between actual growth rate as a fraction of potential growth rate (G_{act}/G_{pot}), against relative nutrient availability, according to equations 14, 15 and 16. Relative nutrient availability is expressed as the ratio of the upper limit on growth as determined by nutrient availability alone (A/n) and the potential growth rate as determined by light availability alone (G_{pot}).

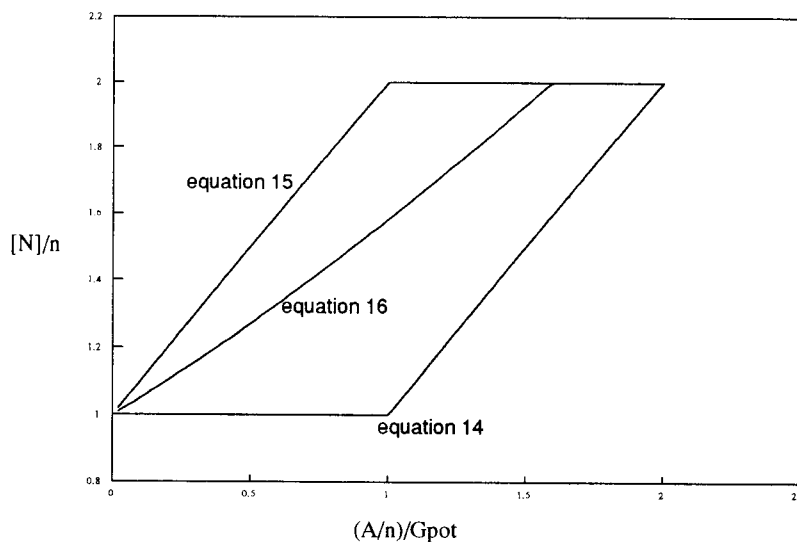


Figure 3.2

The relation between the ratio of actual and minimum nitrogen content ($[N]/n$), against relative nutrient availability, according to equations 14, 15 and 16. Relative nutrient availability is expressed as the ratio of the upper limit on growth as determined by nutrient availability alone (A/n) and the potential growth rate as determined by light availability alone (G_{pot}).

4 GROWTH AND MORTALITY

As discussed in the previous chapter, the outcome of the competition between the various species is determined by the balance between growth and loss rates for these species. These two processes, and the way they are simulated by the model, will therefore be described in this chapter in greater detail.

4.1 Growth processes

Growth is defined as the yearly increase in biomass of the species, and can be divided in increase in carbon and increase in nitrogen. Both the carbon supply (potential productivity) and the nitrogen supply determine actual growth, as shown in the previous chapter. The result of these calculations is the total (carbon and nitrogen) growth of the plant.

Growth, however, is different in the various plant parts, which have different minimum and maximum nitrogen concentrations. The way in which the available carbon and nitrogen are distributed over the various plant parts is described below.

In the model, the available carbon for growth is distributed over the various plant parts according to a fixed distribution key. This means that each plant part always receives a constant fraction of the total available carbon for the plant.

This does not mean that the ratio between the different plant parts is also constant in the standing biomass, because mortality rates for the different plant parts may differ.

Nitrogen distribution over the various plant parts can not be described with a fixed distribution key, because not only does the ratio between available carbon and nitrogen vary, but, as a result of that, the nitrogen content of the various plant parts differs as well.

Distribution of the available nitrogen over the plant parts is calculated in a number of steps. First, knowing the actual carbon growth of the total plant, the minimum amount of nitrogen necessary to make that growth possible is calculated by multiplying the growth of each plant part with its minimum nitrogen content:

$$Nmin_j = \sum_{x=1}^n G_{x,j} NCmin_{x,j} \quad (17)$$

where:

$Nmin_j$ minimum flux of N to species j (kg N.ha⁻¹.yr⁻¹)
 $G_{x,j}$ flux of C to compartment x of species j (kg C.ha⁻¹.yr⁻¹)
 $NCmin_{x,j}$ minimum nitrogen / carbon ratio of that compartment (-)

Likewise the maximum amount of nitrogen that corresponds to this carbon growth is obtained by multiplying carbon growth with the maximum nitrogen content of each plant part:

$$Nmax_j = \sum_{x=1}^n G_{x,j} NCmax_{x,j} \quad (18)$$

where:

$Nmax_j$ maximum flux of N to species j (kg N.ha⁻¹.yr⁻¹)

$NC_{max_{x,j}}$ maximum nitrogen / carbon ratio of the compartment (-)

The actual distribution of available nitrogen over the various plant parts can now be calculated. When the available nitrogen is equal to N_{min_j} , growth in all plant parts occurs at minimum nitrogen content. Likewise, when the available nitrogen equals N_{max_j} , growth occurs at maximum nitrogen content. For intermediate situations a linear interpolation between these two distributions is used. For each plant part the available nitrogen can then be calculated as:

$$N_{x,j} = G_{x,j} \left(NC_{min_{x,j}} + (NC_{max_{x,j}} - NC_{min_{x,j}}) \frac{A_j - N_{min_j}}{(N_{max_j} - N_{min_j})} \right), \quad \text{for } A_j \leq N_{max_j} \quad (19)$$

$$N_{x,j} = G_{x,j} NC_{max_{x,j}}, \quad \text{for } A_j > N_{max_j} \quad (20)$$

where:

A_j total available flux of N for species j ($\text{kg N} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$)

4.2 Mortality, redistribution and litter production

For all plant parts, constant relative mortality rates have been specified. Each year, the total mortality is calculated by multiplying these relative mortality rates with the amount of biomass present.

A constant fraction of the total amount of nitrogen present in dying plant parts, specific for each plant part, is reallocated and can be used for growth again. The total amount of reallocated nitrogen is added to the amount of nitrogen taken up by the plant to obtain the total amount of nitrogen available for growth. The nitrogen that is not reallocated remains in the dying plant parts and becomes part of the litter fraction in the following year.

5 THROUGHFALL AND CANOPY EXCHANGE

Atmospheric input of nitrogen is frequently determined by comparing the composition of throughfall, stemflow and bulk precipitation. Canopy exchange processes may substantially modify the concentrations of throughfall and stemflow, especially for ammonium and nitrate (uptake) and for potassium, magnesium and calcium (release/leaching) (e.g. Heil et al. 1987, 1988; Bobbink et al. 1990a,b). In order to evaluate effects of atmospheric nitrogen deposition it is important to determine canopy exchange.

5.1 Throughfall

Wet and dry deposition of NH_x and NO_x form the nitrogen input for the model. When used in the EXPECT model system, these inputs are derived from the air transport module SRM (Olsthoorn & de Leeuw, 1988). The throughfall fluxes are equal to the summed dry and wet deposition fluxes minus the canopy exchange fluxes. The throughfall fluxes are added to the nitrate and ammonium pools in the organic soil layer and are available for uptake by the plants.

5.2 Process descriptions

In regions where both sulphur dioxide and ammonia emissions occur simultaneously, co-deposition upon (wet) surfaces is to be expected due to their opposite pH-dependent behaviour, which increases the deposition of both chemicals. After deposition ammonium sulphate is formed. This phenomenon has been demonstrated for leaves in windtunnel studies (Adema et al., 1986; Van Hove, 1989) but also for heathland vegetation (e.g. Bobbink et al., 1992). Sulphate and ammonium fluxes in bulk deposition are significantly correlated, in a 1:1 ratio (as equivalents). This was observed for throughfall fluxes in an artificial heather canopy. Measurements with artificial grass canopies also showed a 1:1 ratio for sulphate and ammonium in throughfall (Bobbink et al. 1990b). In a natural Calluna canopy, however, the sulphate throughfall flux was considerably higher than the ammonium flux. This phenomenon was also found in grassland (Seastedt 1985; Heil et al. 1988, 1989) and in some forest studies (Hauhs et al. 1989). The results of these studies indicate canopy uptake of ammonium. Experimental shoot application of ammonium sulphate labeled with ^{15}N clearly demonstrated the foliar uptake of ammonium for Calluna, but also for grasses in other experiments. From these experiments it can be concluded that canopy uptake of ammonium is considerable.

Canopy uptake of nitrate has been demonstrated in grassland vegetations (Bobbink et al., 1990b; Van Dam, 1990). Throughfall fluxes of nitrate in heathland vegetation are sometimes lower and sometimes higher than in bulk deposition. Thus, it is likely that nitrate uptake by heathland vegetation occurs, too, although to a lesser extent than ammonium uptake.

From the results of different studies (Bobbink et al., 1990a,b; Bobbink et al., 1992; Heil and Van Dam, 1986; Heil et al., 1987; Heil et al., 1988; Van der Poel en Zaal, 1990; Thijssen, 1988) the average percentage of ammonium and nitrate deposition that is taken

up by the canopy has been calculated for the following species:

	ammonium	nitrate
<u>Calluna vulgaris</u>	38% ± 5%	28% ± 25%
<u>Molinia caerulea</u>	19% ± 5%	10% ± 80%
<u>Deschampsia flexuosa</u>	16% ± 10%	-

Although no experiments on canopy exchange have been carried out with Erica tetralix it can be assumed that canopy uptake of ammonium will also occur with Erica. Contrary to the grass species Molinia and Deschampsia, Erica is an evergreen species. As a consequence it may be expected that the amount of canopy uptake of ammonium and nitrate will be similar to that of Calluna (which is also an evergreen species and of the same family as Erica), viz. approximately 35% and 25% for ammonium and nitrate, respectively. Canopy uptake of nitrate by Deschampsia is assumed to be zero, but no data for this value were available.

6 SOIL PROCESSES

The soil model describes the carbon and nitrogen cycle in the upper soil layers. The model formulations are largely derived from the formulations of the RESAM model (De Vries et al., 1988). Carbon cycling is taken into account in the mineralization process following the NUCOM2 model descriptions (Berendse, 1988). Since only the nitrogen and carbon cycle are described, the soil model of heathsoil does not produce results with respect to acidification. The main reason is the lack of data on the responses to acidification of heathland soils and vegetation.

In the model two soil layers are distinguished. Interactions between plants and soil take place in the first layer. It consists of a thin, organic layer, and the rest of the rooted zone. The second layer extends to the groundwater level. Mineralization and root uptake of nitrogen take place in the first layer, while nitrification and denitrification take also place in the second layer. Average and maximum groundwater levels are directly linked to the type of vegetation. For an *Erica* vegetation a high groundwater level is used, and for a *Calluna* vegetation a lower groundwater level is used. Groundwater level influences both nitrification and denitrification rates.

The main output variables of the soil model are the nitrogen availability for plants and the nitrate flux from the soil to the groundwater.

6.1 Mineralization

The carbon and nitrogen fluxes from mineralization are calculated separately for each litter compartment. Furthermore, each litter compartment is divided in fresh and old litter. Fresh litter contains the plant parts which result from the mortality process. Part of it mineralizes each year. The remaining part is added to the old litter, which also mineralizes partly each year, but at a lower rate than fresh litter. Year classes for old litter are not distinguished.

Carbon mineralizes as a fixed fraction of the total available amount. The fraction was determined in field and laboratory experiments.

In the mineralization process of nitrogen the litter nitrogen content is taken into account as well as the amount of nitrogen needed for microbial growth. A low nitrogen-carbon ratio decreases N-mineralization until a critical ratio is reached under which N-mineralization does not take place. The nitrogen flux from mineralization is partly ammonified, forming the ammonium flux from mineralization, and partly nitrified, forming the nitrate flux.

6.2 Root uptake

The ammonium and nitrate fluxes from mineralization and throughfall constitute the nitrogen available for uptake by the roots of the vegetation (another fraction is taken up by canopy exchange). The part of the available ammonium and nitrate fluxes taken up by the plants is calculated in the heathland model. This uptake is subtracted from the available ammonium and nitrate fluxes. In the model, uptake of ammonium and nitrate takes place in the same ratio as their availability. The total amount of NH_x and NO_y that is left after root uptake leaches to the second soil layer.

6.3 Nitrification

A part of the ammonium in the soil solution is transformed into nitrate and hydrogen. This process is represented by equation 21. In the first layer nitrification is not calculated. In the second layer the ammonium in the soil solution results from leaching from the first layer and the remainder of the previous year. A high groundwater level is considered as a restraining influence on the process (de Vries et al., 1988). The relation between groundwater level and reduction of nitrification is depicted in figure 6.1.

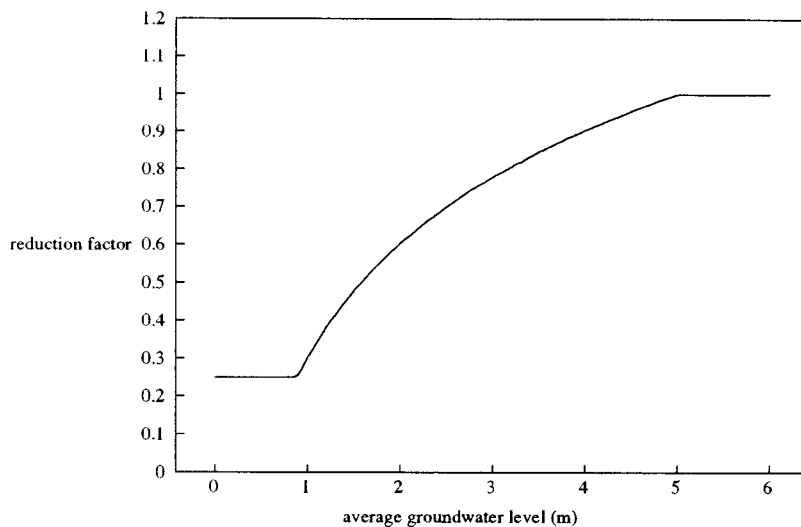
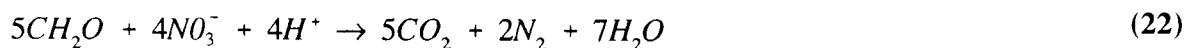


Figure 6.1
Influence of average groundwater level on nitrification rate (De Vries et al., 1988)

6.4 Denitrification

Denitrification is an anaerobic process in which nitrate is transformed into nitrogen and oxygen:



Part of the nitrate in the second soil layer is denitrified. This process is controlled by the groundwater level and pH. Since acidification is not taken into account, pH is omitted as a controlling parameter. A low groundwater level restrains the denitrification process (de Vries et al., 1988). The relation between groundwater level and reduction of denitrification rate is depicted in figure 6.2. The influence of carbohydrates (CH_2O) on denitrification is not taken into account.

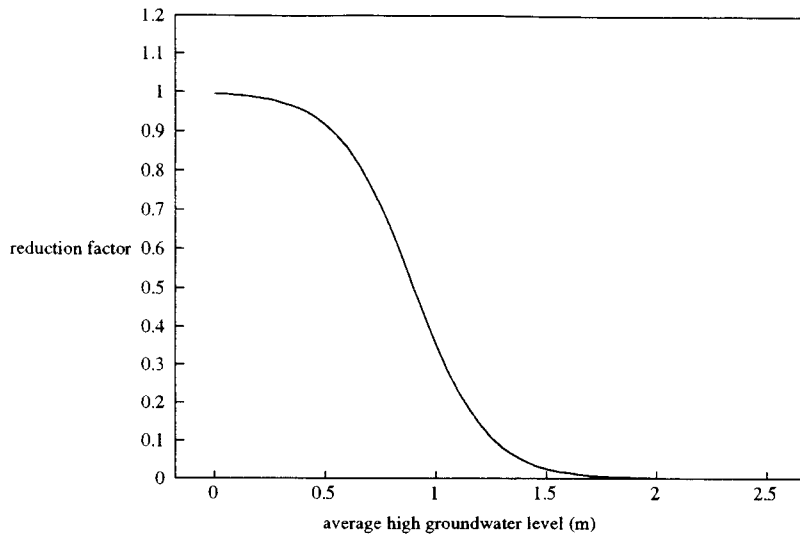


Figure 6.2
Influence of maximum groundwater level on denitrification rate (De Vries et al., 1988)

6.5 Leaching and concentration calculations

The remaining nitrate flux leaches to the groundwater. Pending a more detailed transport description, based on break-through curves, flow through the soil is simply a function of the water flux through the soil. In the model this water flux is controlled by the net precipitation.

To arrive at the yearly averaged nitrate and ammonium concentration and nitrate and ammonium outflow, the following calculation procedure is used.

The total precipitation flux and the total nitrate and ammonium flux are added to the water content and nitrate and ammonium content remaining in the soil layer. This yields the yearly averaged nitrate and ammonium concentration in the soil layer. Nitrate and ammonium outflow are calculated as the total precipitation flux multiplied by this yearly averaged nitrate and ammonium concentration. The remaining nitrate and ammonium content is then calculated by subtracting the nitrate and ammonium outflow from the total amount of nitrate and ammonium calculated earlier.

7 MANAGEMENT PRACTICES

In order to conserve heathlands, different types of management can be considered. For example, reduction of nitrogen availability results in a reduction of growth rates of the various plant species, and as a consequence the circumstances are more favourable for a heather species than for a grass species.

The source of nitrogen enrichment in Dutch heathlands is atmospheric nitrogen deposition. If conservation of heathlands with ericaceous dominance is the management objective, the way to achieve it is the reduction of nutrient availability. This can be realized by periodic removal of the vegetation together with the upper organic soil horizons. Similar results can be achieved by repeated cutting and removal of the vegetation alone, or by grazing.

There are however differences between these management techniques. For example, mowing is commonly non-selective and grazing selective with regard to species and plant parts.

The amount of nutrients removed depends on the management technique. The choice depends strongly on the management goals which one wants to achieve. The ultimate objective is to sustain the dominance of the ericaceous species and to preserve the quality of heathlands.

In table 2 the amount of nitrogen removed from heathland is shown as a result of different management measures.

Table 2. Interval of different management techniques and average amount of nitrogen removed (after Diemont et al., 1982; Van der Zande et al., 1988; Grant, 1987).

type of management	interval (years)	compartments removed
grazing	year round	max. 15 % of production
mowing + litter removal	8-10 (<10)	80-100 % standing crop + 60-80 % litter layer
burning	5-8 (<15)	80-100 % standing crop + 60-100% litter layer
sod-cutting wet heathlands dry heathlands	15-20 (<30) 25-30 (<30 - 50)	100 % of fermentation and litter layer + 50 % of humus layer

In scenario analysis, sod-cutting, i.e. removal of the standing crop and the organic soil layers, is often simulated as a management regime with regular intervals of 20 to 25 years. This frequency is based on the original regime of heather management at the beginning of this century (Diemont et al., 1982). The model Heathsol allows simulation of this management practice at years specified by the user.

As a result of the almost complete removal of the organic layer, the nitrogen content of the soil is extremely low (Diemont et al., 1982; Berendse, 1990). The initial biomass values of Calluna, Erica and of the two grass species are assumed to result from seed bank, seed dispersion, germination and establishment after sod-cutting (De Smidt, 1984;

Bruggink 1987, 1993; Heil, 1984).

In essence, the effect of sod-cutting is modeled by setting the biomass of the plant-compartments and litter compartments back to their initial values.

8 HEATHER BEETLE OUTBREAKS

Calluna can be affected by heather beetles (Lochmaea suturalis). During an outbreak, Calluna plants die almost completely over large areas. Outbreaks of the heather beetle only occur under certain conditions of food availability and micro-climatological conditions (De Smidt 1977; Berdowski 1987). There are no outbreaks in young Calluna stands (< c. 5 years), because percentage cover of the canopy of Calluna must be more than approximately 50 %. When the heather canopy is abundant, the heather beetle affects Calluna randomly (Berdowski & Zeilinga 1987). It was observed that heather beetle outbreaks occurred with intervals of approximately 15 to 20 years when the atmospheric N deposition was relatively low (< 15 kg N ha⁻¹ yr⁻¹). From this, the chance for a heather beetle outbreak to occur was estimated to be 0.06 per year under these circumstances. Furthermore, it has been shown that there is a positive relationship between nutrient availability in the soil and nutrient concentration of the leaves of Calluna, which stimulates outbreaks of the heather beetle (Brunsting & Heil 1985). However, it has also been suggested that very high nitrogen concentrations in Calluna plants make them toxic for the heather beetle, because of high alkaloid concentrations. Data from Brunsting & Heil (1985) indicate that this may happen at a nitrogen availability of c. 115 kg N ha⁻¹ yr⁻¹. Based on these experiments, a linear relationship has been formulated between the probability of the occurrence of heather beetle outbreaks and nutrient availability (upto 100 kg N ha⁻¹ yr⁻¹). This empirical relationship was used in the original CALLUNA model (Heil & Bobbink 1993). A better description of this relationship is by means of an optimum curve, to account for the toxicity at high nitrogen levels.

To account for the effects of both food quantity and food quality on the chance of occurrence of a heather beetle plague, the following equation is used in the model:

$$P = 0.06 F_1 F_2 \quad (23)$$

where

P the chance for a heather beetle outbreak (year⁻¹)

F₁ the influence of food quantity on this chance (-)

F₂ the influence of food quality on this chance (-)

The way in which F₁ and F₂ are calculated is described in the following paragraphs.

8.1 Food availability

It is assumed that the chances for a heather beetle plague to occur are proportional to the amount of biomass of Calluna leaves. Higher availability of food means a higher body weight of the beetles, and as a consequence the number of eggs will increase, which leads to a higher survival rate of the beetle population. We therefore assume a linear relation between the chance for a plague to occur and leaf biomass:

$$F_1 = c B_{leaf} \quad (24)$$

where B_{leaf} is the biomass of Calluna leaves (kg dryweight.ha⁻¹) and c is the coefficient (ha.kg⁻¹). At a background level of 10 kg N ha⁻¹ yr⁻¹ the leaf biomass of a fully grown Calluna vegetation is approximately 5000 kg.ha⁻¹ (dryweight) after 15 to 20 years (cf.

Chapman 1970; Chapman & Webb 1978; Gimingham 1972). Since the chance on a beetle plague under these circumstances was set to 0.06 ($F_1 = 1$), it follows that c equals 1/5000.

8.2 Food quality

The relationship between chance on outbreak and food quality will change due to changes in nitrogen concentration of the Calluna leaves.

When the nitrogen concentration in the leaves increases the nitrogen will be converted into amino acids that are difficult to digest, such as arginine. At first the food quality increases, but at a later stage it decreases, because the digestibility of the food decreases. When we describe this optimum curve by a third order polynome, the influence of food quality can be calculated as follows:

$$F_2 = (c_0 + c_1 N_{leaf} + c_2 N_{leaf}^2 + c_3 N_{leaf}^3) \quad (25)$$

where N_{leaf} is the nitrogen content of the leaves (in % of dryweight) and c_n are coefficients, the values of which are derived below.

From results of fertilization experiments (Brunsting & Heil, 1985) it was shown that heather beetles perform better on food plants with higher nitrogen concentration. The larvae grow faster, which results both in shorter larval periods and higher adult weights. The results suggest that there may be a direct effect of the food quality on mortality too. From these results, it is assumed that the survival of the heather beetles doubles when nitrogen availability to Calluna plants increases from 10 to 55 kg N ha⁻¹ yr⁻¹, and that the survival decreases when nitrogen availability increases to more than 110 kg N ha⁻¹ yr⁻¹. The corresponding average nitrogen concentrations of Calluna leaves are given in table 8.1.

amount of nitrogen applied (in kg N ha ⁻¹ yr ⁻¹)	nitrogen concentration in <u>Calluna</u> leaves (percentage of dry weight)
10 (background)	1.2 ± 0.11
55	1.5 ± 0.15
90	1.7 ± 0.20
110	2.1 ± 0.22

Table 8.1.

Relation between amount of nitrogen applied and nitrogen concentration of Calluna leaves (Brunsting & Heil, 1985; Bobbink et al., 1990).

The amount of food in the utilization experiment (Brunsting & Heil, 1985) was constant. Therefore, when the chance on beetle outbreaks doubles at a deposition level of 55 kg N ha⁻¹ yr⁻¹, it follows that this doubling occurs as a result of the increase of the nitrogen concentration of Calluna leaves from 1.2 % to 1.5 %. When the nitrogen concentration of Calluna leaves becomes higher than 1.7 % this chance will start to decrease again. Therefore, at a nitrogen content of 1.2 % F_2 should be equal to 1 and at 1.5% it should be 2. For nitrogen contents of 1.7 % and 2.1% we assumed values of 2.5 and 1 respectively.

The constants of this third order polynome (figure 8.1) are:
 $c_0 = 23.75$, $c_1 = -54.292$, $c_2 = 41.111$ and $c_3 = -9.722$

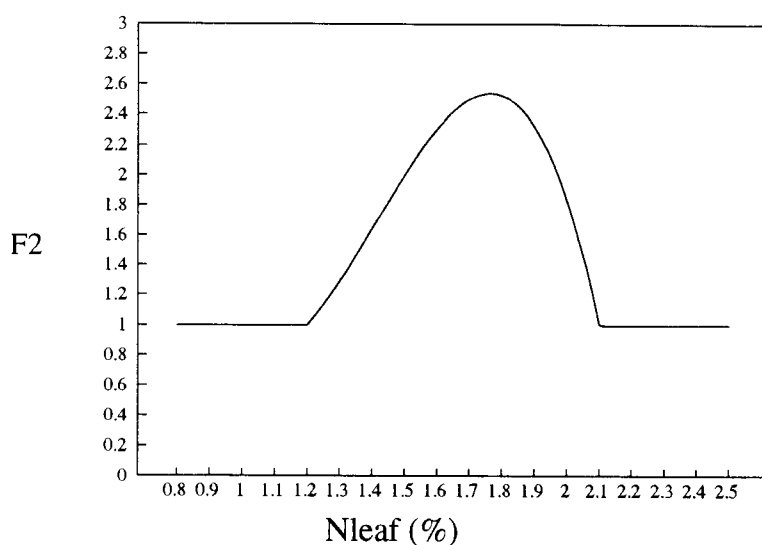


Figure 8.1.

The third order polynome describing the relationship between nitrogen content of Calluna leaves (N_{leaf}) and increase in the chance of occurrence of heather beetle outbreaks.

8.3 Amount of litter

As mentioned before there are no heather beetle outbreaks in young Calluna stands ($c. < 5$ years), because the amount of litter, which functions as a hiding place against drought, must be more than ca. 3500 kg dry weight ha^{-1} . Data for a clear relationship between percentage survival of the heather beetle and amount of litter are lacking. Therefore an on/off relationship is assumed.

The final equation then becomes:

$$P = 0, \quad \text{when litter} < 3500 \text{ kg} \cdot \text{ha}^{-1}, \text{ otherwise:} \quad (26)$$

$$P = 0.06 (2 \cdot 10^{-4} B_{leaf}) (1.2 - 1.6 N_{leaf} + 1.2 N_{leaf}^2 - 0.4 N_{leaf}^3)$$

Where P is the overall chance on heather beetle outbreaks, B_{leaf} is the biomass of Calluna leaves (dryweight) and N_{leaf} is nitrogen concentration of Calluna leaves (percentage N of dryweight).

8.4 Effects of heather beetle outbreaks on the canopy

During an outbreak of the heather beetle Calluna plants are infested and may die-off. The heather beetle is a monophagous feeding insect which eats the green parts of Calluna plants. Infested plants may develop new shoots in autumn, but almost all heavily infested plants die next spring (Berdowski 1987). In the model, all Calluna plants are assumed to die when a heather beetle plague occurs, and the biomass of the Calluna vegetation is

added to the fresh litter.

9 RESULTS

This chapter provides some examples of the model behaviour. Since the model output has not yet been validated, these results should be regarded as preliminary. It is shown however, the model behaves as expected and confirms the possibilities for its use in scenario analysis. The values of the model parameters were obtained from a variety of (partly unpublished) experiments performed by Aerts, Berendse and Heil. A sensitivity analysis of the model is presently being carried out.

The results presented in this chapter were obtained using the nitrogen deposition scenario from 'Environmental Outlook II' (RIVM, 1991). This scenario yields dry and wet NO_x and NH_y depositions from 1950 to 2010, for 20 regions in the Netherlands. Here the average value for the 20 regions is used (figure 10.1).

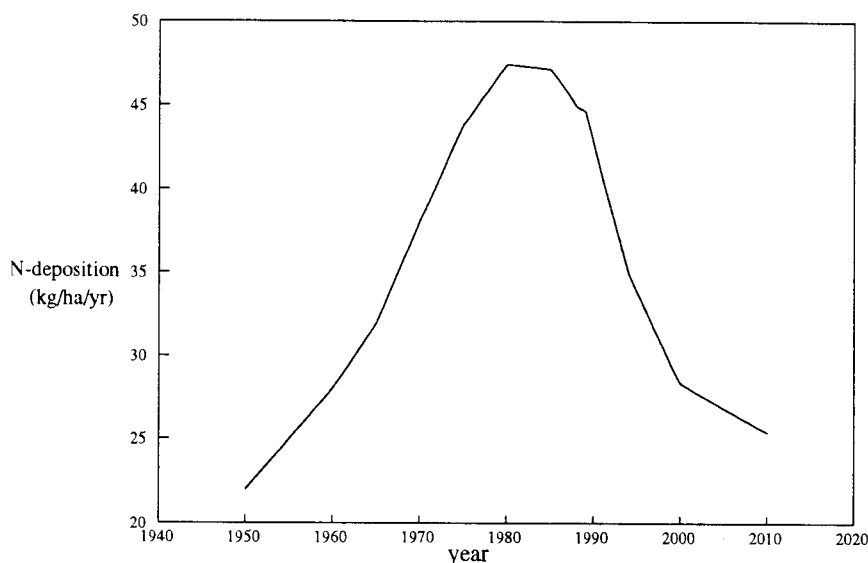
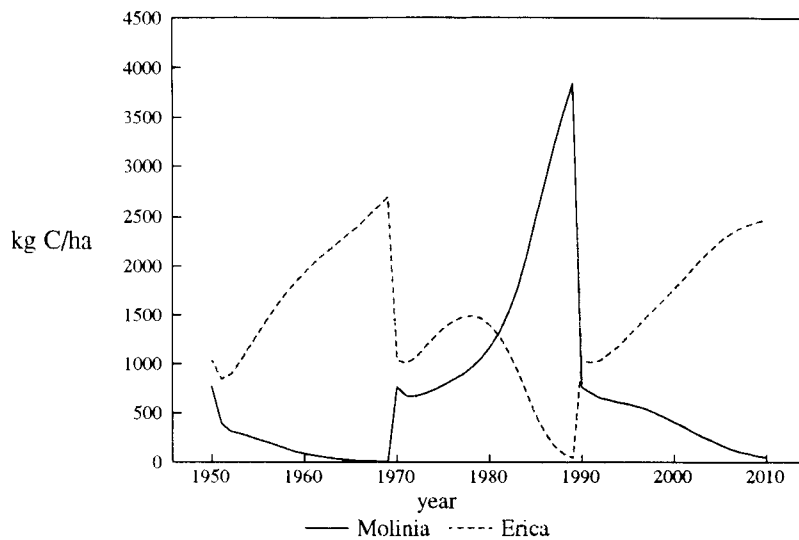


Figure 9.1
Nitrogen deposition scenario, averaged over all heathland areas in The Netherlands (RIVM, 1991).

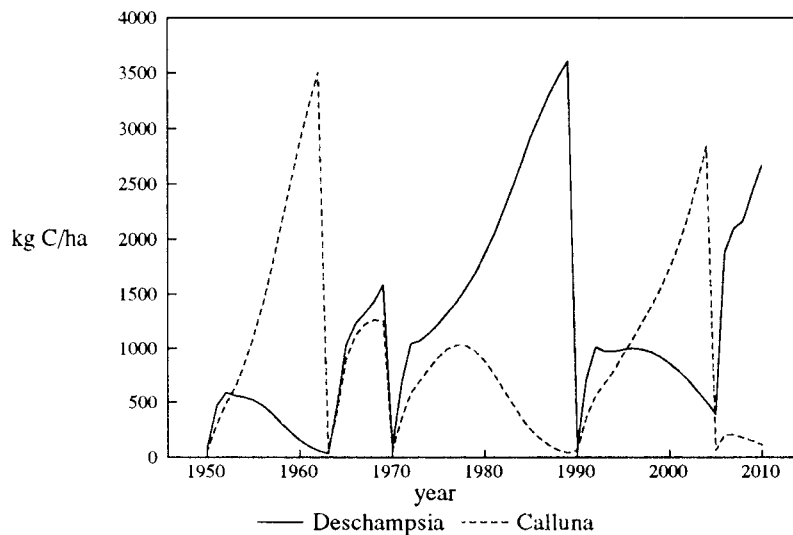
As in the 'Environmental Outlook II' a sod-cutting interval of 20 years is used. To observe the long-term behaviour of the model 60-year simulations without sod-cutting were executed.

9.1 The carbon budget

The development of the total biomass of both heather and grass-species is shown in figure 9.2a and 9.2b for a *Calluna-Deschampsia* and an *Erica-Molinia* vegetation respectively.



a



b

Figure 9.2

Biomass of Erica and Molinia (a) and Calluna and Deschampsia (b), with a sod-cutting interval of 20 years. Nitrogen deposition as in figure 9.1.

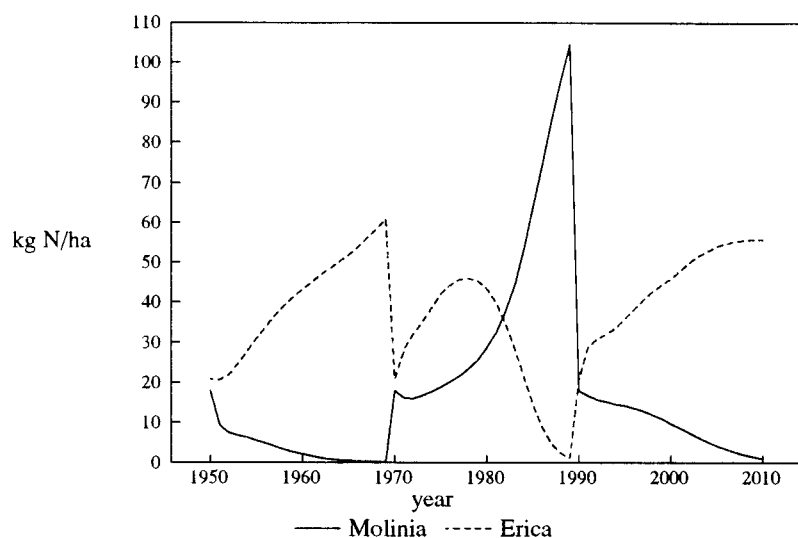
In both cases, the heather species dominates in the periods with relatively low nitrogen deposition (1950 to 1970 and 1990 to 2010), while in the period 1970-1990, the grass species benefits from the increased nitrogen deposition and becomes dominating. However, after several years of dominance, Calluna is struck by a heather beetle plague. When this happens the grass starts to dominate. The occurrence of a heather beetle plague is modeled as a stochastic phenomenon, as described in chapter 8. Therefore the simulation result will be different for each model run.

It can also be seen that after sod-cutting the initial biomass of both Molinia and Erica is rather high. This is caused by the fact that the values used for initialization are in fact values of a vegetation several years old. Unfortunately no other data were available. That the initial values are too high can also be seen from the dip in biomass the first years after

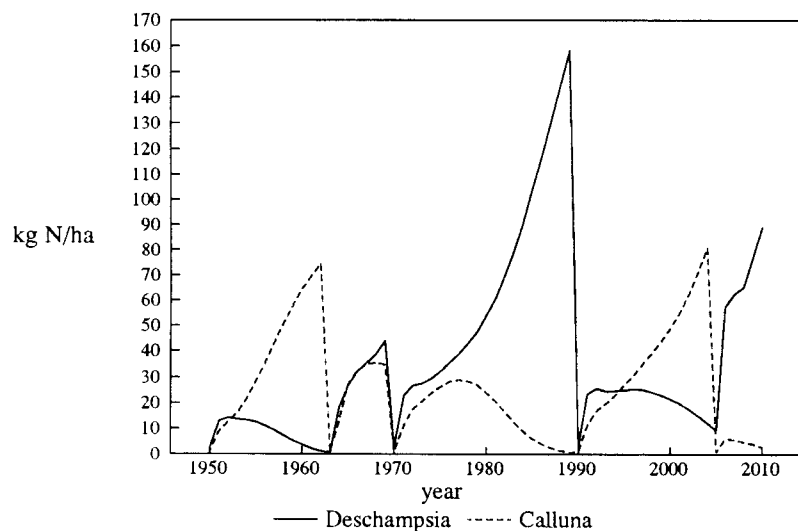
sod-cutting; the nitrogen flux from mineralization and deposition is still too low to maintain this biomass. After a few years however, when litter starts to build up and mineralization increases, growth resumes. Therefore in the longer run this effect disappears. However, better initialization values for *Erica* and *Molinia* would yield more realistic biomass patterns in the first years after sod-cutting.

9.2 The nitrogen budget

The nitrogen content of all species (figure 9.3a and 9.3b) closely follows the biomass pattern.



a



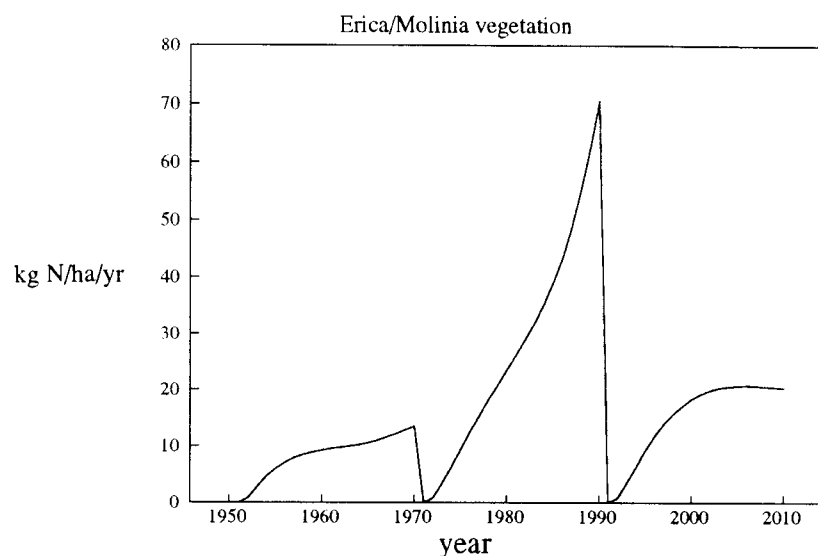
b

Figure 9.3

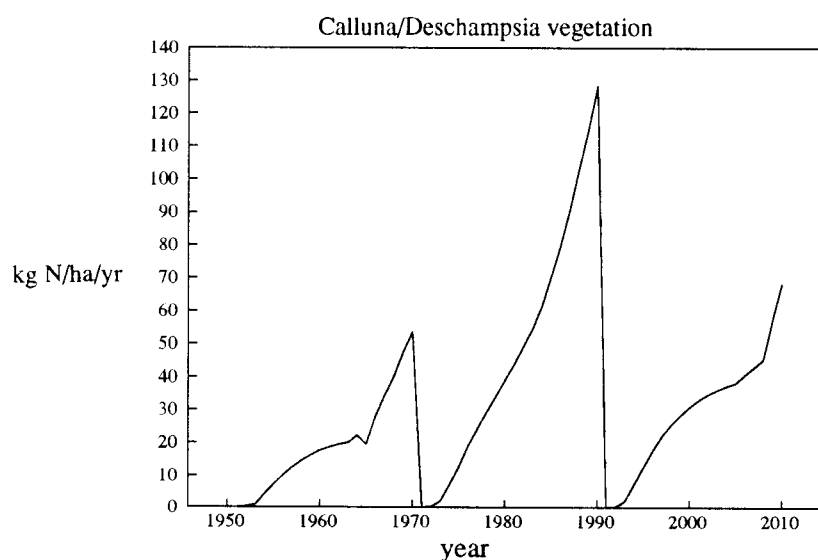
Nitrogen content of *Erica* and *Molinia* (a) and *Calluna* and *Deschampsia* (b), with a sod-cutting interval of 20 years. Nitrogen deposition as in figure 9.1.

Only *Deschampsia* at the end of the 1970-1990 period clearly shows an ongoing increase in nitrogen content, while biomass growth starts leveling off.

Total nitrogen mineralization increases during each growth period, especially during periods with high deposition (figure 9.4a and 9.4b), due to a gradual accumulation of nitrogen in the litter (figure 9.5a and 9.5b).



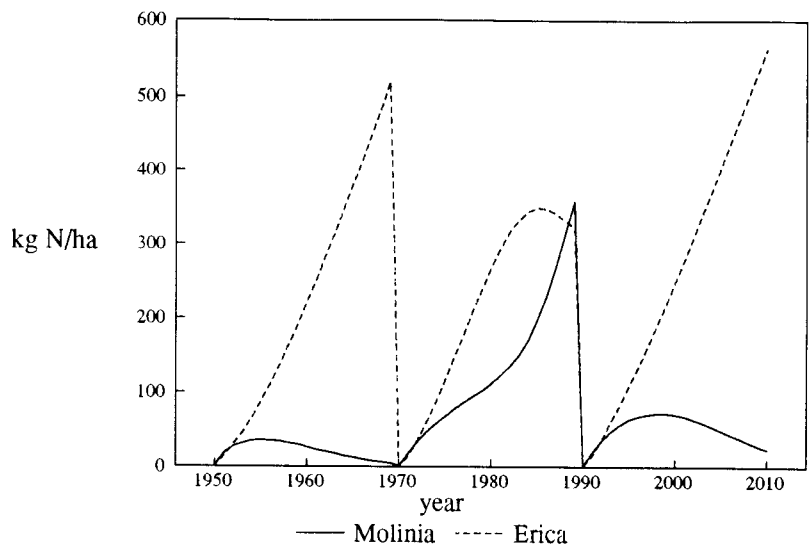
a



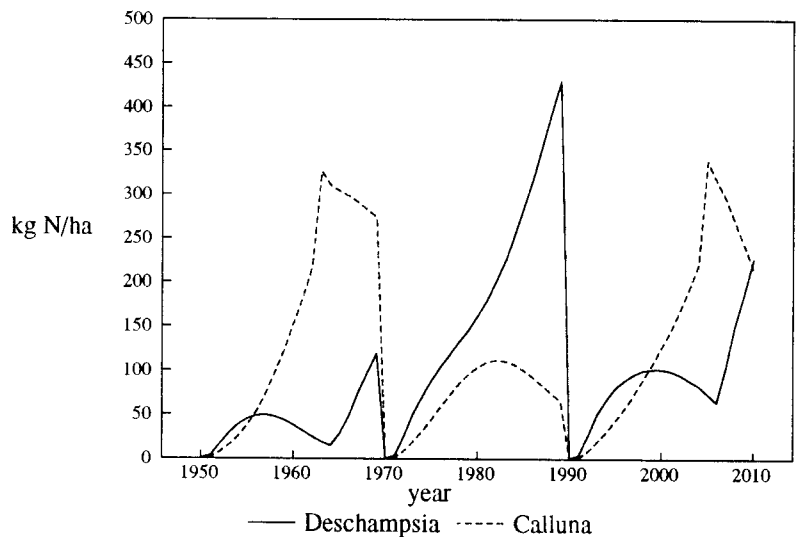
b

Figure 9.4

Total nitrogen mineralization of an Erica/Molinia vegetation (a) and a Calluna/Deschampsia vegetation (b), with a sod-cutting interval of 20 years. Nitrogen deposition as in figure 9.1.



a



b

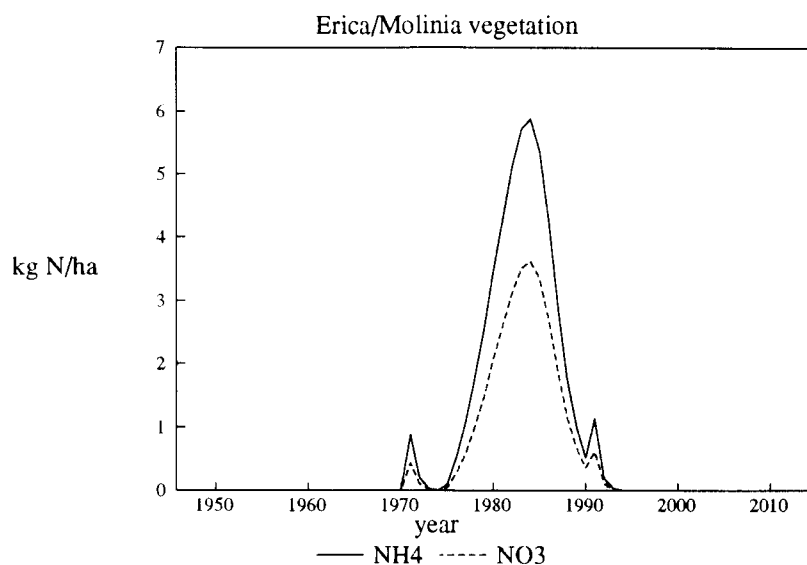
Figure 9.5

Total litter nitrogen content of an Erica/Molinia vegetation (a) and a Calluna/Deschampsia vegetation (b), with a sod-cutting interval of 20 years. Nitrogen deposition as in figure 9.1.

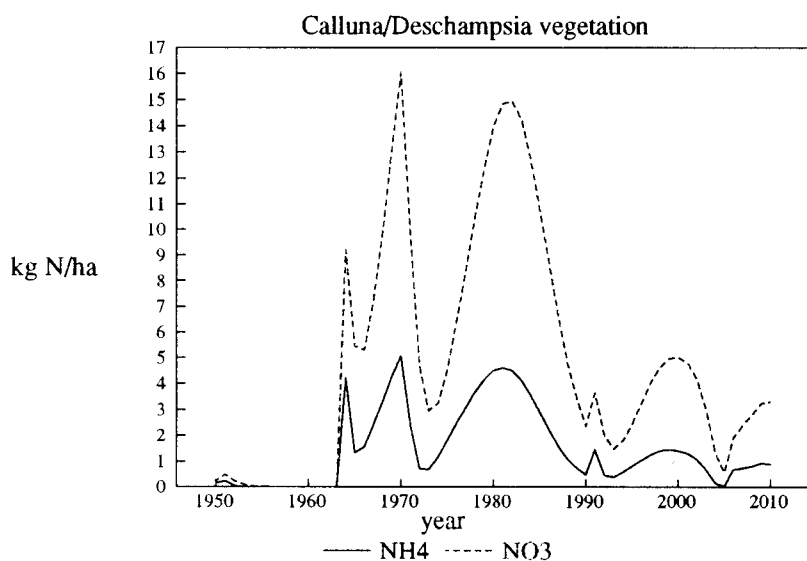
The balance between nitrogen availability and nitrogen uptake is reflected in the leaching of nitrogen from the soil profile (figure 9.6a and 9.6b). The peaks at and immediately after sod-cutting and heather beetle plagues reflect the young and emerging vegetations that are not yet able to use all available nitrogen for their growth. In the case of the occurrence of a heather beetle plague this effect is enhanced by the large amount of newly formed litter from decaying heather plants that starts mineralizing.

At low deposition levels, after a few years all nitrogen available from deposition and mineralization is taken up by the vegetation. At higher deposition levels however, the growth of the vegetation (in this case the grass species) at first can not keep up with the increase in available nitrogen. When deposition decreases and vegetation biomass increases, however, a larger portion of the available nitrogen is taken up by the vegetation,

and leaching decreases again.



a



b

Figure 9.6

Leaching of nitrogen from soil profile under an Erica/Molinia vegetation (a) and a Calluna/Deschampsia vegetation (b), with a sod-cutting interval of 20 years. Nitrogen deposition as in figure 9.1.

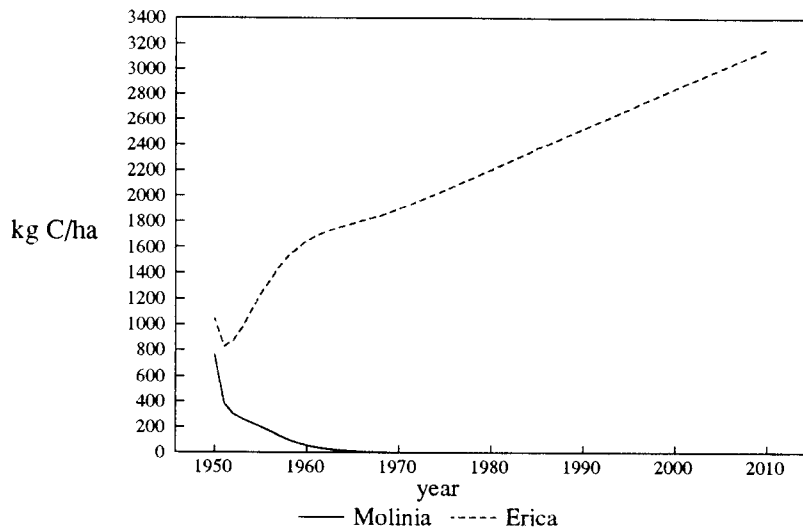
9.3 Long-term behaviour

As mentioned before, a sod-cutting interval of 20 years was used in all of the above simulations. However, by removing all living biomass every 20 years the long-term autonomous behaviour of the model is not shown.

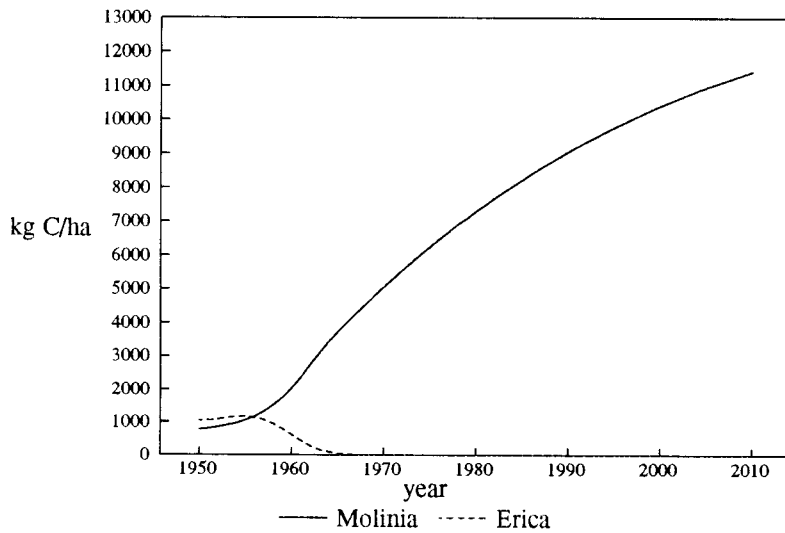
Therefore simulations have also been executed without sod-cutting. Two constant deposition levels were used, in order to eliminate the influence of changing deposition levels.

The low and high deposition levels are the average nitrogen deposition on heathlands in the Netherlands in 1950 and 1985 respectively, as used in the 'Environmental Outlook II' (RIVM, 1991).

Since in a Calluna vegetation, heather beetle outbreaks set back the vegetation to its initial biomass, these results are not shown here. The results for an Erica and Molinia vegetation are shown in figure 9.7a and 9.7b.



a



b

Figure 9.7

Biomass of Erica and Molinia, without sod-cutting, with a constant nitrogen deposition level of 1950 (a) and with a constant nitrogen deposition level of 1985 (b). Deposition levels in 1950 and 1985 as in figure 9.1.

From these figures, it is clear that the deposition levels determine which species becomes dominant. Biomass levels for Molinia under the high deposition level seem to become rather high after a long time. However, deposition levels in reality have only reached so

high values for a much shorter time period.

10 FUTURE DEVELOPMENTS

10.1 Sensitivity and uncertainty analysis

The sensitivity of the model outputs to changes in model inputs is currently being analyzed using the UNCSAM software package (Jansen et al., 1992). Results of this study will be used to determine which parameters should receive special attention during calibration of the model, and to check if unexpected sensitivities exist.

Uncertainty analysis can probably only be carried out to a very limited extent, due to insufficient knowledge of uncertainty in model parameters. From the results of the sensitivity analysis it will become clear for which parameters the model outputs are most sensitive. With this information a limited uncertainty analysis might still be relevant.

10.2 Calibration and validation

A first impression of the model behaviour has been given in the previous chapter. In general, the model 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. Increase in biomass seems slow for all species however.

Further calibration and validation of the model will be carried out in the near future with single- species time series on biomass development. It is impossible to calibrate the situation with competition (two species vegetation) accurately, because of the lack of sufficient data. Therefore, the model will be calibrated and validated by comparing single species simulations with measurements only.

10.3 Regionalization

Initialization of the previous heather models for scenario analysis has thusfar been done by assuming sod-cutting had just occurred in all heather fields in the Netherlands.

Sod-cutting sets the model back to its original values, and makes it possible for heather species to resume dominance, but also allows grass species to become dominant when they were not (the 1970 situation). In reality such situations sod-cutting would never be carried out in such situations.

For a more accurate simulation, initialization of the model should reflect the regional differences in vegetation composition. For this purpose, remote sensing techniques are presently applied to provide actual data on the species composition and coverage for all heathland areas in the Netherlands.

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APPENDIX B. PROCESS FORMULATIONS

In chapters 3 to 8 the process formulations with their theoretical and empirical background have been described in a general way. In this appendix an overview of all formulations is given in a more formalistic way. The processes are dealt with in the same order as they are executed in the program. For the rationale behind these formulations the reader is referred to the main text of the report.

B.1 Throughfall 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 canopy exchange fraction of compound i by species j (-)

B_j biomass of species j ($\text{kgC}\cdot\text{ha}^{-1}$)

Bc_j biomass of species j where the canopy is closed ($\text{kgC}\cdot\text{ha}^{-1}$)

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

where

T_i throughfall of compound i (NH_x or NO_y) ($\text{kgN}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$)

D_i deposition of compound i ($\text{kgN}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$)

B.2 Mineralization

Mineralization is calculated separately for each litter compartment, both for 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 ($\text{kg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$)

B_{xj} : biomass of compartment x of species j ($\text{kg C}\cdot\text{ha}^{-1}$)

R_{xj} : mineralization rate of compartment x of species j (yr^{-1})

The nitrogen flux is calculated as:

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

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 (-)
- $NC_{crit_{xj}}$ critical NC ratio of compartment x of species j (-)
- R_{xj} : Mineralization rate of compartment x of species j (yr⁻¹)
- B_{xj} : biomass of compartment x of species j (kg C.ha⁻¹)
- RF: respiration fraction (-)

B.3 Mortality

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

where

- M_{xj} mortality rate of compartment x of species j (kgC.ha⁻¹.yr⁻¹)
- B_{xj} biomass of the compartment (kgC.ha⁻¹)
- MR_{xj} relative mortality rate of the compartment (yr⁻¹)

The corresponding nitrogen flux is calculated as:

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

where

- MN_{xj} nitrogen flux in dying tissue (kgN.ha⁻¹.yr⁻¹)
- NC_{xj} nitrogen content of the compartment (kgN.(kg C)⁻¹)

B.4 Redistribution

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

where

- R_j total redistribution in species j (kgN.ha⁻¹.yr⁻¹)
- Rf_{xj} fraction redistribution in compartment x of species j (-)

B.5 Competition for nitrogen

$$A_j = E_j + R_j + S_j$$

where

- A_j nitrogen available for growth of species j (kgN.ha⁻¹.yr⁻¹)
- S_j nitrogen available from the soil:

$$S_j = S \frac{L_j B_j}{\sum L_j B_j}$$

where

S total nitrogen available from soil

L_j specific root length for species j ($m \cdot (kgC \cdot ha^{-1})^{-1}$)

B.6 Competition for light

The fraction intercepted light is calculated for each species as:

$$F_j = F_{s_j} + F_{m_j}$$

where

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

F_{s_j} fraction intercepted in single-species vegetation (-)

F_{m_j} fraction intercepted in mixed-species vegetation (-)

$$F_{s_j} = S \frac{LAI_j}{\sum LAI_j} (1 - e^{-\sum k_j LAI_j})$$

where

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

LAI_j leaf area index of species j (-)

k extinction coefficient (-)

The first term ($LAI_j / \sum LAI_j$) gives the fraction of the single-species vegetation that is formed by this species. The second term ($1 - \text{EXP}(\sum -k_j \cdot LAI_j)$) gives the fraction of light intercepted according to Beer's law.

$$F_{m_j} = (1 - S) (U_j + L_j)$$

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

$$LAI_U = \frac{(H_{tall} - H_{short})^d}{H_{tall}^d} LAI_{tall}$$

while $LAI_U = 0$ for the shorter species.

Leaf area index 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:

$$U_j = 1 - e^{-kLAIU_j}$$

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

where

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

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

B.7 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 (kg C.ha⁻¹.year⁻¹)

Gmax_j maximum growth rate of species j in monoculture (kg C.ha⁻¹.year⁻¹)

Actual growth is then calculated 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.year⁻¹)

n_j minimum average nitrogen content of species j (-)

Carbon growth for each plant part is then calculated as:

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

where

f_{xj} fraction carbon distributed to part x (-)

A_j total available flux of N for species j (kg N.ha⁻¹.yr⁻¹)

Nitrogen growth is calculated as:

$$N_{xj} = G_{xj} (NCmin_{xj} + (NCmax_{xj} - NCmin_{xj}) \frac{A_j - Nmin_j}{(Nmax_j - Nmin_j)}), \quad for A_j \leq Nmax_j$$

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

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)

$NC_{max,x,j}$ maximum nitrogen / carbon ratio of the compartment (-)

B.8 Nitrification

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

$$NO_3 = NH_4_{soil} NF$$

$$NF = 0.25, \text{ for } GW < 0.45$$

$$NF = {}^{10}\log(2 GW), \text{ for } 0.45 < GW < 2.5$$

$$NF = 1, \text{ for } GW > 2.5$$

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 fraction (yr ⁻¹)
GW	groundwater level (m)

B.9 Denitrification

The nitrogen flux is calculated as:

$$N = NO_3_{soil} DF$$

with:

$$DF = \frac{1}{1 + e^{6GW_u - 0.9}}$$

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)

B.10 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:

$C_{NO_3,l}$	concentration of nitrate in layer l (kg N.m ⁻³)
$M_{NO_3,l}$	Total mass of nitrate in layer l (kg N.ha ⁻¹)
m_l	Moisture content of layer l (-)

t_l thickness of layer l (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:

$L_{NO_3,l}$ Leaching of Nitrate from layer l (kg N.ha⁻¹)
 10^4 conversion factor from m^2 to hectare