

Landscape forming processes and diversity of forested landscapes - description and application of the model FORSPACE



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Kramer, K., H. Baveco, R.J. Bijlsma, A.P.P.M. Clerkx, J. Dam, J. van Goethem, T.A. Groen, G.W.T.A. Groot Bruinderink, I.T.M. Jorritsma, J. Kalkhoven, A.T. Kuiters, D. Lammertsma, R.A. Prins, M. Sanders, R. Wegman, S.E. van Wieren, S. Wijdeven and R. van der Wijngaart

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## ABSTRACT

K. Kramer, H. Baveco, R.J. Bijlsma, A.P.P.M. Clerkx, J. Dam, J. van Goethem, T.A. Groen, G.W.T.A. Groot Bruinderink, I.T.M. Jorritsma, J. Kalkhoven, A.T. Kuiters, D. Lammertsma, R.A. Prins, M. Sanders, R. Wegman, S.E. van Wieren, S. Wijdeven and R. van der Wijngaart, 2001. *Landscape forming processes and diversity of forested landscapes - description and application of the model FORSPACE*. Wageningen, Alterra, Green World Research. Alterra-rapport 216. 170 pp. 36 figs.; 4 tables; 21 refs.

In the project "Landschapsvormende processen en biodiversiteit" ("Landscape forming processes and bioersity") the spatial interactions between autonomous development of a vegetation and landscape forming processes were investigated and their implications for (bio)diversity at the landscape level were evaluated. For this purpose the model FORSPACE was developed which is a spatial explicit process model that describes vegetation dynamics and the impacts of landscape forming processes. In this study emphasis was paid to the effects of grazing by large herbivores and fire on the vegetation. Two approaches to analyse diversity at the landscape scale were developed: 1) a spatial analysis evaluating the time-evolution of dominant vegetation types, and 2) a metapopulation approach that describes the population dynamics of indicator species at the landscape scale depending on the availability of habitat.

This report focuses on the methodological aspects of the study and thus acts as a reference for future applied studies. The model structure is described in detail, as well as the approach of spatial analysis and of the metapopulation dynamics of an indicator species. Much emphasis is paid on the validation of the driving processes for trees, herbs and grasses by evaluating controlled simulation experiments. In a case-study on the 200 ha of the Imbos, an area in the centre of the Netherlands, the impacts of grazing by herbivores and its interaction with different fire frequencies were evaluated.

Keywords: disturbance, grazing, fire, ungulates, spatial-explicit modelling, biodiversity, landscape dynamics, metapopulations, spatial analysis, forest dynamics, landscape forming processes

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## Summary

In natural systems landscape forming processes (lfp's) such as fire, grazing by large herbivores, storms, flooding etc. are an inherent feature shaping the landscape. However, in man-made landscapes lfp's cannot operational anymore to their full extend. Fires are suppressed, trees planted after large storms, the density of large herbivores are controlled by hunting, dikes and dams are build to control the water. Moreover, manmade landscapes are usually fragmented, prohibiting the spread of lfp's. The hypothesis is that in the absence of lfp's in natural area's a landscape develops with relatively low diversity compared to a landscape where lfp's do operate to their full extend. An important question for the management of an actual natural area in an agricultural or urban surrounding is: What is the role of relevant lfp's for the (bio)diversity of the landscape? A manager may wish to know with what frequency and extend of controlled lfp's the natural reference situation can mimicked to some degree for his actual situation. Furthermore, he may also wish to know what extend and frequency of lfp's are acceptable given other management goals than biodiversity such as timber production, recreational values and carbon sequestration. If the hypothesis is correct it should be possible to define an optimal level of extend and frequency of lfp's such that the constraints of biodiversity, productivity, recreational values and carbon sequestration are met for a given bounded landscape. Such an optimisation of management constraints cannot be found by means of an experimental design, but can only by means of process-based modelling at the landscape level.

The aim of this study was to analyse the role of lfp's in forested landscapes and to evaluate their role both on the spatial distribution of vegetation types and on the meta-population dynamics of indicator species at the landscape level. For this purpose the spatial explicit process model FORSPACE, an acronym for *Forest dynamics in spatially changing environments*, was developed. FORSPACE is a generic model describing the principle processes that govern growth of plants (herbs, shrubs and trees), and their dispersal, germination, establishment, and mortality. For herbivores, birth and mortality and the dynamics body weight depending on consumption and costs. The parameterisation is currently restricted to the dominant plant species of nutrient poor and dry sandy soils in the Netherlands, including Scots pine, birch, oak and beech, and several herb- and grass species. The lfp's evaluated are the impacts of grazing by large herbivores (bovine, horse, red deer, roedeer and wild boar), and of fire.

In this study much emphasis was paid to describe the principal processes realistically and concisely, making use of parameters that are physically realistic, *i.e.* measurable in the field. Another constraint was that the initial characterisation should be as simple as possible, such that detailed field inventories can be avoided. In another study the use of remote sensing for initialisation of the models was evaluated (Sanders & Kramer, 2000). To test the realism of the model behaviour we performed extensive tests under controlled conditions, *e.g.* monocultures of trees and predefined mixtures. Growth in terms of basal area development, diameter increment, volume increment

etc., which can be compared to statistics provided by growth and yield tables. For the parameter values of herbs and grasses advantage was taken from the database of the Dutch Forest reserves programme (Broekmeyer, 1999).

### *Case study*

A case study was done to evaluate the effects of grazing and fire on the vegetation dynamics using the model FORSPACE. The case study was performed on 200 ha of the Imbos, a natural reserve in the centre of The Netherlands. The scenario's included: 1) autonomous development of the vegetation, thus without grazing and without fire; 2) grazing without fire, by each of the herbivore species mentioned above separately and by all species simultaneously; 3) fire without grazing, with different fire frequencies; and 4) fire with grazing with all herbivores present, also with different fire frequencies. These scenario's were based on a spatial analysis of the succession of adjacent vegetation types, and based on the meta-population dynamics of an indicator species, *i.e.* an ant species.

The results showed that,  
for herbivores:

- there is a strong effect of interaction between herbivore species: if all species are present then realistic values are attained. For single species runs, FORSPACE predicts that much higher densities can be attained than currently found in the field
- the interaction between fire and grazing indicated that 200 ha is too small to contain sustainable populations of bovine and horse, even with the lowest fire frequency
- grazing by a single species appeared not to stop the vegetation development into a closed forest with sparse understory, whilst mixed species grazing slows down this process
- in mixed-species grazing, there were stronger population fluctuations projected compared to the single-species situation. This was especially the case for species with low body weight (roedeer, red deer)
- the 200 ha study area is too small for a sustainable wild boar population

for trees:

- the rate of spread of beech and oak over the landscape is strongly reduced by the presence of herbivores. Apparently, many seedlings and saplings are eaten before they can reach the tree layer. The presence of herbivores does not affect the propagation of birch and pine over the landscape very much. For these species there is in general a steady decline in occupied plots due to competition with either beech or oak occurring in the same plot. Furthermore, there are only small differences between herbivore species in their effect on the propagation of a tree species. The same is true for differences between herbivore species in their effect on the average cover of occupied plots. The absence or presence of herbivores does affect the average cover of plots occupied by beech and oak.
- grazing has a strong impact on the propagation of tree species in the shrublayer. Grazing reduces the number of plots that are occupied by beech and oak, and

increases this for birch and pine. There appears to be no significant effect of grazing on cover of occupied plots in the shrub layer, and also little differentiation between herbivore species.

- the presence of herbivores has little or no impact on propagation of beech and oak in the herblayer, however grazing strongly increases the opportunities of germination and establishment of pine. Again there is little differentiation between herbivore species in their effect on the propagation of tree species over the landscape.
- the effect of fire in the absence of grazing is a strong increase of the rate at which a tree species spreads over the landscape compared to the no-grazing/no-fire. The lower fire frequency used ( $P=0.001$ ) has a stronger effect than the higher fire frequency ( $P=0.01$ ) because in the former case larger areas are burnt. In the scenarios where there is both grazing and fire there is a strong effect on the forest development. This is especially the case for beech and oak, whereas this situation appears to be relatively beneficial for pine compared to the other species.
- in the shrublayer, birch and to a lesser degree pine take advantage of the occurrence of fire. For beech and oak there is a strong interaction between grazing and the occurrence of fire, so that the number of plots with trees in the shrub layer is much reduced in the presence of herbivores.
- in the herblayer, for both beech and oak there appears to be little interaction between grazing and fire, whereas for birch and to a lesser extent for pine the combination of grazing and fire is beneficial for the propagation of these species over the landscape rather than fire only. Comparing the no grazing/no fire scenario with the no grazing/fire scenario there appears to be little difference in the rate of spread of both birch and pine in the herb layer.

Summarising: the spread of both beech and oak forests appears to be reduced by grazing, and this effect is stronger if an occasional forest fire occurs. These effects are due to the effect of herbivores on the shrub layer, rather on the trees of these species in the herb layer. Birch and pine take advantage of the occurrence of fire, but are much less affected by grazing, or grazing is beneficial for their spread because of its negative impact on beech and oak.

for herbs:

- the presence of herbivores increases the propagation of *Calluna*, but reduces this for *Deschampsia*, Grass and *Vaccinium*. The long-term differences between the impacts of different herbivores is negligible except for *Deschampsia*. In that case roedeer has the least impact, whereas horse and bovine appear to reduce its propagation the most. The strong propagation potential of Grass and *Deschampsia* consistently set back by grazing. Furthermore, the presence of herbivores has a strong advantageous effect on the average cover of Grass in the plots it already occupies. Grazing slightly reduces the cover of *Deschampsia*, but has no effect on either *Calluna* nor *Vaccinium*. For the latter two species the development of the forest has a stronger impact on their cover than grazing has.
- the interacting effects of the presence of herbivores and the occurrence of fire on the number of occupied plots by a herbs and grasses is that for *Deschampsia*, Grass and *Vaccinium* the rate of spread over the landscape is the fastest for the

scenario with a low fire frequency and without herbivores. For *Calluna* the presence of herbivores in combination with fire is beneficial for its propagation. Comparing the no-fire-scenarios with the fire-scenarios, the results show that fire is detrimental for the propagation of *Calluna*, *Deschampsia* and *Vaccinium*, but beneficial for Grass. Although *Calluna*'s competitive ability increases in the grazing-no-fire-scenarios relative to the other herb species, the scenario with grazing only is the most beneficial for *Calluna*. The presence of herbivores strongly reduces the potential propagation of Grass and *Deschampsia* by consistently removing seedlings from newly invaded plots.

### *Spatial analysis*

Several standard procedures were introduced useful in many spatio-temporal analyses of raster-based model output, especially so when applied to a set of model scenarios such as grazing and fire regimes. All tables and queries can be used to build more complex queries that will solve specific ecological questions such as:

- what is the turnover of the cover type of isolated plots, *eg* gaps in a forest, patches of birch?
- where are the most (in)stable plots located per cover type?
- what is the turnover of edge habitat?
- how many suitable habitat (expressed as a combination of cover types and/or edge habitat) is available through time within a certain radius of plots with specific characteristics, *eg* edge-habitat plot pairs?

From the perspective of species, spatio-temporal dynamics will affect opportunities for establishment, growth, survival and dispersal. A major challenge to both field ecologists and theoretical biologist is therefore to express ecological requirements of species and constraints on establishment, growth etc. into constraints on spatio-temporal features of (suitable) habitat at the landscape level. The procedures introduced in this chapter will be extended to meet this challenge.

### *Metapopulation dynamics*

The results show that scenarios with herbivores present lead to a combination of a slowly changing habitat landscape with a high fraction of habitat for red forest ants. Starting from a single habitat site, species with local dispersal will thus spread through the whole landscape (though it may take some time for temporary corridors between habitat clusters to appear, due to the low habitat turnover rate). Fire is expected to cause occasional increases in the fraction of habitat, followed by a slow decrease back to equilibrium values. Thus, fire should lead to an on average higher habitat incidence, and faster spread of species through the landscape. Species with less "local" dispersal strategies, for instance with the ability to colonize sites outside the direct neighborhood, may prosper equally well in such landscapes (ignoring possible trade-offs between dispersal-capacity and other life-history parameters).

For scenarios without herbivores the fraction of habitat is generally (very) low. Thus the actual spatial configuration, in terms of clusters of habitat sites, very much determines metapopulation incidence (and persistence). Starting from a single habitat site, a species with local dispersal will spread relatively fast through the landscape

(due to the short habitat life span) but will attain only a low incidence. The habitat landscape may well be below the thresholds for the fraction of habitat or for the habitat life span, or the effective  $R_0$  (the average number of propagules a local population produces during its life span) may be well below 1. In such cases, the metapopulation is unlikely to persist. Species with less “local” dispersal strategies are expected to do much better in these landscapes, as they will colonize isolated habitat sites or isolated clusters of habitat sites. It is clear that the scenario, no herbivores and no fire, offers no perspectives for species that depend on the openness of the forest landscape. However, once fires occur, the perspectives improve, as temporarily the landscape may offer a spanning cluster of habitat, and the possibility of a rapid spread. The actual metapopulation dynamics in such case will probably be very much dependent on the spatial and temporal correlation of fire events.

### *Future development*

Future developments of FORSPACE could include the parameterisation for other plant species, so that the model can also be applied at *eg* dune and river landscapes. Different forms of forest management can be included, and the recreational value of the area can be quantified *eg* by some measure of spatial heterogeneity and species composition. The amount of carbon sequestered by the forest landscape can be evaluated relatively easily. However, the soil module should be improved for an accurate assessment of the amount of carbon in the soil. A further extension of the model could include the vulnerability of a forest to storms depending on the forest structure. Despite these possibilities to extend the model, the current version can be used to support decision making for many relevant situations in the management of natural area's.





# 1 Introduction

In current nature management it is often aimed to create large natural areas with little human interference, possibly after an initial re-structuring of a man-made landscape. Another aim in nature management is to attain the highest diversity feasible for the area. Both aims do not necessarily match because in many cases a long history of human management has increased the diversity of an area by frequent disturbances such as thinning and felling in a forest and other activities outside the forest, thereby creating a small-scale heterogeneous landscape. The natural autonomous development of a large area without human interference may be that a closed forest develops with relatively few species. The highest diversity may occur if different stages of succession are simultaneously present, distributed over the landscape in patches of different size and occurring with different frequencies in time. In absence of human disturbance, such a simultaneous presence of succession stages could be attained by other factors that disturb the autonomous development of the vegetation, including grazing by large herbivores, fire, storms etc.. In the Netherlands little is known on the impacts of these factors on natural development of the vegetation. Forest grazing by large herbivores is a relatively new management practice, and there is much debate on how grazers may have affected the prehistoric landscape (Vera, 1997). The occurrence of forest fires is suppressed whenever possible because of the loss of timber and other property such as farms and houses etc in the forest. The impacts of storms are reduced as much as possible, traditionally by clearing and replanting of a damaged forest, but more recently by creating a forest structure that is less vulnerable to storm damage. If landscape forming processes are allowed to occur, they will have strong interactions. *E.g.* herbivores may affect regeneration after a fire and vice versa has an extensive forest fire a strong impact on the availability of forage for herbivores.

The aim of this study was to gain a better understanding on the spatial interactions between vegetation development and landscape forming processes, and their importance for diversity at the landscape level. Therefore, a process-based model was developed that describes these interactions. The model was named FORSPACE, which is an acronym for: *Forest dynamics in spatially changing environments*. Two methods were developed for the analysis of diversity at the landscape level. One is a spatial analysis on the succession of vegetation types and edges between vegetation types, including frequency distributions of shifts from one to other vegetation types. The other considers a method for metapopulation dynamics of either plant- or animal species that are dependent on the balance between colonising emerging patches with suitable habitat and extinction at patches with deteriorating habitat.

General questions that can be answered using FORSPACE include: how develops diversity, expressed in several measures, of a forest landscape affected by interacting landscape forming processes? What is the effect of initial configurations of the landscape on its later development? Or: what initial measurements can be taken such that a diverse landscape develops? What is the size of a reserve that can contain a sustainable metapopulation of a target species? Which scale and frequency of

landscape forming processes maximise landscape heterogeneity? What is the size of a reserve that can incorporate landscape forming processes? If the actual size of the reserve is too small, what may the management regime be to attain a maximal landscape heterogeneity?

In this report, a full description is presented of the model FORSPACE and the two methods for assessing diversity at the landscape level. In the chapter *Model documentation*, first an outline is given on the general concepts and the processes considered. For a general reader this section should be sufficient to understand the modelling principles. Next, mathematical equations are presented for nearly all calculations that are performed by the model. The structure of the presentation of the equations matches the code of the model so that this chapter is a full documentation for a reader who is interested in the details of the model.

To apply FORSPACE for a realistic landscape, the vegetation of this landscape needs to be initialised. The future development of the vegetation depends very much on the vegetation that is present and therefore needs to be described accurately. However, a detailed survey of the vegetation over thousands of hectares is usually not feasible. Therefore the chapter *Initialisation of a realistic landscape* describes how a landscape can be initialised realistically with as little as information as possible (maps on cover and height per species, and soil).

A spatial explicit process-based model such as FORSPACE can have many outputs as it contains detailed information for each plant species for every layer in every 20x20m plot. All these features have their own time evolution and spatial distribution over the landscape. In the chapter on *Model dynamics* the dynamics of some of the most important model features are described for small areas for standardised conditions.

The next chapter *A case study: the Imbos* presents the results of applications of FORSPACE for a realistic area. The impacts of grazing by herbivores on vegetation dynamics and its interactions with fire were analysed by evaluating a range of scenarios. This analysis allowed to draw general conclusions on the effects of grazing, with and without interaction with occasional forest fires, on the development of vegetation of dry sandy soils in The Netherlands.

FORSPACE is not only an useful tool to gain insight of the dynamics and distribution of species, it can also be used to evaluate the time evolution of statistics relevant at the landscape level. Such statistics include the degree of connectedness between similar patches and the spatial heterogeneity of the landscape. Other questions at the landscape level include: how long is a certain vegetation type present at a given location? Into which vegetation types does it develop? What is the turnover time and frequency distribution of transitions from one to another vegetation type?, etc.. In the chapter *Spatial analysis*, a methodology is presented to analyse the spatial output enabling to answer such questions. This approach was applied to some of the scenarios as presented in the case study on the Imbos.

A landscape may contain habitat for certain rare and vulnerable plant and animal species that the manager of the area wishes to protect. Such patches of habitat may consist of different tree species or vegetation types depending on the requirements of the animal- or plant species of interest to survive and to fulfil its life cycle. These patches of habitat are connected with patches of non-habitat through which the

target species may or may not be able to migrate to colonise unoccupied habitat patches. The vegetation of the occupied areas may, however, change in time and not be suitable anymore for the target species, either by autonomous development of the vegetation or by landscape forming processes. The survival of the target species at the landscape scale thus depends on rate at which new, unoccupied, habitat emerges that can be reached through dispersion from occupied habitat patches, and the rate at which the species goes extinct at occupied habitat patches, either because of random fluctuation due to a small population size or because the quality of the habitat deteriorates for the species. In the chapter on *Metapopulation dynamics*, a methodology will be presented that describes the population dynamics of a target species for dynamically changing landscapes. This approach was applied to some of the scenarios as presented in the case study on the Imbos.

This report serves as a background document for future publications in which FORSPACE plays a role. In this report little emphasis is paid to the large amount of literature available on spatial modelling, plant-herbivore interactions, the role of disturbances and their mutual importance for understanding diversity. Only the most important sources of literature that represent the ideas that are applied in FORSPACE are indicated. It is anticipated that in future publications in the open literature, addressing the general questions posed above, do contain a detailed referencing and confrontation of the results with published knowledge.

The base version of FORSPACE presented here is parameterised such that it can be used to evaluate management scenarios for forest at relatively dry sandy soils in the Netherlands. The role of water limitations for the functioning of the forest is described in Groen, Kramer & Heitköning (2000).

Much attention has been paid to the generality and realism of the description of the processes so that the parameters of the relationships have all physical, *i.e.* measurable, dimensions. Therefore, in its current stage only a few plant species are parameterised and the landscape forming processes described include grazing and fire only. However, the base version allows an expansion of species, the incorporation of other landscape forming processes, and the evaluation of new scenarios.



## 2 Model description

### 2.1 General concepts

FORSPACE is a spatial-explicit model that aims to give a realistic description of the processes that determine forest dynamics at a the scale of a landscape (up to 1000-ths of hectares). Gap-dynamics are an important aspect that determines the growth of individual trees and the succession of plant species in time. The forest dynamics as described in FORSPACE are also based on the dynamics of the vegetation on plots with a size of 20x20 m. However to be able to represent an entire landscape, FORSPACE does not track individual trees or shrubs but rather height cohorts of identical individuals per species. The vertical structure of a forest is represented by having different cohorts per species in the herb-, shrub- and tree layer. A cohort can shift to a higher layer (*e.g.* from shrub layer to tree layer) if it reaches the limit of its own layer and a cohort of individuals of the same species does not occur in a the higher layer. Thus, the cohort-structure has the consequence that height-growth may stagnate due to the presence of individuals of the same species in the higher layer. This is only realistic if the spatial resolution is limited to gaps that can contain maximally one or a few large adult trees. In such situations the tree layer may indeed physically block the height growth of the shrub layer. For a larger resolution, say 1 hectare, this assumption is not valid. For herbs and grasses, however, the concept of individuals cannot be maintained. Hence for these plant species the number of metre square that are occupied in the herb layer are simulated.

Grazing by herbivores is an important aspect of forest dynamics because they have a strong impact on the natural regeneration of seedlings from trees and shrubs. Moreover, some herbivore species graze heavily on saplings and thereby affect which tree species grow into the canopy, out of reach of large herbivores. On the other hand, the forest provides the food for the large herbivores, not only as foliage of the trees but also of the plants in the understory. The productivity of the herbs and grasses in the understory is driven by the amount of light available on the forest floor. Thus, there are strong interactions between the dynamics in the density of populations of herbivores and the dynamics in the density of herbs, grasses, shrubs and trees, and the succession of plant species within a plot. Therefore much attention has been paid to develop a mechanistic description of these interactions.

As abiotic factor disturbing the autonomous development of the vegetation, a simple fire model was developed (Dam 1997, Van Goethem, 2000) based on fire models presented in the literature. Although fire is currently not an important factor in forests in the Netherlands, the forests may become more vulnerable for fire in the future due to global warming. Furthermore, small-scale prescribed burning may be used to create spatial heterogeneity and to avoid large wild fires.

The following sections present a general outline of the model characteristics whereas details are presented in the chapters on *Initialisation*, *Dynamics*, *Integration* and *Derived variables*. The *Fire* submodel is described in a separate chapter.

FORSPACE operates with a monthly time step. The *static features* of the model that do not change in time include properties of the herbivore species, the plant species, the number of patches forming the area of interest. The *dynamic features* of the model include the rates of change of the number and biomass of both juvenile and adult herbivores and the biomass of plants, and hence available metabolic energy for the herbivores. See the Appendix for an overview of the static and dynamic features of the herbivores and plants. Output can be requested for all dynamic features of the model, for spatial variables as maps and but both as time series either as maptotals or mapaverage or as output for a single plot.

The model consists of the description of *continuous processes* that are considered to be the most important for the dynamics of the populations herbivores and plants, and *discrete events* for both herbivores and plants. This results into interactions between plant species through competition for light, between herbivore species through competition for food, and between herbivores and plants through available metabolic energy for the herbivores and the alterations in biomass and structural features of the plants as a consequence of grazing. Abiotic factors such as fire disturb these interactions by the removal of plant biomass and by making space available for new individuals.

The continuous processes of the herbivores include: *diet choice, digestion, respiration (including costs for transport), pregnancy, lactation and change of weight*. The discrete events for the herbivores consider *birth and mortality*. It is assumed that the diet choice of the herbivores is based on the digestibility of the plants. Plots containing plants that are higher digestible have a better quality than plots containing plants with a lower digestibility. The amount of digestible plant material is not taken into consideration for the selection of a plot to avoid that plots with a large amount of food with a low digestibility are selected instead of plots containing a small amount of highly digestible food (cf. Van Wieren, 1996).

The continuous processes of the plants include: *production and dispersion of seeds, interception of light, change of biomass* of foliage, stalks or stems, branches and roots, *change in crown radius, and height growth*. The change in biomass and structural features are linked. The discrete events for the plant consider the conditions required for *germination of seeds*, as well as *mortality*. The rate of change in biomass of the plants directly depends on the amount of light absorbed. The light absorbed is converted into plant biomass, allowing an increase in plant height and crown radius. The processes are described for individual plants, which can be extrapolated to plot features by following the number of individual plants per plot. For herbs and grasses the concept of individuals is not relevant, so for these species their coverage, in m<sup>2</sup> per plot, is considered. Increase of cover of herb- and grass-species is the consequence of either lateral expansion, based on growth and an optimal foliage density to increase in radius, or of germination and establishment of seedlings, if the conditions are favorable and seeds are available.

## 2.2 Herbivores

The population of a herbivore species is structured into two cohorts: juveniles (0-1 year-old) and adults (> 1 year-old). All animals within a cohort are identical, *i.e.* have

the same biomass and the same parameter values. For the adult cohort, however, the number of animals for every age is tracked. By convention is the total amount of food available for the animals expressed in metabolic energy (MJ), providing a standard currency by which the vegetation in the plots can be valued for the herbivores in a consistent and comparable manner. This is done because a given amount of plant dry matter may have a different amount of metabolic energy for different herbivore species. The metabolic energy available at a plot is the product of plant biomass and available metabolic energy per kg dry plant biomass for the animal species. This convention is applicable to the available *metabolic energy*, *i.e.* all digestible plant biomass (depending on the plant species) at the plot for the herbivore species, and *consumed metabolic energy*, the amount of food that the herbivore population actually eats. Its *requirement* is then the energy that is required to cover the costs for growth, respiration (including the costs for transport), lactation and pregnancy. *Maximum food intake*, the maximum amount of food that the herbivore population can eat on a daily base is, however, expressed in kg dry matter.

*Grazing* refers to the effect of the herbivore on the vegetation from the point of view of individual plants, and is the amount of plant biomass removed from the plant by herbivores, expressed in kg dry matter. Thus, this definition of grazing includes *browsing* *i.e.* the removal of foliage and small branches of trees and shrubs by herbivores. The amount of plant biomass grazed by a herbivore is constrained by the total digestible plant biomass present at the plot and the maximum intake of plant dry matter by the herbivore.

Whether a plot is selected by a herbivore species to graze on depends on the *quality of the plot*. This depends on digestibility of the plants for the herbivore species only, not on the amount of digestible plant material. The quality of a plot reflects the suitability of a plot for a particular herbivore species relative to the suitability of the other plots in the area to which the species has access. The quality of a plot is expressed on a scale from zero to unity by dividing the cumulative digestibility of the plants at the plot by the maximal cumulative digestibility found in the area. It is assumed that herbivores have perfect knowledge of the area wherein they live and hence are able to graze upon different plots in order of decreasing quality. Furthermore, it is assumed that the herbivores can travel through the entire plot on a monthly base. Thus, they can indeed reach all plots within the timestep used by the model. For the selection of plots to consume food the plots with the highest quality are selected first and all available metabolic energy is eaten before the animals move to plots with lower quality. This pattern continues until the maximum uptake is achieved.

### 2.3 Plants

Plants convert carbon dioxide and water into plant biomass by intercepting energy in the form of light from the sun. *Photosynthesis* is described in FORSPACE by radiation use efficiency, and depends on temperature based on a lower and upper temperature threshold. The amount of intercepted light depends on the leafiness of the canopy, which is described as the surface of the foliage per unit ground surface (*leaf area index*, LAI). The surface of the foliage is calculated from its biomass and surface area per unit biomass (*specific leaf area*, SLA). The extinction of light from the top of the

canopy downward takes an exponential course as a function of the LAI and an extinction coefficient. Thus, the amount of light intercepted for each layer of foliage can be calculated, and via photosynthesis the amount of assimilates produced at the prevailing temperature. In the model three height levels are taken into account: the herb, shrub and tree layer. Each layer can consist of several plant species. As mentioned, a cohort of identical individuals describes a species in a given layer. The total amount of assimilates produced in each layer is distributed proportional to the relative amount of foliage per species and per layer. After subtraction of assimilates required to replenish the reserves from the total amount of assimilates, the remaining assimilates are converted into plant matter. Preference is given to *allocation* to foliage to attain the optimal foliage density and to enable height growth. *Allocation* to roots, branches, stalks and sapwood are extracted from the remaining assimilates, according to fractions that change with the size of the individual. The *allocation* to heartwood is a fraction of the current amount of sapwood.

Foliage and stalks are available for grazing or can be decomposed. The turnover of root and branches depends on a fixed turnover coefficient. All biomass lost due to turnover, is converted into dead organic matter. It fills up the layers the litter-, fermentation- and humus layer, dependent upon the nature of the biomass decomposed.

Plant *dynamic features* are divided in biomass and structural features. The structural features of a plant consider its height, crown length, crown radius, and diameter at breast height (dbh). Also the age is tracked. A species-specific function is used for height growth that describes the increase in height depending on current height and the *soil-type* of the plot. Besides these individual characteristics, also the number of plants per plot is followed.

*Coverage* is the fraction of the ground surface covered by an individual. This affects the opportunities a species has to germinate and establish in the plot, and the fraction of the plot that intercepts light for each layer (*i.e.* canopy closure). The rate of increase of crown radius, and thus coverage, depends on its maximum rate of increase in surface, which depends on the *soil-type* and the *competition* the species experiences from the presence of other species. Plants compete for light depending on their height and amount of foliage in a given layer. A water module can be included optionally (see Groen, Kramer and Heitköning, 2000). In that case the plants also compete for water, which depends on the rooting dept and amount of fine roots in each of the three soil layers.

Beside continuous processes that determine the dynamics of plant individuals, discrete events occur. These events are represented by a stochastic approach, *i.e.* by assuming a probability distribution from which the probability that the event occurs is 'drawn'. If this probability exceeds a threshold then the event occurs, and state variables are adjusted according to conditional decision rules. The discrete events considered for the plants include dispersion and germination of seeds, and mortality.

*Dispersion* of seeds is the spread of seeds over the landscape. It is determined by de number of seeds produced by the plant species and the distance over which the seeds are dispersed. Both aspects are species-specific and stochastig. The number of seeds produced is drawn from an empirical distribution but also depends on the size of the individual plant. For the dispersal of seeds over the landscape, an exponential decline in number of seeds with distance is assumed without a directional preference. The



seeds are dispersed in clumps to save computing time. The clump size is dependent on the number of seeds produced such that each individual plant disperses maximally 100 clumps.

*Germination* in a plot depends on the availability of the species requirements. This is based on quantitative rules that take the following factors into account: **soil-type**, height of the litter-layers, available light at the soil-surface, total vegetation coverage and month of the year. If the plot's environment is favourable for the species then the species will be established in the herb layer with fixed initial characteristics concerning biomass of the different plant components, and plants *structural features*.

*Mortality* is the death of individuals present in the plot; competition; age-related mortality and a too low growth of trees can cause this; fire; and for species in the herb layer also by trampling. Mortality due to competition between seedlings and saplings in the herb and shrub layer is determined based on the self-thinning rule, or  $-3/2$  power 'law'. The theory is based on the assumption that at high density the average individual total biomass in a plot determines the maximum number of individuals. If the average weight increases, the maximum number of individuals decreases. Whenever the total current number of plants in a layer exceeds the maximum number, the surplus of plants dies. For age-related mortality of trees and shrubs, the mortality increases as the individual approaches its maximum age. This occurs during a species specific mortality period, *eg* the last 75 years before the maximum age is attained. During the mortality period the mortality rate of that species increases linearly. Mortality can also be caused by large-scale disturbances such as fire. A species is killed by fire depending on the species (bark thickness) and flame height.

*Grazing* is the removal of plant biomass by the animal, in plant dry matter equivalents. Thus affecting structural features of the plant such as its height, crown base and crown diameter. Due to the removal of foliage the ability to intercept light is reduced and thereby photosynthesis. Furthermore, the coverage of the individual can be reduced due to trampling. In case of grasses and herbs, a minimum length of the vegetation is taken into account to be accessible, depending on the herbivore species. Thus, the biomass below this threshold is not accessible for grazing.

FORSPACE was developed using the package PCRaster (Karssenbergh 1996), a Geographic Information System for personal computers that works on raster base and allows the easy development of dynamic spatial models and linking with ARC-INFO. PCRaster includes a simple programming language with many features for cartographic calculus and spatial statistics.



## 3 Initialisation

### 3.1 General features

#### 3.1.1 SoilTypes

Some of the coefficients ( $MxRSrfTr$ ,  $MxRSrfSrb$ ,  $MxRSrfHrb$ ) are dependent upon the soil-type. Currently, 8 soil-types are distinguished, but this can be extended depending on the area.  $SoilTypes$  is initialised by a soiltype map that specifies for each plot the soiltype it belongs to.

#### 3.1.2 MapArea

$MapArea$  specifies the size of the area of interest.

#### 3.1.3 Begin of the growing season

$BgnSsn$  is the month in which the growing season starts. It can optionally be made dependent on wet (later flushing) or dry areas. By default, it is initialised for dry areas.

### 3.2 Herbivores

#### 3.2.1 Number

$NIniPerAge$  [#/population] specifies the initial number of animals in the entire area per species and per age. A population of herbivores is structured into two cohorts: juveniles (0-1 year old) and adults (> 1 year old). All animals within a cohort are identical, *i.e.* they have the same biomass and the same parameter values. For the adult cohort, however, the number of animals for every age is tracked.

#### ***number of reproducing herbivores per species per age***

The number of reproducing herbivores per species per age,  $NRprPerAge$  [#/population], is a fraction of the number of herbivores per species per age.

$$NRprPerAge_{b,a} = NIniPerAge_{b,a} \cdot RprAbl_{b,a} \quad (1)$$

( $NIniPerAge, RprAbl$ )

### ***total number of reproducing herbivores per species***

**NRpr** [#/population] is the sum over the ages of the number of reproducing herbivores per species per age.

$$NRpr_b = \sum_a NRprPerAge_{b,a} \quad (2)$$

(NRprPerAge)

### ***total number of herbivores per age-group***

Herbivores are divided into two age groups or cohorts: juveniles and adults. Herbivores with the age of 1 year belong to juveniles, whilst individuals of all other ages are adults. **NPerGroup** [#/population] is the sum over all ages per species, belonging to a specific group.

$$NPerGroup_{b,g} = \sum_a NPerAge_{b,a} \quad (3)$$

(NPerAge)

## **3.2.2 Weight**

**WghPerGroup** [kg/population] is the weight of all herbivores per species and per age group of the total amount of herbivores of that species in the area. For initialisation, all individual adult herbivores are considered to have the same individual weight. The initial number of juveniles is set to zero.

$$WghPerGroup_{b,Ad} = NPerGroup_{b,Ad} \cdot CAvrWghInd_b \quad (4)$$

$$WghPerGroup_{b,Jv} = 0$$

(NPerGroup, CAvrWghInd)

## **3.2.3 Age of juveniles**

The **Age** [months] of a juvenile herbivore is expressed in months (1-12) and is set to zero at the start of the simulation.

$$Age_{b,Jv} = 0 \quad (5)$$

## **3.3 Plants**

### **3.3.1 Site index**

The site index, **StxTr**, **StxSrb** [m<sup>3</sup>/yr], of a plot is the maximum average increase in stem volume during the life of a tree. Some of the coefficients depend upon the site index of the plot (**CRHghTr**, **MxHghTr**, **MxHghSrb**, **CRueSrb**, **CRueTr**).

### **3.3.2 Radiation use efficiency**

The coefficients **CRueHrb**, **CRueSrb**, **CRueTr** [kg DM/MJ(PAR)] determine the rate of conversion of light into plant biomass, provided the temperature is sufficiently

high. The radiation use efficiency is site specific for shrub and tree species ([StxSrb](#), [StxTr](#)).

### 3.3.3 Height

The coefficients [CRHghTr](#), [CRHghSrb](#) and [CRHghHrb](#) [m/month] specify the rate of height growth per species and site index ([StxTr](#), [StxSrb](#)). It represents the slope of the age dependent height growth curve of a species. The coefficients [C1HghWshTr](#) and [C1HghWshSrb](#) determine the relationship between height and shoot weight for the initialisation of biomass and numbers.

### 3.3.4 Maximum increase in surface

[MxRSrfTr](#), [MxRSrfSrb](#) [m<sup>2</sup>/individual] represent the maximum increase in individual crown area per individual plant. It is depend on [soiltypes](#) only. For herbs, the rate of increase in radius is more readily observed in the field instead to the increase of surface. Hence, [MxRSrfHrb](#), is based on the parameter [CMxRdsHrb](#).

### 3.3.5 Maximal height

[MxHghTr](#), [MxHghSrb](#) and [MxHghHrb](#) [m] indicate the maximum heights of tree-shrub and herb-species per layer. The maximum height depends on the site index. For trees and shrubs in the herb-layer and for trees in the shrub-layer, the maximum heights equal the layer-heights: [HghHl](#) and [HghSl](#).

### 3.3.6 Probability of germination

The probability of germination of seeds from trees, shrubs and herbs [CPGrm](#) ([CPGrmTr](#), [CPGrmSrb](#), [CPGrmHrb](#) [0-1]) depends on the [soiltype](#).

### 3.3.7 Coverage

Vegetation input is supplied in terms of coverage and [height](#) per species. The coverage information [CvrTrPerLayer](#), [CvrSrbPerLayer](#) and [CvrHrbPerLayer](#) [fraction], is imported from maps describing the initial situation. Besides the coverage per species, also the coverage per layer is calculated. It is checked that the coverage per layer in the input files does not exceed unity. If so, each species cover is reduced proportionally to its contribution to the total coverage. The cumulative cover over all plants (trees plus shrubs plus herbs) is subsequently calculated ([CvrTl](#), [CvrSl](#), [CvrHl](#)).

$$\begin{aligned}
CvrTl &= \sum_t CvrTrPerLayer_{TrTl,t} \\
CvrSl &= \sum_t CvrTrPerLayer_{TrSl,t} + \sum_s CvrSrbPerLayer_{SrbSl,s} \\
CvrHl &= \sum_t CvrTrPerLayer_{TrHl,t} + \sum_s CvrSrbPerLayer_{SrbHl,s} + \sum_h CvrHrbPerLayer_{HrbHl,h}
\end{aligned} \tag{6}$$

### 3.3.8 Height

The initial height information is assigned to **HghTrPerLayer**, **HghSrbPerLayer** and **HghHrbPerLayer** by means of input maps per species named **HghIniTr**, **HghIniSrb** and **HghIniHrb**. Plant heights are initialised under the condition that the species is present (coverage exceeds zero).

### 3.3.9 Maximum height

**MxHghTl**, **MxHghSl** and **MxHghHl** [m] indicate the maximum height over all plant species in a given layer per plot.

### 3.3.10 Age

For initialisation, the age of trees and shrubs, **AgeTr**, **AgeSrb** [year] is derived from its height. Age is rounded to integer numbers. The relation between age and height for trees is expressed by the inverted Chapman-Richards function (Janssen *et al*, 1996).

$$\begin{aligned}
AgeTr_{il,t} &= \frac{\ln \left\{ I - \left( \frac{HghTrPerLayer_{il,t}}{MxHghTr_{TrTl,t}} \right)^{\frac{1}{C8HghTr_t}} \right\}}{C7HghTr_t} \\
AgeSrb_{sl,s} &= \frac{\ln \left\{ I - \left( \frac{HghSrbPerLayer_{sl,s}}{MxHghSrb_{SrbSl,s}} \right)^{\frac{1}{C8HghSrb_s}} \right\}}{C7HghSrb_s}
\end{aligned} \tag{7}$$

(**HghTrPerLayer**, **HghSrbPerLayer**, **MxHghTr**, **MxHghSrb**,  
**C7HghTr**, **C8HghTr**, **C7HghSrb**, **C8HghSrb**)

### 3.3.11 Crown length

The initial length of a crown (**LngCnHrb**, **LngCnSrb**, **LngCnTr** [m]) of an individual plant is set at either the maximum crown length of the species

( $CMxLngCnTr, CMxLngCnHrb, CMxLngCnSrb, CMxLngCnHrb$ ), or the height of the individual in that layer ( $HghHrbPerLayer, HghSrbPerLayer, HghTrPerLayer$ ), whatever is the lowest.

### 3.3.12 Crown base

If the initial height of the individual plant exceeds the maximum length of the crown of the species then the height of the crown base ( $BseCnHrb, BseCnSrb, BseCnTr$  [m]) is set at the plant's height minus the maximum crown length. Otherwise, the height of the crown base is set at ground level (zero metres).

### 3.3.13 Minimal crown base

The minimum crown base ( $MnBseCnTr, MnBseCnSrb$  [m]) is the lowest crown base of any individual in either the tree- or shrub layer

### 3.3.14 Procedure to determine initial weights

Allometric relationships are used for the initial partitioning of biomass over the different plant components (foliage, branches, sapwood and heartwood for trees, stalks for herbs, roots and reserves. Here, an outline is presented. The following equations detail this outline.

Firstly, the aboveground biomass (shoot) is related to the plant's height. Secondly, optimal ratios of both foliage and branches to the shoot are determined. Thirdly, these optimal ratios are weighted to calculate the initial fractions of the shoot consisting of stem, foliage and branches. Fourthly, the partitioning of the stem into sapwood and heartwood depends on the minimum height above which heartwood is formed. In that case, the fixed proportion of the stem that consists of heartwood is weighted with the actual length of the plant above the height where heart wood formation starts.

The initial weight of foliage of an individual plant can only be determined if the crown radius is known, which is dependent on the initial number of plants.

### 3.3.15 Weight of the shoot

The initial weight of the above ground biomass, consisting of foliage plus branches plus stem for trees and shrubs ( $WshTr, WshSrb$  [kg DM/individual]) is calculated based on an allometric relationship with the plant's height.

$$\begin{aligned} WshTr_{tl,t} &= C1HghWsh_t \cdot HghTrPerLayer_{tl,t}^{C2HghWsh_t} \\ WshSrb_{sl,s} &= C1HghWsh_s \cdot HghSrbPerLayer_{sl,s}^{C2HghWsh_s} \end{aligned} \quad (8)$$

### 3.3.16 Optimal ratio of foliage to stem

The optimal ratio between foliage and stem (**OptRatioWflWstTr**, **OptRatioWflWstSrb** [fraction]) follows an allometric relationship with the weight of the shoot (Van Hees, pers. comm.).

$$OptRatioWflWstTr_{tl,t} = e^{C1AllTr_i + C2AllTr_i \cdot \ln(WshTr_{tl,t}) + C3AllTr_i \cdot \ln(WshTr_{tl,t})^2 + C4AllTr_i \cdot \ln(WshTr_{tl,t})^3} \quad (9)$$

$$OptRatioWflWstSrb_{sl,s} = e^{C1AllSrb_s + C2AllSrb_s \cdot \ln(WshSrb_{sl,s}) + C3AllSrb_s \cdot \ln(WshSrb_{sl,s})^2 + C4AllSrb_s \cdot \ln(WshSrb_{sl,s})^3}$$

### 3.3.17 Optimal ratio of branches to stem

The optimal ratio between branches and the stem (**OptRatioWbrWstTr**, **OptRatioWbrWstSrb** [fraction]) has an allometric relationship with the weight of the shoot.

$$OptRatioWbrWstTr_{tl,t} = e^{C5AllTr_i + C6AllTr_i \cdot \ln(WshTr_{tl,t}) + C7AllTr_i \cdot \ln(WshTr_{tl,t})^2 + C8AllTr_i \cdot \ln(WshTr_{tl,t})^3} \quad (10)$$

$$OptRatioWbrWstSrb_{sl,s} = e^{C5AllSrb_s + C6AllSrb_s \cdot \ln(WshSrb_{sl,s}) + C7AllSrb_s \cdot \ln(WshSrb_{sl,s})^2 + C8AllSrb_s \cdot \ln(WshSrb_{sl,s})^3}$$

### 3.3.18 Fraction stem

The initial fraction of the shoot that consist of the stem (**FWstWshTr**, **FWstWshSrb** [fraction]) depends on the optimal ratio of both foliage and branches with the shoot.

$$FWstWshTr_{tl,t} = \frac{1}{1 + OptRatioWflWstTr_{tl,t} + OptRatioWbrWstTr_{tl,t}} \quad (11)$$

$$FWstWshSrb_{sl,s} = \frac{1}{1 + OptRatioWflWstSrb_{sl,s} + OptRatioWbrWstSrb_{sl,s}}$$

### 3.3.19 Fraction foliage

The initial fraction of the shoot that consists of foliage for evergreen tree and shrub species (**FWflWshTr**, **FWflWshSrb** [fraction]) depends on the optimal ratio between foliage and the shoot, and the fraction of the shoot consisting of the stem.

$$FWfWshTr_{tl,t} = OptRatioWflWstTr_{tl,t} \cdot FWstWshTr_{tl,t} \quad (12)$$

$$FWfWshSrb_{sl,s} = OptRatioWflWstSrb_{sl,s} \cdot FWstWshSrb_{sl,s}$$

$$WflTr_{tl,t} = FWflWshTr_{tl,t} \cdot WshTr_{tl,t} \quad (13)$$

$$WflSrb_{sl,s} = FWfWshSrb_{sl,s} \cdot WshSrb_{sl,s}$$



### 3.3.20 Fraction branches

The initial fraction of the shoot that consists of branches for trees and shrubs ( $FWbrWshTr$ ,  $FWbrWshSrb$  [fraction]) depends on the optimal ratio between branches and the shoot, and the fraction of the shoot consisting of the stem.

$$\begin{aligned} FWbrWshTr_{il,t} &= OptRatioWbrWstTr_{il,t} \cdot FWstWshTr_{il,t} \\ FWbrWshSrb_{sl,s} &= OptRatioWbrWstSrb_{sl,s} \cdot FWstWshSrb_{il,t} \end{aligned} \quad (14)$$

### 3.3.21 Weight of branches

The initial weight of the branches ( $WbrTr$ ,  $WbrSrb$ ,  $WbrHrb$  [kg DM/individual]) is a fraction of the shoot.

$$\begin{aligned} WbrTr_{il,t} &= FWbrWshTr_{il,t} \cdot WshTr_{il,t} \\ WbrSrb_{sl,s} &= FWbrWshSrb_{sl,s} \cdot WshSrb_{sl,s} \end{aligned} \quad (15)$$

$$WbrHrb_{hl,h} = CFWbrHrb_h \cdot \frac{CMxLaiHrb_{hl,h}}{CSlaHrb_h} \cdot \frac{HghPerLayerHrb_{hl,h}}{MxHghHrb_{hl,h}} \quad (16)$$

(CFWbrHrb, CMxLaiHrb,CSlaHrb)

The current-year branches ( $WnwbrTr$ ,  $WnwbrSrb$  [kg DM/individual]) are an important food source for roe-deer. The initial weight thereof are initially set at 10% of the total individual branch biomass.

### 3.3.22 Weight of stem or stalk

The initial weight of the stem of trees and shrubs ( $WstTr$ ,  $WstSrb$ ,  $WstHrb$  [kg DM/individual]) is a fraction of the shoot. The initial weight of the stalks of herbs depends on the optimal amount of foliage.

$$\begin{aligned} WstTr_{il,t} &= FWstTr_{il,t} \cdot WshTr_{il,t} \\ WstSrb_{sl,s} &= FWstSrb_{sl,s} \cdot WshSrb_{sl,s} \end{aligned} \quad (17)$$

$$WstHrb_{hl,h} = CFWstHrb_h \cdot \frac{CMxLaiHrb_h}{CSlaHrb_h} \cdot \frac{HghPerLayerHrb_{hl,h}}{MxHghHrb_{hl,h}} \quad (18)$$

(CFWstHrb,CMxLaiHrb,CSlaHrb,RdsHrb)

### 3.3.23 Weight of heartwood

The initial weight of heartwood of trees and shrubs ( $WhwTr$ ,  $WhwSrb$ [kg DM/individual]) is a fraction of the stem. However, heartwood formation starts from a species-specific minimum height onwards until a maximum height. The fraction of the stem consisting of heartwood increases linearly between these limits.

$$WhwTr_{it,t} = \frac{HghTrPerLayer_{it,t} - CMnHghWhwTr_t}{CMxHghWhwTr_t - CMnHghWhwTr_t} \cdot CFHwStTr_{it,t} \cdot WstTr_{it,t} \quad (19)$$

$$WhwSrb_{sl,s} = \frac{HghSrbPerLayer_{sl,s} - CMnHghWhwSrb_s}{CMxHghWhwSrb_s - CMnHghWhwSrb_s} \cdot CFHwStSrb_{sl,s} \cdot WstSrb_{sl,s}$$

(CMnHghWhwTr, CMxHghWhwTr, CFHwStTr, WstTr, CMnHghWhwSrb, CMxHghWhwSrb, CFHwStSrb, WstSrb)

### 3.3.24 Weight of sapwood

The initial weight of the sapwood of trees and shrubs ( $WswSrb$ ,  $WswTr$  [kg DM/individual]) is the part of the stem not consisting of heartwood.

$$WswTr_{it,t} = WstTr_{it,t} - WhwTr_{it,t} \quad (20)$$

$$WswSrb_{sl,s} = WstSrb_{sl,s} - WhwSrb_{sl,s}$$

### 3.3.25 Weight of roots

The initial weight of the roots of trees and shrubs ( $WrtTr$ ,  $WrtSrb$ ,  $WrtHrb$  [kg DM/individual]) is a fixed proportion of the stem. The initial weight of the roots of herbs is assumed the same as the initial weight of the stalk.

$$WrtTr_{it,t} = \frac{0.35 \cdot WshTr_{it,t}}{1 - 0.35} \quad (21)$$

$$WrtSrb_{sl,s} = \frac{0.35 \cdot WshSrb_{sl,s}}{1 - 0.35}$$

$$WrtHrb_{sl,s} = 1 \cdot WstHrb_{sl,s} \quad (22)$$

### 3.3.26 Procedure to determine initial number of individuals

In this paragraph an outline is presented on how the initial number of individuals per layer and per plot is determined. The following equations present the exact details how the maximum number, initial dbh, individual stem volume, distance between trees and initial number of trees is calculated in the model.

The initial number of trees and shrubs ( $NTrPerLayer$ ,  $NSrbPerlayer$  [# /plot]) is based on the space between them. It is assumed that the trees and shrubs are regularly spaced, *i.e.* are 'planted' in a triangle manner. The size of the triangle depends on the plants' diameter at breast height, which itself is determined from the stem volume of the individual plant. Furthermore, the initial number should never exceed a maximum number and is set at at maximally 5000 individuals per plot.

### 3.3.27 Stem volume of individual plants

The initial stem volume of individual trees and shrubs ( $VlmIndTr$ ,  $VlmIndSrb$  [m<sup>3</sup>/individual]) is determined by the weight of the stem and the wood density of the species.

$$\begin{aligned} VlmIndTr_{il,t} &= WstTl_{il,t} / CDnsWdTr_t \\ VlmIndSrb_{sl,s} &= WstSrb_{sl,s} / CDnsWdSrb_s \end{aligned} \quad (23)$$

( $CDnsWdTr, CDnsWdSrb$ )

### 3.3.28 Diameter at breast height

Dbh of trees and shrubs ( $DbhTr, DbhSrb$  [cm]) is the diameter of the stem at breast height ( $CHghDbh$ , 1.35m) (Janssen *et al.* 1996), and is based on the initial stem volume of an individual tree or shrub.

$$\begin{aligned} DbhTr_{il,t} &= \left( \frac{1000 \cdot VlmIndTr_{il,t}}{HghTrPerLayer_{il,t}^{C2DbhTr_t} \cdot e^{C3DbhTr_t}} \right)^{1/C1DbhTr_t} \\ DbhSrb_{sl,s} &= \left( \frac{1000 \cdot VlmIndSrb_{sl,s}}{HghSrbPerLayer_{sl,s}^{C2DbhSrb_s} \cdot e^{C3DbhSrb_s}} \right)^{1/C1DbhSrb_s} \end{aligned} \quad (24)$$

( $C1DbhTr, C2DbhTr, C3DbhTr, C1DbhSrb, C2DbhSrb, C3DbhSrb$ )

### 3.3.29 Average distance between individuals

An even-spaced distance between trees and shrubs ( $DstTr$ ,  $DstSrb$  [m]) is assumed depending on their dbh (Janssen *et al.* 1996).

$$\begin{aligned} DstTr_{il,t} &= C9DstTr_t \cdot DbhTr_{il,t} + C10DstTr_t \\ DstSrb_{sl,s} &= C9DstSrb_s \cdot DbhSrb_{sl,s} + C10DstSrb_s \end{aligned} \quad (25)$$

( $C9DstTr, C10DstTr, C9DstSrb, C10DstSrb$ )

### 3.3.30 Number of individuals

The initial number of trees and shrubs ( $NTr$ ,  $NSrb$  [# /plot]) depends on their coverage and the distance between the individuals (Janssen *et al.* 1996). This values is rounded downward to the nearest integer value, and should not exceed the maximum number.

$$NTr_{it,t} = CvrTrPerLayer_{it,t} \cdot \left( \frac{10745.7}{DstTr_{it,t}} \right)^2 \cdot \frac{PlotSize}{10000} \quad (26)$$

$$NSrb_{sl,s} = CvrSrbPerLayer_{sl,s} \cdot \left( \frac{10745.7}{DstSrb_{sl,s}} \right)^2 \cdot \frac{PlotSize}{10000}$$

(CvrTrPerLayer, CvrSrbPerLayer, DstTr, DstSrb)

The 'number' of herbs (NHrb [# / plot]) is the number of square metres a cohort of a herb occupies on a plot.

$$NHrb_{hl,h} = CvrHrbPerLayer_{hl,h} \cdot PlotSize \quad (27)$$

Subsequently, the number of individuals per species group and layer (NTrPerLayer, NSrbPerLayer, NHrbPerLayer) are derived, as well as the total of trees, shrubs and herbs per layer (NTI, NSI, NHI)

$$NTrPerLayer_{it} = \sum_t NTr_{it,t}$$

$$NSrbPerLayer_{sl} = \sum_s NSrb_{sl,s} \quad (28)$$

$$NHrbPerLayer_{hl} = \sum_h NHrb_{hl,t}$$

$$NTI = NTrPerLayer_{TrTI}$$

$$NSI = NTrPerLayer_{TrSI} + NSrbPerLayer_{SrbSI} \quad (29)$$

$$NHI = NTrPerLayer_{TrHI} + NSrbPerLayer_{SrbHI} + NHrbPerLayer_{HrbHI}$$

### 3.3.31 Stem volume

VlmTr and VlmSrb [m<sup>3</sup>/plot] is the initial total stem volume of trees and shrubs per unit area.

$$VlmTr_{it,t} = VlmIndTr_{it,t} \cdot NTr_{it,t}$$

$$VlmSrb_{sl,s} = VlmIndSrb_{sl,s} \cdot NSrb_{sl,s} \quad (30)$$

### 3.3.32 Crown radius

The initial crown radius of an individual plant (RdsTr, RdsSrb, RdsHrb [m]) is calculated assuming a cylindrical crown.

$$\begin{aligned}
RdsTr_{il,t} &= \sqrt{\frac{(CvrTrPerLayer_{il,t} \cdot PlotSize) / NTr_{il,t}}{\pi}} \\
RdsSrb_{sl,s} &= \sqrt{\frac{(CvrSrbPerLayer_{sl,s} \cdot PlotSize) / NSrb_{sl,s}}{\pi}} \\
RdsHrb_{hl,h} &= \sqrt{\frac{(CvrHrbPerLayer_{hl,h} \cdot PlotSize) / NHrb_{hl,h}}{\pi}}
\end{aligned} \tag{31}$$

### 3.3.33 Optimal density of foliage

The optimal density of the foliage of trees, shrubs and herbs (**OptDnsFlTr**, **OptDnsFlSrb**, **OptDnsFlHrb** [m2 foliage/m3 crown]) is a derived parameter based on the maximal leaf area index and the maximal crown length of the species.

$$\begin{aligned}
OptDnsFlTr_{il,t} &= \frac{CMxLaiTr_{il,t}}{CMxLngCnTr_t} \\
OptDnsFlSrb_{sl,s} &= \frac{CMxLaiSrb_{sl,s}}{CMxLngCnSrb_s} \\
OptDnsFlHrb_{hl,h} &= \frac{CMxLaiHrb_{hl,h}}{MxHghHrb_h}
\end{aligned} \tag{32}$$

(CMxLaiTr, CMxLaiSrb, CMxLaiHrb,  
CMxLngCnTr, CMxLngCnSrb, CMxLngCnHrb)

### 3.3.34 Weight of foliage

If the tree, shrub or herb species is wintergreen then the initial weight of foliage (**WflTr**, **WflSrb**, **WflHrb** [kg DM/individual]) is determined from the optimal foliage density of an individual plant of a given height and radius. For deciduous trees the initial foliage weight is set to zero.

$$\begin{aligned}
WflTr_{il,t} &= \frac{OptDnsFlTr_{il,t} \cdot \pi \cdot (RdsTr_{il,t})^2 \cdot LngCnTr_{il,t}}{CSlaTr_t} \\
WflSrb_{sl,s} &= \frac{OptDnsFlSrb_{sl,s} \cdot \pi \cdot (RdsSrb_{sl,s})^2 \cdot LngCnSrb_{sl,s}}{CSlaSrb_s} \\
WflHrb_{hl,h} &= \frac{OptDnsFlSrb_{sl,s} \cdot \pi \cdot (RdsSrb_{sl,s})^2 \cdot LngCnSrb_{sl,s}}{CSlaSrb_s}
\end{aligned} \tag{33}$$

(CSlaHrb)

### 3.3.35 Maximum weight of reserves

The maximum weight of the reserves ( $MxWrsTr$ ,  $MxWrsSrb$ ,  $MxWrsHrb$  [kg DM/individual]) is the amount of dry matter that is required for flushing of new foliage in spring. As herbs may have no crown at the start of the simulation (Januari) the height growth at the start of the growing season is taken to determine the level of the reserves, rather than the actual crown length.

$$MxWrsTr_{tl,t} = \frac{OptDnsFlTr_{tl,t} \cdot \pi \cdot RdsTr_{tl,t}^2 \cdot LngCnTr_{tl,t}}{CSlaTr_t}$$

$$MxWrsSrb_{sl,s} = \frac{OptDnsFlSrb_{sl,s} \cdot \pi \cdot RdsSrb_{sl,s}^2 \cdot LngCnSrb_{sl,s}}{CSlaSrb_s} \quad (34)$$

$$MxWrsHrb_{hl,h} = \frac{OptDnsFlHrb_{hl,h} \cdot \pi \cdot RdsHrb_{hl,h}^2 \cdot CRHgh_{hl,h}}{CSlaHrb_h} \quad (CSlaHrb)$$

### 3.3.36 Weight of reserves

The initial weight of the reserves ( $WrsSrb$ ,  $WrsSrb$ ,  $WrsHrb$  [kg DM/individual]) is set at the maximum weight of the reserves. The reserves are only used to produce new foliage. This can be flushing in spring for deciduous plants, but also a reflush if foliage is removed by grazing or other disturbances. The reserves are tracked as a separate pool, but are considered to be part of both the sapwood and the roots. Hence, if stems or roots are removed then so are the reserves. The fraction of reserves in the roots and sapwood are distributed proportional to the size of the sapwood and roots.

### 3.3.37 Plant weight

The individual total plant weight ( $WghTr$ ,  $WghSrb$ ,  $WghHrb$  [kg DM/individual]) is the sum of the weight of the foliage, branches, stems, roots and reserves.

### 3.3.38 Total weight of all trees, shrubs and herbs per layer

$TotWghTr$ ,  $TotWghSrb$  [kg DM/plot] is the sum of the weights of the individuals of either trees or shrubs in a layer.

$$TotWghTr_{tl} = \sum_t NTr_{tl,t} \cdot WghTr_{tl,t}$$

$$TotWghSrb_{sl} = \sum_s NSrb_{sl,s} \cdot WghSrb_{sl,s} \quad (35)$$

### ***total weight over all plants in a layer***

$WghTl, WghSl, WghHl$  [kg/plot] is the sum of the weight of all individuals in a layer.

$$\begin{aligned}WghTl &= TotWghTr_{TrTl} \\WghSl &= TotWghTr_{TrSl} + TotWghSrb_{SrbSl} \\WghHl &= TotWghTr_{TrSl} + TotWghSrb_{SrbSl}\end{aligned}\tag{36}$$

### **3.3.39 Crown volume**

The volume of the crown of an individual plant ( $VlmCnHrb, VlmCnSrb, VlmCnTr$  [m<sup>3</sup>]) is determined from the length and radius of the crown, assuming a cylindrical crown.

$$\begin{aligned}VlmCnTr_{tl,t} &= LngCnTr_{tl,t} \cdot \pi \cdot RdsTr_{tl,t}^2 \\VlmCnSrb_{sl,s} &= LngCnSrb_{sl,s} \cdot \pi \cdot RdsSrb_{sl,s}^2 \\VlmCnHrb_{hl,h} &= LngCnHrb_{hl,h} \cdot \pi \cdot RdsHrb_{hl,h}^2\end{aligned}\tag{37}$$

### **3.3.40 Maximal crown volume**

The maximal volume of the crown of an individual plant ( $MxVlmCnHrb, MxVlmCnSrb, MxVlmCnTr$  [m<sup>3</sup>]) is a derived parameter determined from the maximal length and maximal radius of the crown, assuming a cylindrical crown.

$$\begin{aligned}MxVlmCnTr_{tl,t} &= CMxLngCnTr_{tl,t} \cdot \pi \cdot CMxRdsTr_{tl,t}^2 \\MxVlmCnSrb_{sl,s} &= CMxLngCnSrb_{sl,s} \cdot \pi \cdot CMxRdsSrb_{sl,s}^2 \\MxVlmCnHrb_{hl,h} &= CMxLngCnHrb_{hl,h} \cdot \pi \cdot CMxRdsHrb_{hl,h}^2\end{aligned}\tag{38}$$

### **3.3.41 Density of foliage**

The initial density of the foliage of trees, shrubs and herbs ( $DnsFlTr, DnsFlSrb, DnsFlHrb$  [m<sup>2</sup> foliage/m<sup>3</sup> crown], is the surface of foliage per unit volume of the crown.

$$\begin{aligned}DnsFlTr_{tl,t} &= \frac{WflTr_{tl,t} \cdot CSlaTr_t}{VlmCnTr_{tl,t}} \\DnsFlSrb_{sl,s} &= \frac{WflSrb_{sl,s} \cdot CSlaSrb_s}{VlmCnSrb_{sl,s}} \\DnsFlHrb_{hl,h} &= \frac{WflHrb_{hl,h} \cdot CSlaHrb_h}{VlmCnHrb_{hl,h}}\end{aligned}\tag{39}$$

( $CSlaTr, CSlaSrb, CSlaHrb$ )

### 3.3.42 Leaf area index

#### **leaf area index per layer**

The initial leaf area index of trees, shrubs and herbs in a given layer (**LaiTrPerLayer**, **LaiSrbPerLayer**, **LaiHrbPerLayer** [m<sup>2</sup> foliage/m<sup>2</sup> ground]) depends on the density of the foliage and the length of the crown.

$$\begin{aligned}
 \text{LaiTrPerLayer}_{il,t} &= \text{DnsFlTr}_{il,t} \cdot \text{LngCnTr}_{il,t} \\
 \text{LaiSrbPerLayer}_{sl,s} &= \text{DnsFlSrb}_{sl,s} \cdot \text{LngCnSrb}_{sl,s} \\
 \text{LaiHrbPerLayer}_{sl,s} &= \text{DnsFlHrb}_{sl,s} \cdot \text{LngCnHrb}_{sl,s}
 \end{aligned} \tag{40}$$

#### **leaf area index over all trees, shrubs and herbs**

**LaiTr**, **LaiSrb**, **LaiHrb** [m<sup>2</sup> foliage/m<sup>2</sup> ground] is the sum of the LAI per layer over either trees, shrubs and herbs.

$$\begin{aligned}
 \text{LaiTr}_{il} &= \frac{\sum_t \left( \text{LaiTrPerLayer}_{il,t} \cdot \text{NTr}_{il,t} \cdot \pi \cdot \left( \text{RdsTr}_{il,t} \right)^2 \right)}{\text{PlotSize}} \\
 \text{LaiSrb}_{sl} &= \frac{\sum_s \left( \text{LaiSrbPerLayer}_{sl,s} \cdot \text{NSrb}_{sl,s} \cdot \pi \cdot \left( \text{RdsSrb}_{sl,s} \right)^2 \right)}{\text{PlotSize}} \\
 \text{LaiHrb}_{hl} &= \frac{\sum_h \left( \text{LaiHrbPerLayer}_{sl,s} \cdot \text{NHrb}_{sl,s} \cdot \pi \cdot \left( \text{RdsHrb}_{sl,s} \right)^2 \right)}{\text{PlotSize}}
 \end{aligned} \tag{41}$$

#### **leaf area index over all individuals in a layer**

**LaiTl**, **LaiSl**, **LaiHl** [m<sup>2</sup> foliage/m<sup>2</sup> ground] is the sum of all individuals in a layer.

$$\begin{aligned}
 \text{LaiTl} &= \text{LaiTr}_{TrTl} \\
 \text{LaiSl} &= \text{LaiTr}_{TrSl} + \text{LaiSrb}_{SrbSl} \\
 \text{LaiHl} &= \text{LaiTr}_{TrSl} + \text{LaiSrb}_{SrbSl} + \text{LaiHrb}_{HrbHl}
 \end{aligned} \tag{42}$$

#### **total leaf area index over all layers**

**TotLai** [m<sup>2</sup> foliage/m<sup>2</sup> ground] is the sum of the Lai over all layers.

$$\text{TotLai} = \text{LaiTl} + \text{LaiSl} + \text{LaiHl} \tag{43}$$

### 3.3.43 Number of seeds

The initial number of seeds of tree species (**NsdTr** [# /plot]) is determined by the number of trees in a plot and the production of seeds per tree. This number is scaled to the size of the tree based on its height. Furthermore, the deterministic amount of seeds as represented by Eqn. (44) is multiplied by a uniformly distributed factor (0-1) for each plot to represent the stochastic nature of the amount of seeds present in a plot. As the simulation starts at Januari, the number of seeds is still very high in the month in which they can germinate



$$NsdTr_t = CMxPrdNsdTr_t \cdot NTr_{TrTL,t} \cdot \frac{HghTr_{TrTL,t}}{MxHghTr_t} \quad (44)$$

(CMxPrdNsdTr)

### 3.3.44 Basal area

The initial basal of trees and shrubs (**BslTr**, **BslSrb** [m<sup>2</sup>/plot]) is the area of the stems of all individuals of a plot. The total basal area (**TotBslTr**, **TotBslSrb** [m<sup>2</sup>/plot]) is the basal area accumulated over all tree and shrub species and layers, whereas **Bsl** is the total basal area over all woody plants present on a plot.

$$BslTr_{it,t} = \pi \cdot \left( \frac{0.5 \cdot DbhTr_{it,t}}{100} \right)^2 \cdot NTr_{it,t} \quad (45)$$

$$BslSrb_{sl,s} = \pi \cdot \left( \frac{0.5 \cdot DbhSrb_{sl,s}}{100} \right)^2 \cdot NSrb_{sl,s}$$

$$TotBslTr = \sum_{it,t} BslTr_{it,t} \quad (46)$$

$$TotBslSrb = \sum_{sl,s} BslSrb_{sl,s}$$

$$Bsl = TotBslTr + TotBslSrb \quad (47)$$

### 3.3.45 Litter

The initial weight of the amount of litter per layer (**Wlt** [kg DOM/plot]) is read from an input map. The height of the litter layers (**HghLt** [m]) is important to determine the possibility of seeds to germinate.

$$HghLt_l = \frac{Wlt_l}{CDnsLt_l \cdot PlotSize} \quad (48)$$

### 3.3.46 Weight of dead wood

The initial weight of dead wood (**Wdw** [kg DM/plot]) is read from an input map.

### 3.3.47 Initialising annual totals

#### *current year new weight*

The initial weight of current-year new weight of trees, shrubs and herbs (**WnwTr**, **WnwSrb**, **WnwHrb** [kg DM/individual]) is set at zero.

***annual net primary production per individual***

The annual net primary production of trees, shrubs and herbs (ANppTr, ANppSrb, ANppHrb [kg DM/individual/year]) is initialised at zero.

***annual net primary production per unit area***

The total annual net primary production of trees, shrubs and herbs per unit area (TotANppTr, TotANppSrb, TotANppHrb [kg DM/plot/year]) is initialised at zero.

***height growth***

The initial rate of height growth (RHghTr, RHghSrb, RHghHrb [m/month]) is initialised at zero.

***annual rate of change of stem volume***

The annual rate of change of stem volume, *i.e.* current annual increment (AGVImTr, AGVImSrb [m<sup>3</sup>/plot/year]) is initialised at zero.

## 4 Dynamics

### 4.1 General features

#### 4.1.1 Month of the year

$Mnt$  [1..12] indicates the month of the year.

#### 4.1.2 Photosynthetic active radiation

Photosynthetic radiation  $Par$  [MJ/m<sup>2</sup> ground/month] drives photosynthesis, and is assumed to follow a fixed cosine pattern over the year.

$$Par = 30 \cdot 0.5 \cdot 10^6 \cdot \left( 10 + 8 \cdot \cos \left( 2 \cdot \pi \cdot \frac{Mnt + 6}{12} \right) \right) \quad (49)$$

#### 4.1.3 Temperature

Temperature ( $Tmp$  [°C]) is assumed to follow a fixed cosine pattern over the year.

$$Tmp = 10 + 15 \cdot \cos \left( 2 \cdot \pi \cdot \frac{Mnt + 6}{12} \right) \quad (50)$$

#### 4.1.4 Snow

The fraction of the month during which the soil is covered with  $snow$  [-], such that the vegetation is not accessible for grazing.

## 4.2 Herbivores

### 4.2.1 Digestibility

The digestibility of trees, shrubs, herbs, seeds and roots for a herbivore ( $DgsTr$ ,  $DgsSrb$ ,  $DgsHrb$ ,  $DgsSd$ ,  $DgsRt$  [MJ/kg DM plant]) represents the metabolic energy of the edible part of a plant for a herbivore. It is a coefficient that depends on the month of the year, and is found in look-up tables. For trees and shrubs the edible parts of the plant consist of the foliage and the current-year branches. It is assumed that during the growing season a fixed proportion of branches is consumed while grazing foliage. Depending on the herbivore, the branches of some deciduous trees and shrubs species are edible during winter.

$$\begin{aligned}
DgsTr_{b,t} &= DgsTrTbl_{b,t}(b,t,Mnt) \\
DgsSrb_{b,s} &= DgsSrbTbl_{b,s}(b,s,Mnt) \\
DgsHrb_{b,h} &= DgsHrbTbl_{b,h}(b,h,Mnt) \\
DgsSd_{b,t} &= DgsSdTbl_{b,t}(b,t,Mnt) \\
DgsRt_{b,h} &= DgsRtTbl_{b,h}(b,h,Mnt)
\end{aligned} \tag{51}$$

#### 4.2.2 Availability

Availability is the amount of food accessible in a plot for a herbivore species, expressed in MJ per plot. This food may consist of foliage, current-year new branches, large trees seeds (acorns and beechnuts) and roots. Food may be covered with snow during winter. Food can also be out of reach either if it is below a minimum grazing height, *eg* very short grazed grass, or above the maximum grazing height of the herbivore.

##### **availability of foliage**

The availability of foliage of trees, shrubs and herbs per layer ([AvlFlTrPerLayer](#), [AvlFlSrbPerLayer](#), [AvlFlHrbPerLayer](#) [MJ/plot] consists of the following:

- (1) for trees and shrubs in the herb layer it is assumed that all foliage is available, *ie* there is no correction for the accessible part of crown
- (2) for trees and shrubs in both the shrub and tree layer the availability depends on the height of the base of the crown and the maximum grazing height of the herbivore
- (3) for herbs a minimum grazing height constraints the availability of foliage
- (4) for juvenile herbivores it is assumed that they only graze on trees, shrubs and herbs that occur in the herb-layer

$$\begin{aligned}
AvlFlTrPerLayer_{b,g,t,t} &= (1 - Snow) \cdot DgsTr_{b,t} \cdot WflTr_{t,t} \cdot NTr_{t,t} \cdot \frac{CMxHghGrz_b - BseCnTr_{t,t}}{LngCnTr_{t,t}} \\
AvlFlSrbPerLayer_{b,g,sl,s} &= (1 - Snow) \cdot DgsSrb_{b,s} \cdot WflSrb_{sl,s} \cdot NSrb_{sl,s} \cdot \frac{CMxHghGrz_b - BseCnSrb_{sl,s}}{LngCnSrb_{sl,s}} \\
AvlFlHrbPerLayer_{b,g,hl,h} &= (1 - Snow) \cdot DgsHrb_{b,h} \cdot WflHrb_{hl,h} \cdot NHrb_{hl,h} \cdot \left( 1 - \frac{CMnGrzHgh_b}{LngCnHrb_{hl,h}} \right)
\end{aligned} \tag{52}$$

(CMxHghGrz, BseCnTr, BseCnSrb, BseCnHrb, LngCnTr, LngCnSrb, LngCnHrb)

##### **availability of branches**

The availability of branches of trees and shrubs ([AvlNwbrTrPerLayer](#), [AvlNwbrSrbPerLayer](#) [MJ/plot] depends on the current-year new growth of branches. It is assumed that during the growing season a fixed proportion of new branches is consumed while grazing foliage. During winter, for some deciduous trees branches are eaten depending on the herbivore species, with a lower digestibility than the summer value.

$$AvlNwbrTrPerLayer_{b,g,tl,t} = (1 - Snow) \cdot DgsTr_{b,t} \cdot WnwbrTr_{tl,t} \cdot NTr_{tl,t} \cdot \frac{CMxHghGrz_b - BseCnTr_{tl,t}}{HghTl - BseCnTr_{tl,t}} \quad (53)$$

$$AvlNwbrSrbPerLayer_{b,g,sl,s} = (1 - Snow) \cdot DgsSrb_{b,s} \cdot WnwbrSrb_{sl,s} \cdot NSrb_{sl,s} \cdot \frac{CMxHghGrz_b - BseCnSrb_{sl,s}}{HghSl - BseCnSrb_{sl,s}}$$

### **availability of foliage plus branches**

To determine the amount of foliage and branches that is grazed (Eqns. (73) and (74), respectively), the fraction of foliage and branches in the available food needs to be known.

$$\begin{aligned} AvlTrPerLayer_{b,g,tl,t} &= AvlFlTrPerLayer_{b,g,tl,t} + AvlNwbrTrPerLayer_{b,g,tl,t} \\ AvlSrbPerLayer_{b,g,sl,s} &= AvlFlSrbPerLayer_{b,g,sl,s} + AvlNwbrSrbPerLayer_{b,g,sl,s} \\ AvlHrbPerLayer_{b,g,hl,h} &= AvlFlHrbPerLayer_{b,g,hl,h} + AvlNwbrHrbPerLayer_{b,g,hl,h} \end{aligned} \quad (54)$$

fraction foliage:

$$\begin{aligned} FAvlFlTrPerLayer_{b,g,tl,t} &= \frac{AvlFlTrPerLayer_{b,g,tl,t}}{AvlTrPerLayer_{b,g,tl,t}} \\ FAvlFlSrbPerLayer_{b,g,sl,s} &= \frac{AvlFlSrbPerLayer_{b,g,sl,s}}{AvlSrbPerLayer_{b,g,sl,s}} \\ FAvlFlHrbPerLayer_{b,g,hl,h} &= \frac{AvlFlHrbPerLayer_{b,g,hl,h}}{AvlHrbPerLayer_{b,g,hl,h}} \end{aligned} \quad (55)$$

fraction branches:

$$\begin{aligned} FAvlBrTrPerLayer_{b,g,tl,t} &= 1 - FAvlFlTrPerLayer_{b,g,tl,t} \\ FAvlBrSrbPerLayer_{b,g,sl,s} &= 1 - FAvlFlSrbPerLayer_{b,g,sl,s} \\ FAvlBrHrbPerLayer_{b,g,hl,h} &= 1 - FAvlFlHrbPerLayer_{b,g,hl,h} \end{aligned} \quad (56)$$

### **availability of seeds**

For seeds as a food source for large herbivores ( $AvlSdPerLayer$  [MJ/plot]) only the seeds from trees are taken into account. Typically, only beechnuts and acorns have a digestibility that exceeds zero. The seeds are only found in the herb layer.

$$AvlSdPerLayer_{b,g,TrHl,t} = (1 - Snow) \cdot DgsSd_{b,t} \cdot CWsdTr_t \cdot NsdTr_t \quad (57)$$

### **availability of roots**

For roots as a food source for large herbivores ( $AvlRtPerLayer$  [MJ/plot]), only roots of herbs are taken into account.

$$AvlRtPerLayer_{b,g,hl,h} = (1 - Snow) \cdot DgsRt_{b,h} \cdot WrtHrb_{hl,h} \cdot NHrb_{hl,h} \quad (58)$$

### **availability of trees, shrubs and herbs per herbivore group**

The availability of trees, shrubs, and herbs is accumulated for the herbivore groups. *i.e.* adults and juveniles ( $AvlTrPerGroup$ ,  $AvlSrbPerGroup$ ,  $AvlHrbPerGroup$  [MJ/plot]).

$$\begin{aligned} AvlTrPerGroup_{b,g} &= \sum_{tl,t} AvlTrPerLayer_{b,g,tl,t} + \sum_{tl,t} AvlSdPerLayer_{b,g,TrHl,t} \\ AvlSrbPerGroup_{b,g} &= \sum_{sl,s} AvlSrbPerLayer_{b,g,sl,s} \\ AvlHrbPerGroup_{b,g} &= \sum_{hl,h} AvlHrbPerLayer_{b,g,hl,h} + \sum_{hl,h} AvlRtPerLayer_{b,g,hl,h} \end{aligned} \quad (59)$$

### **availability per herbivore and age-group**

$Avl$  [MJ/plot] is the availability per herbivore species and group totaled over the trees, shrubs and herbs.

$$Avl_{b,g} = AvlTrPerGroup_{b,g} + AvlSrbPerGroup_{b,g} + AvlHrbPerGroup_{b,g} \quad (60)$$

### **availability per plot**

$TotAvl$  [MJ/plot] is the sum of the availabilities over the herbivores and age-groups.

$$TotAvl = \sum_{b,g} Avl_{b,g} \quad (61)$$

### **availability of the area**

$TotAvlArea$  [MJ/area] is the total availability of the entire area for all herbivores

$$TotAvlArea = \text{maptotal}(TotAvl) \quad (62)$$

## **4.2.3 Preference**

The preference of a herbivore for the trees (including seeds from trees), shrubs and herbs (including roots from herbs) ( $PrfTr$ ,  $PrfSrb$ ,  $PrfHrb$  [MJ/kg]) is based on the digestibility of these food sources in a plot. It is thus not dependent on the *amount* of food with a given digestibility. The reason for this choice is that if both digestibility and amount are taken into account, a plot with a large amount of food with low digestibility can have the same or a higher preference than a plot with high digestibility but a small amount of food. This is not in accordance with observations on food selection by herbivores.

$$\begin{aligned} PrfTr_b &= \sum_{tl,t} (DgsTr_{b,t} + DgsSd_{b,t}) \\ PrfSrb_b &= \sum_{sl,s} DgsSrb_{b,s} \\ PrfHrb_b &= \sum_{hl,h} (DgsHrb_{b,h} + DgsRt_{b,h}) \end{aligned} \quad (63)$$

### ***preference of a herbivore for a plot***

$Prf$  [MJ/kg] is the preference of a plot totalled over the trees, shrubs and herbs occurring in the plot

$$Prf_b = PrfTr_b + PrfSrb_b + PrfHrb_b \quad (64)$$

### ***maximum preference***

$MxPrf$  [MJ/kg] indicates the plot with the highest preference in the entire area for a herbivore species.

## **4.2.4 Quality**

The quality of a plot ( $Qtl$  [0..1]) is the preference of a plot relative to the plot with the highest preference in the area.

$$Qtl_b = \frac{Prf_b}{MxPrf_b} \quad (65)$$

## **4.2.5 Maximum intake**

Maximum intake ( $MxNtk$  [kg plant DM/month]) is the maximum amount of food that an individual animal can consume. For juveniles the maximum intake increases with the **age** of the animal.

$$MxNtk_{b,Ad} = CMxNtkAd_b \cdot NPerGroup_{b,Ad}$$
$$MxNtk_{b,Jv} = \frac{CMxNtkJv_b \cdot NPerGroup_{b,Jv}}{12 - Age_{b,Jv} + 1} \quad (66)$$

## **4.2.6 Consumption**

Consumption is the actual removal of food from trees, seeds of trees, shrubs, herbs and roots of herbs ( $CnsTrPerLayer$ ,  $CnsSdPerLayer$ ,  $CnsSrbPerLayer$ ,  $CnsHrbPerLayer$ ,  $CnsRtPerLayer$  [MJ/plot/month]) from a plot by a herbivore species. The selection of plots by the herbivore is done by a 'top-down search': all high quality plots are selected first. The top-down search is done with a step-size of 0.2 quality class (1.0-0.8; 0.8-0.6, etc.). To avoid over-consumption because several herbivore species may wish to consume the same food item, the availability of the food source is scaled with the total availability of food in the plot for all herbivores. Similarly, to avoid over-intake it is checked if by consumption of food, the maximum intake of the herbivore is not exceeded.

$$\begin{aligned}
CnsTrPerLayer_{b,g,tl,t} &= AvlTrPerLayer_{b,g,tl,t} \cdot \frac{Avl_{b,g}}{TotAvl} \\
CnsSdPerLayer_{b,g,TrHl,t} &= AvlSdPerLayer_{b,g,TrHl,t} \cdot \frac{Avl_{b,g}}{TotAvl} \\
CnsSrbPerLayer_{b,g,sl,s} &= AvlSrbPerLayer_{b,g,sl,s} \cdot \frac{Avl_{b,g}}{TotAvl} \\
CnsHrbPerLayer_{b,g,hl,h} &= AvlHrbPerLayer_{b,g,hl,h} \cdot \frac{Avl_{b,g}}{TotAvl} \\
CnsRtPerLayer_{b,g,hl,h} &= AvlRtPerLayer_{b,g,hl,h} \cdot \frac{Avl_{b,g}}{TotAvl}
\end{aligned} \tag{67}$$

#### **consumption per herbivore and age group**

**CnsTr**, **CnsSd**, **CnsSrb**, **CnsHrb**, **CnsRt** [MJ/plot/month] is the consumption of trees, seeds, shrubs, herbs and roots per herbivore and age group in all layers of the vegetation.

$$\begin{aligned}
CnsTr_{b,g} &= \sum_{tl,t} CnsTrPerLayer_{b,g,tl,t} \\
CnsSd_{b,g} &= \sum_{TrHl,t} CnsSdPerLayer_{b,g,TrHl,t} \\
CnsSrb_{b,g} &= \sum_{sl,s} CnsSrbPerLayer_{b,g,sl,s} \\
CnsHrb_{b,g} &= \sum_{hl,h} CnsHrbPerLayer_{b,g,hl,h} \\
CnsRt_{b,g} &= \sum_{hl,h} CnsRtPerLayer_{b,g,hl,h}
\end{aligned} \tag{68}$$

#### **consumption over all plants**

**Cns** [MJ/plot/month] is the consumption of a herbivore and age group totaled over all food items in the plot.

$$Cns_{b,g} = CnsTr_{b,g} + CnsSd_{b,g} + CnsSrb + CnsHrb_{b,g} + CnsRt_{b,g} \tag{69}$$

#### **4.2.7 Intake**

Intake of trees, seeds from trees, shrubs, herbs and roots from herbs (**NtkTrPerLayer**, **NtkSdPerLayer**, **NtkSrbPerLayer**, **NtkSrbPerLayer**, **NtkHrbPerLayer**, **NtkRtPerLayer** [kg DM/plot/month]) is the amount of plant dry matter that is removed by herbivores.



$$\begin{aligned}
NtkTrPerLayer_{b,g,tl,t} &= \frac{CnsTrPerLayer_{b,g,tl,t}}{DgsTr_{b,t}} \\
NtkSdPerLayer_{b,g,TrHl,t} &= \frac{CnsSdPerLayer_{b,g,TrHl,t}}{DgsSd_{b,t}} \\
NtkSrbPerLayer_{b,g,sl,s} &= \frac{CnsSrbPerLayer_{b,g,sl,s}}{DgsSrb_{b,s}} \\
NtkHrbPerLayer_{b,g,hl,h} &= \frac{CnsHrbPerLayer_{b,g,hl,h}}{DgsHrb_{b,h}} \\
NtkRtPerLayer_{b,g,hl,h} &= \frac{CnsRtPerLayer_{b,g,hl,h}}{DgsRt_{b,h}}
\end{aligned} \tag{70}$$

### **intake of the area**

**NtkTrArea**, **NtkSdArea**, **NtkSrbArea**, **NtkHrbArea**, **NtkRtArea** [kg DM/area/month] is the intake of trees, seeds of trees, shrubs, herbs and roots of herbs per herbivore and age-group accumulated over the entire area.

$$\begin{aligned}
NtkTrArea_{b,g} &= \sum_{tl,t} \text{maptotal} (NtkTrPerLayer_{b,g,tl,t}) \\
NtkSdArea_{b,g} &= \sum_{TrHl,t} \text{maptotal} (NtkSdPerLayer_{b,g,TrHl,t}) \\
NtkSrb_{b,g} &= \sum_{sl,s} \text{maptotal} (NtkSrbPerLayer_{b,g,sl,s}) \\
NtkHrbArea_{b,g} &= \sum_{hl,h} \text{maptotal} (NtkHrbPerLayer_{b,g,hl,h}) \\
NtkRtArea_{b,g} &= \sum_{hl,h} \text{maptotal} (NtkRtPerLayer_{b,g,hl,h})
\end{aligned} \tag{71}$$

### **4.2.8 Grazing**

Grazing of trees, seeds of trees, shrubs, herbs and roots of herbs (**GrzTr**, **GrzSd**, **GrzSrb**, **GrzHrb**, **GrzRt** [kg DM/plot/month]) is the removal of biomass of plants accumulated over the herbivores and age-groups that graze in a plot.

$$\begin{aligned}
GrzTr_{tl,t} &= \sum_{b,g} NtkTrPerLayer_{b,g,tl,t} \\
GrzSd_{TrHl,t} &= \sum_{b,g} NtkSdPerLayer_{b,g,TrHl,t} \\
GrzSrb_{sl,s} &= \sum_{b,g} NtkSrbPerLayer_{b,g,sl,s} \\
GrzHrb_{hl,h} &= \sum_{b,g} NtkHrbPerLayer_{b,g,hl,h} \\
GrzRt_{hl,h} &= \sum_{b,g} NtkRtPerLayer_{b,g,hl,h}
\end{aligned} \tag{72}$$

### **grazing of foliage**

**GrzFlTr**, **GrzFlSrb**, **GrzFlHrb** [kg DM/plot/month] indicates the amount of foliage grazed from trees, shrubs and herbs. It is assumed that juvenile herbivores graze in the herb layer only.

$$\begin{aligned}
GrzFlTr_{tl,t} &= \sum_{b,g} FAvlFlTr_{b,g,tl,t} \cdot NtkTrPerLayer_{b,g,tl,t} \\
GrzFlSrb_{sl,s} &= \sum_{b,g} FAvlFlSrb_{b,g,sl,s} \cdot NtkSrbPerLayer_{b,g,sl,s} \\
GrzFlHrb_{sl,s} &= \sum_{b,g} FAvlFlHrb_{b,g,sl,s} \cdot NtkHrbPerLayer_{b,g,hl,h}
\end{aligned} \tag{73}$$

### **grazing of branches**

**GrzBrTr**, **GrzBrSrb**, **GrzBrHrb** [kg DM/plot/month] indicates the amount of current-year new branches grazed from trees, shrubs and herbs. It is assumed that juvenile herbivores graze in the herb layer only.

$$\begin{aligned}
GrzBrTr_{tl,t} &= \sum_{b,g} FAvlBrTr_{b,g,tl,t} \cdot NtkTrPerLayer_{b,g,tl,t} \\
GrzBrSrb_{sl,s} &= \sum_{b,g} FAvlBrSrb_{b,g,sl,s} \cdot NtkSrbPerLayer_{b,g,sl,s} \\
GrzBrHrb_{hl,h} &= \sum_{b,g} FAvlBrHrb_{b,g,hl,h} \cdot NtkHrbPerLayer_{b,g,hl,h}
\end{aligned} \tag{74}$$

In the model, there is a check for possible over-intake. Over-intake is defined as  $NtkArea > MxNtk_{b,g}$ . If this occurs then the actual amount of intake is reduced proportional to  $MxNtk_{b,g}/NtkArea_{b,g}$ . Consequently, consumption and grazing are corrected to match the corrected amount of intake.

Similarly, there is a check for over-consumption in the model. Over-consumption is defined as  $TotCnsArea > TotAvlArea$ . If this occurs then the amount of consumption is reduced proportional to  $TotAvlArea/TotCnsArea$ . Consequently, grazing and intake are corrected to match the amount of grazing.

## 4.2.9 Age of juveniles

**Age** [mnt] of juveniles is the number of month counted from the date of birth (= end of pregnancy) onwards. The shift to adult age-group after 12 months, *i.e.* the month at which new young are born.

## 4.2.10 Weight

The weight of an individual herbivore (**WghInd** [kg]) of a given age is calculated as the total weight of the population divided by the number of animals of that herbivore species and age-group. Hence all individuals in the juvenile age-group have the same weight, and all individuals in the adult age-group have the same weight.

$$WghInd_{b,g} = \frac{WghPerGroup_{b,g}}{NPerGroup_{b,g}} \quad (75)$$

### **average weight**

The average weight of an adult is an input parameter (**CAvrWghInd** [kg]). The average weight of a juvenile is assumed to increase linearly from the weight at birth until half the maximum individual weight of a juvenile in 1 year time.

$$AvrWghInd_{b,Jv} = CBrtWghInd_{b,Jv} + \frac{(CMxWghInd_{b,Jv} / 2 - CBrtWghInd_{b,Jv})}{12 - Age_{b,Jv} + 1} \quad (76)$$

(**CBrtWghInd, CMxWghInd**)

### **minimal weight**

The minimum weight (**CMnWghInd** [kg/individual]) is the weight below which mortality occurs. For an adult this is a parameter. For a juvenile it is set as half the average weight.

$$MnWghInd_{b,Jv} = AvrWghInd_{b,Jv} / 2 \quad (77)$$

For adult animals **CMnWghInd** is a parameter.

## 4.2.11 Fraction pregnant

The fraction of the population that is pregnant (**FPrG** [fraction]) is not constant but decreases during starvation. A linear decrease between the average weight of an individual and its minimum weight is assumed.

$$FPrG_b = CMxFPrG_b, \quad WghInd_{b,Ad} \geq CAvrWghInd_b$$

$$FPrG_b = CMxFPrG_b \cdot \frac{WghInd_{b,Ad} - CMnWghInd_{b,Ad}}{CAvrWghInd_b - CMnWghInd_{b,Ad}}, \quad (78)$$

$$CMnWghInd_{b,Ad} \leq WghInd_{b,Ad} < CAvrWghInd_b$$

$$FPrG_b = 0, \quad WghInd_{b,Ad} \leq CMnWghInd_{b,Ad}$$

(**CMxFPrG, CAvrWghInd, CMnWghInd**)

#### 4.2.12 Pregnancy

Pregnancy (**Prg** [MJ/population/month]) is the energy required for growth of the foetus. It depends on the fraction of reproducing animals that are pregnant, the monthly cost for pregnancy, and is allometrically proportional to the body weight of the female animal.

$$Prg_b = FPr_g_b \cdot NRpr_{b,Ad} \cdot CPr_g_b \cdot WghInd_{b,Ad}^{0.71}, CBgnPrg_b \leq Mnt \leq CEndPrg_b \quad (79)$$

(CPr\_g, CBgnPrg, CEndPrg)

#### 4.2.13 Birth

**NBrt** [# /yr] is the number of young born annually. It depends on the maximum number of young produced by the reproducing number of female animals in the population, and the fraction of female animals that is pregnant. The number of young can be reduced by predation.

$$NBrt_b = CMxNYng_b \cdot FPr_g_b \cdot NRpr_b \cdot (1 - CPrdJv_b) \quad (80)$$

(CMxNYng, CPrdJv)

#### 4.2.14 Mortality

Mortality is the loss of individuals from the population (**NMrt**, [# /month]). It can occur due to two reasons: (1) If the body weight (**WghPerGroup** [kg/individual]) of an individual animal falls below the minimum weight. The maximum number of individuals (**MxN** [# /plot]) is the total weight of the population divided by the minimum body weight. Mortality occurs if this maximum is less than the actual numbers. (2) If the maximum age is reached (see Eqn.(164)).

$$MxN_{b,g} = \frac{WghPerGroup_{b,g}}{MnWghInd_{b,g}} \quad (81)$$

$$NMrt_{b,g} = NPerGroup_{b,g} - MxN_{b,g}, MxN_{b,g} < N_{b,g} \quad (82)$$

(CBrtWghInd, CMnWghInd, CMxWghInd)

#### 4.2.15 Lactation

Lactation (**Lct** [MJ/population/month]) is the transfer of energy from the parent to the young. It depends on the number of juveniles the monthly cost for lactation, and is allometrically proportional to the body weight of the female animal.

$$Lct_b = NPerGroup_{b,Jv} \cdot CLct_b \cdot WghInd_{b,Ad}^{0.81}, CEndPrg_b < Mnt \leq CEndLct_b \quad (83)$$

(CLct, CEndPrg, CEndLct)

#### 4.2.16 Maintenance

Maintenance (**MntPerGroup** [MJ/population/month]) is the energy required to cover metabolic costs for animals to stay alive. It depends on the monthly cost of maintenance, the number of animals, and is allometrically proportional to the body weight.

The coefficient of maintenance is however not a constant. A linearly decrease from a maximum to a minimum value is assumed if the weight of an individual decreases from the average body weight to the minimum body weight.

In case of birth of young, maintenance for juveniles is based on the number of newborn.

$$\begin{aligned}
 CMnt_{b,g} &= CMxMnt_b, & WghInd_{b,g} > AvrWghInd_{b,g} \\
 CMnt_{b,g} &= CMnMnt_{b,g} + \left( \frac{WghInd_{b,g} - MnWghInd_{b,g}}{AvrWghInd_{b,g} - MnWghInd_{b,g}} \right) \cdot (CMxMnt_b - CMnMnt_b) & (84) \\
 & & MnWghInd_{b,g} \leq WghInd_{b,g} \leq AvrWghInd_{b,g} \\
 CMnt_{b,g} &= CMnMnt_b, & WghInd_{b,g} < MnWghInd_{b,g}
 \end{aligned}$$

(CMnt,CMxMnt ,CMnMnt)

$$MntPerGroup_{b,g} = CMnt_{b,g} \cdot NPerGroup_{b,g} \cdot WghInd_{b,g}^{0.75} \quad (85)$$

#### 4.2.17 Requirement

Requirement (**Rqr** [MJ/population/month]) is the total amount of energy to meet the costs for pregnancy, lactation and maintenance. Hence for juveniles, only the cost for maintenance is relevant.

$$\begin{aligned}
 Rqr_{b,Ad} &= Prg_b + Lct_b + MntPerGroup_{b,Ad} \\
 Rqr_{b,Jv} &= MntPerGroup_{b,Jv}
 \end{aligned} \quad (86)$$

#### 4.2.18 Rate of change in weight

Rate of change of weight per herbivore species and age group (**RWgh** [kg/population/month]) is the net result of input of energy by consumption and loss by requirements.

$$\begin{aligned}
 RWgh_{b,Ad} &= \frac{CnsArea_{b,Ad}}{CGrw_b} - \frac{Rqr_{b,Ad}}{CRsp_b} \\
 RWgh_{b,Jv} &= \frac{Lct_b + CnsArea_{b,Jv}}{CGrw_b} - \frac{Rqr_{b,Jv}}{CRsp_b}
 \end{aligned} \quad (87)$$

(CGrw,CRsp)

#### 4.2.19 Reduction in length of crown due to grazing

The structure of the vegetation is changed due to grazing. It is assumed the reduction in the length of the crown due to grazing on trees, shrubs and herbs ( $RdcLngCnGrzTr$ ,  $RdcLngCnGrzSrb$ ,  $RdcLngCnGrzHrb$  [m]) is proportional to the amount of plant biomass that is grazed based on a uniform distribution of foliage density over the height of the crown.

$$\begin{aligned}
 RdcLngCnGrzTr_{tl,t} &= \left( \frac{GrzTr_{tl,t}}{(WflTr_{tl,t} + WnwBrTr_{tl,t}) \cdot NTr_{tl,t}} \right) \cdot LngCnTr_{tl,t} \\
 RdcLngCnGrzSrb_{sl,s} &= \left( \frac{GrzSrb_{sl,s}}{(WflSrb_{sl,s} + WnwBrSrb_{sl,s}) \cdot NSrb_{sl,s}} \right) \cdot LngCnSrb_{sl,s} \quad (88) \\
 RdcLngCnGrzHrb_{hl,h} &= \left( \frac{GrzHrb_{hl,h}}{WflHrb_{hl,h} \cdot NHrb_{hl,h}} \right) \cdot LngCnHrb_{hl,h}
 \end{aligned}$$

#### 4.2.20 Minimum height of grazing

The minimum height of grazing ( $MnHghGrz$  [m]) is the lowest height to which the vegetation can be reduced due to grazing by the herbivores that are grazing in a plot.

$$MnHghGrz = \min(CMnHghGrz_b) \quad (89)$$

(CMnHghGrz)

#### 4.2.21 Maximum height of grazing

The maximum height of grazing ( $MxHghGrz$  [m]) is the maximum height to which the base of the crowns of shrubs and trees can be increased due to grazing by the herbivores that are grazing in a plot.

$$MxHghGrz = \max(CMxHghGrz_b) \quad (90)$$

(CMxHghGrz)

### 4.3 Plants

#### 4.3.1 Allocation

Allocation is the distribution of assimilates that are produced by photosynthesis over the growing plant components: foliage, branches, sapwood for trees or stalks for herbs, roots and reserves. The reserves have priority over the other plant organs. The assimilates not allocated to the reserves are used to produce new weight ( $Wnw$  [kg/individual]). Optimal ratio's between plant components are assumed for the allocation of new weight over foliage, branches and sapwood of trees and shrubs (Eqns. (9)-(10))

### **to roots**

A fixed fraction of the allocation to the roots is assumed for trees, shrubs and herbs ( $AlcWrtTr$ ,  $AlcWrtSrb$ ,  $AlcWrtHrb$  [-]), relative to the allocation of assimilates to the shoot. However, if the maximum height of the layer is achieved, then allocation to roots equals unity.

$$\begin{aligned} AlcWrtTr_{tl,t} &= CFRtShTr_t \\ AlcWrtSrb_{sl,s} &= CFRtShSrb_s \\ AlcWrtHrb_{hl,h} &= CFRtShHrb_h \end{aligned} \quad (91)$$

### **to stalks of herbs**

For woody herbs like Ericaceae, a fixed allocation to the stalk is assumed ( $AlcWstHrb$ [-]), relative to the allocation to the shoot.

$$AlcWstHrb_{hl,h} = CFStShHrb_h \cdot (1 - AlcWrtHrb_{hl,h}) \quad (92)$$

### **to branches of herbs**

For woody herbs like *Ericaceae*, a fixed allocation to the branches is assumed ( $AlcWbrHrb$ [-]), relative to the allocation to the shoot.

$$AlcWbrHrb_{hl,h} = (1 - CFStShHrb_h) \cdot (1 - AlcWrtHrb_{hl,h}) \quad (93)$$

## **4.3.2 Mortality**

Mortality is the reduction in number of plants that occur on a plot [# /plot/month]. Mortality can due to: self-thinning, age-related decline, fire, or trampling by large herbivores.

### **self-thinning**

It is assumed that self-thinning is only applicable to the high numbers of trees and shrubs in the herb and shrub layer. Thus, trees in the treelayer have no mortality due to self-thinning. The maximum number of individuals per layer ( $MxNSI, MxNHI$  [# /plot]) is determined according to the self-thinning rule (Eqn. (94)). This rule relates the maximum numbers of plants to the average individual weight, over all species, per layer. The average individual weight per layer ( $AvrWghIndSI, AvrWghIndHI$  [kg/individual]) is based on the branches, stem and roots, thus excluding foliage.

If the actual number of plants in a layer ( $NSI, NHI$ ) exceeds the maximum number as defined by the self-thinning rule, then this excess represents mortality by self-thinning (Eqn. (96)).

$$\begin{aligned} MxNSI &= PlotSize \cdot 10^{-2/3 \cdot \log_{10}(AvrWghIndSI \cdot 1000) + CThnSI} \\ MxNHI &= PlotSize \cdot 10^{-2/3 \cdot \log_{10}(AvrWghIndHI \cdot 1000) + CThnHI} \end{aligned} \quad (94)$$

The distribution of the maximum number of trees and shrubs per layer ( $MxNTr$ ,  $MxNSrb$  [# /plot]) depends on their coverage and is inversely related to their individual biomass. Thus, the bigger individuals obtain less numbers and vice versa.

$$\begin{aligned}
 MxNTr_{TrSl,t} &= MxNSl \cdot CvrTrPerLayer_{TrSl,t} \cdot \frac{1/WghStRtBr_{TrSl,t}}{\sum_t 1/WghStRtBrSl_t} \\
 MxNTr_{TrHl,t} &= MxNHL \cdot CvrTrPerLayer_{TrHl,t} \cdot \frac{1/WghStRtBr_{TrHl,t}}{\sum_t 1/WghStRtBrHl_t} \\
 MxNSrb_{SrbSl,s} &= MxNSl \cdot CvrSrbPerLayer_{SrbSl,s} \cdot \frac{1/WghStRtBr_{SrbSl,s}}{\sum_t 1/WghStRtBr_{TrSl,s} + \sum_s 1/WghStRtBr_{SrbSl,s}} \\
 MxNSrb_{SrbHl,s} &= MxNHL \cdot CvrSrbPerLayer_{SrbHl,s} \cdot \frac{1/WghStRtBr_{SrbHl,s}}{\sum_t 1/WghStRtBr_{TrHl,s} + \sum_s 1/WghStRtBr_{SrbHl,s}}
 \end{aligned} \tag{95}$$

$$\begin{aligned}
 NMrtThnSl &= \max(0, NSl - MxNSl) \\
 NMrtThnHl &= \max(0, NHL - MxNHL)
 \end{aligned} \tag{96}$$

The mortality due to self-thinning is distributed over the species proportional to the number of individuals a species contributes to the total number of individuals in that layer.

For trees:

$$\begin{aligned}
 NMrtThnTr_{TrSl,t} &= \frac{NTr_{TrSl,t}}{NSl} \cdot NMrtThnSl \\
 NMrtThnTr_{TrHl,t} &= \frac{NTr_{TrHl,t}}{NHL} \cdot NMrtThnHl
 \end{aligned} \tag{97}$$

For shrubs:

$$\begin{aligned}
 NMrtThnSrb_{SrbSl,s} &= \frac{NSrb_{SrbSl,s}}{NSl} \cdot NMrtThnSl \\
 NMrtThnSrb_{SrbHl,s} &= \frac{NSrb_{SrbHl,s}}{NHL} \cdot NMrtThnHl
 \end{aligned} \tag{98}$$

### **maximum age**

Trees and shrubs die when they approach their maximum age ( $NMrtAgeTr$ ,  $NMrtAgeSrb$  [# /plot]). It is assumed that from a given phase onward the fraction of mortality due to ageing in trees and shrubs ( $FMrtAgeTr$ ,  $FMrtAgeSrb$  [0-1]) increases linearly from zero at the onset of the mortality phase toward unity at the maximum age. Mortality for herbs ( $FMrtAgeHrb$ ) is assumed to be constant



$$\begin{aligned}
FMrtAgeTr_{il,t} &= \begin{cases} 0 & , AgeTr_{il,t} < (CMxAgeTr_t - CMrtPhsTr_t) \\ \frac{AgeTr_{il,t} - CMxAgeTr_t + CMrtPhsTr_t}{CMrtPhsTr_t} & , AgeTr_{il,t} \geq (CMxAgeTr_t - CMrtPhsTr_t) \end{cases} \quad (99) \\
FMrtAgeSrb_{sl,s} &= \begin{cases} 0 & , AgeSrb_{sl,s} < (CMxAgeSrb_s - CMrtPhsSrb_s) \\ \frac{AgeSrb_{sl,s} - CMxAgeSrb_s + CMrtPhsSrb_s}{CMrtPhsSrb_s} & , AgeSrb_{sl,s} \geq (CMxAgeSrb_s - CMrtPhsSrb_s) \end{cases} \\
FMrtAgeHrb_{hl,h} &= CFMrtAgeHrb_h
\end{aligned}$$

(CMxAgeTr, CMxAgeSrb, CMrtPhsTr, CMrtPhsSrb, CFMrtAgeHrb)

$$\begin{aligned}
NMrtAgeTr_{il,t} &= FMrtAgeTr_{il,t} \cdot NTr_{il,t} \\
NMrtAgeSrb_{sl,s} &= FMrtAgeSrb_{sl,s} \cdot NSrb_{sl,s} \\
NMrtAgeHrb_{hl,h} &= FMrtAgeHrb_{hl,h} \cdot NHrb_{hl,h}
\end{aligned} \quad (100)$$

### **fire**

see chapter *Fire*

### **trampling by herbivores**

Herbivores may affect the structure of the vegetation not only by grazing but also by trampling. It is assumed that mortality of herbs by trampling (NMrtTrmHrb [# /plot]) is proportional to the amount of biomass removed by grazing as the residence time of a herbivore in a plot is proportional to the amount of food grazed. The trampling effect is plant-species specific.

$$NMrtTrmHrb_{hl,h} = \frac{GrzHrb_h}{WghHrb_h} \cdot NHrb_{hl,h} \quad (101)$$

### **total mortality**

The loss of individual trees, shrubs and herbs (NMrtTr, NMrtSrb, NMrtHrb [# /plot]) from a plot is the sum of the mortality by self-thinning, age, fire and trampling.

$$\begin{aligned}
NMrtTr_{il,t} &= NMrtThnTr_{il,t} + NMrtAgeTr_{il,t} + NMrtFrTr_{il,t} + NMrtRDbhTr_{il,t} \\
NMrtSrb_{sl,s} &= NMrtThnSrb_{sl,s} + NMrtAgeSrb_{sl,s} + NMrtFrSrb_{sl,s} + NMrtRDbhSrb_{sl,s} \\
NMrtHrb_{hl,h} &= NMrtTrmHrb_{hl,h} + NMrtAgeHrb_{hl,h} + NMrtFrHrb_{hl,h}
\end{aligned} \quad (102)$$

### **4.3.3 Rate of increase in height**

Height growth is the increase in height (RHghTr, RHghSrb, RHghHrb [m/month]) during the growing season. Height growth in the shrub- and herb layer is linear and stops if the individual reaches either its maximum height or the height of one of these layers.

The coefficient for increase in height for trees depends on the site index. For shrubs and herbs it depends on the month of the year and is read from a lookup table, thus determining height growth phenology.

$$\begin{aligned}
CRHghSrb_s &= \text{tbl}(CRHghSrbTbl_s, Mnt) \\
CRHghHrb_h &= \text{tbl}(CRHghHrbTbl_h, Mnt)
\end{aligned}
\tag{103}$$

$$\begin{aligned}
RHghTr_{il,t} &= CRHghTr_{il,t} \cdot \frac{MxHghTr_{TrTl,t} - HghPerLayerTr_{il,t}}{MxHghTr_{TrTl,t}}, \quad tl = TrTl \\
RHghTr_{il:TrSl,t} &= CRHghTr_{il,t}, \quad tl = TrHl, TrSl \\
RHghSrb_{sl,s} &= CRHghSrb_{sl,s} \\
RHghHrb_{hl,h} &= CRHghHrb_{hl,h}
\end{aligned}
\tag{104}$$

(CRHghTr, CRHghSrb, CRHghHrb)

#### 4.3.4 Rate of change in crown base

The crown base of trees and shrubs (**RBseCnTr**, **RBseCnSrb** [m/month]) increases due to height growth when the crown reaches its maximum length. It is assumed that the crown base of herbs is always at zero metres height, hence there is no increase in crown base.

$$\begin{aligned}
RBseCnTr_{il,t} &= RHghTr_{il,t} - CMxLngCnTr_{il,t} + LngCnTr_{il,t} \\
RBseCnSrb_{sl,s} &= RHghSrb_{sl,s} - CMxLngCnSrb_{sl,s} + LngCnSrb_{sl,s} \\
RBseCnHrb_{hl,h} &= 0
\end{aligned}
\tag{105}$$

#### 4.3.5 Leaf area index

The leaf area index (**Lai** [m<sup>2</sup> fl/m<sup>2</sup> gr]) is the surface of foliage per unit ground surface. It is important to determine the amount of light that is intercepted and absorbed by the vegetation. Subsequently, the absorbed light is distributed over the individuals in a layer. This distribution depends on the relative contribution to the Lai in that layer. An individual tree and shrub may contribute to several layers depending on its height and the length of its crown. *E.g* an individual tree with its top in the tree layer contributes to the TrTl-cohort, however, it can have its crown base in the shrub- or even herb layer. Therefore, an upper, middle and lower part of the crown of an individual plant is distinguished. For a tree, the upper part is the part that contributes to the Lai of the tree layer, its middle part contributes to the shrub layer and its lower part contributes to the herb layer.

For trees:

$$\begin{aligned}
LaiUppTr_{TrTL,t} &= DnsFlTr_{TrTL,t} \cdot \min \left( \begin{array}{l} LngCnTr_{TrTL,t}, \\ HghTrPerLayer_{TrTL,t} - HghSl \end{array} \right) \\
LaiMidTr_{TrTL,t} &= DnsFlTr_{TrTL,t} \cdot \min \left( \begin{array}{l} LngCnTr_{TrTL,t}, \\ HghSl - HghHl, \\ HghSl - BseCnTr_{TrTL,t}, \\ HghTrPerLayer_{TrTL,t} - HghHl \end{array} \right) \\
LaiLowTr_{TrTL,t} &= DnsFlTr_{TrTL,t} \cdot \min \left( \begin{array}{l} LngCnTr_{TrTL,t}, \\ HghHl, \\ HghHl - BseCnTr_{TrTL,t}, \\ HghTrPerLayer_{TrTL,t} \end{array} \right) \\
LaiMidTr_{TrSl,t} &= DnsFlTr_{TrSl,t} \cdot \min \left( \begin{array}{l} LngCnTr_{TrSl,t}, \\ HghSl - HghHl, \\ HghSl - BseCnTr_{TrSl,t}, \\ HghTrPerLayer_{TrSl,t} - HghHl \end{array} \right) \\
LaiLowTr_{TrSl,t} &= DnsFlTr_{TrSl,t} \cdot \min \left( \begin{array}{l} LngCnTr_{TrSl,t}, \\ HghHl, \\ HghHl - BseCnTr_{TrSl,t}, \\ HghTrPerLayer_{TrSl,t} \end{array} \right) \\
LaiLowTr_{TrHl,t} &= DnsFlTr_{TrHl,t} \cdot \min \left( \begin{array}{l} LngCnTr_{TrHl,t}, \\ HghHl, \\ HghHl - BseCnTr_{TrHl,t}, \\ HghTrPerLayer_{TrHl,t} \end{array} \right)
\end{aligned} \tag{106}$$

For shrubs:

$$\begin{aligned}
 LaiMidSrb_{SrbSl,s} &= DnsFlSrb_{SrbSl,s} \cdot \min \left( \begin{array}{l} LngCnSrb_{SrbSl,s}, \\ HghSl - HghHl, \\ HghSl - BseCnSrb_{SrbSl,s}, \\ HghSrbPerLayer_{SrbSl,s} - HghHl \end{array} \right) \\
 LaiLowSrb_{SrbSl,s} &= DnsFlSrb_{SrbSl,s} \cdot \min \left( \begin{array}{l} LngCnSrb_{SrbSl,s}, \\ HghHl, \\ HghHl - BseCnSrb_{SrbSl,s}, \\ HghSrbPerLayer_{SrbSl,s} \end{array} \right) \\
 LaiLowSrb_{SrbHl,s} &= DnsFlSrb_{SrbHl,s} \cdot \min \left( \begin{array}{l} LngCnSrb_{SrbHl,s}, \\ HghHl, \\ HghHl - BseCnSrb_{SrbHl,s}, \\ HghSrbPerLayer_{SrbHl,s} \end{array} \right)
 \end{aligned} \tag{107}$$

For herbs:

$$LaiLowHrb_{HrbHl,h} = DnsFlHrb_{HrbHl,h} \cdot \min \left( \begin{array}{l} LngCnHrb_{HrbHl,h}, \\ HghHl, \\ HghHl - BseCnHrb_{HrbHl,h}, \\ HghHrbPerLayer_{HrbHl,h} \end{array} \right) \tag{108}$$

#### 4.3.6 Absorbed radiation

The absorbed radiation by trees in the upper layer of the canopy [**ArUppTr** [MJ(par)/individual/month]) is the amount of photosynthetic active radiation an individual tree absorbs per month in this layer. The total absorbed radiation by trees in the upper layer (**TotArUppTr** [MJ(par)/month/layer]) is the accumulated value over all individuals in this layer.

It is assumed that the amount of light decreases exponentially with leaf area index over the depth of the canopy (Lambert-Beer). Thus, the amount of photosynthetic radiation that is not absorbed in the upper layer is available for the middle layer (**ParMid** [J(par)/plot/month]).

For trees in the upper layer:

$$ArUppTr_{TrTl,t} = Par \cdot \left(1 - e^{-CExt \cdot LaiUppTr_{TrTl,t}}\right) \cdot \pi \cdot RdsTr_{TrTl,t}^2 \tag{109}$$

$$TotArUppTr = \sum_t NTr_{TrTl,t} \cdot ArUppTr_{TrTl,t} \tag{110}$$

Resulting Par for the middle layer:

$$ParMid = \frac{Par \cdot PlotSize - TotArUppTr}{PlotSize} \quad (111)$$

Both trees and shrubs can have a part of their canopy in the middle layer and absorbed light there ( $ArMidTr$ ,  $ArMidSrb$  [MJ(par)/individual/month]). Similarly to the upper layer, is the total absorbed radiation by trees and shrubs in the middle layer ( $TotArMidTr$ ,  $TotArMidSrb$  [MJ(par)/month/layer]) is the accumulated value over individual trees and shrubs, respectively, in this layer. The amount of photosynthetic radiation available for the lower layer is then the amount that was available for the middle layer minus what is absorbed both by trees and shrubs in the middle layer ( $ParLow$  [MJ(par)/plot/month]).

For trees in the middle layer:

$$ArMidTr_{TrTL,t} = ParMid \cdot \left(1 - e^{-CExt \cdot LaiMidTr_{TrTL,t}}\right) \cdot \pi \cdot RdsTr_{TrTL,t}^2 \quad (112)$$

$$ArMidTr_{TrSL,t} = ParMid \cdot \left(1 - e^{-CExt \cdot LaiMidTr_{TrSL,t}}\right) \cdot \pi \cdot RdsTr_{TrSL,t}^2$$

$$TotArMidTr = \sum_t NTr_{tl,t} \cdot ArMid_{tl,t} \quad (113)$$

For shrubs in the middle layer:

$$ArMidSrb_{SrbSL,s} = ParMid \cdot \left(1 - e^{-CExt \cdot LaiMidSrb_{SrbSL,s}}\right) \cdot \pi \cdot \left(RdsSrb_{SrbSL,s}\right)^2 \quad (114)$$

$$TotArMidSrb = \sum_s NSrb_{SrbSL,s} \cdot ArMid_{SrbSL,s} \quad (115)$$

Resulting Par for the lower layer:

$$ParLow = \frac{ParMid \cdot PlotSize - TotArMidTr - TotArMidSrb}{PlotSize} \quad (116)$$

Finally, trees, shrubs and herbs can have a part of their canopy in the lower layer and absorb part of the available light there ( $ArLowTr$ ,  $ArLowSrb$ ,  $ArLowHrb$  [MJ(par)/individual/month]). The total absorbed radiation by trees, shrubs and herbs in the lower layer ( $TotArLowTr$ ,  $TotArLowSrb$ ,  $TotArLowHrb$  [MJ(par)/month/layer]) is the accumulated value over all individual trees, shrubs and herbs in this layer.

For trees in the lower layer:

$$ArLowTr_{tl,t} = ParLow \cdot \left(1 - e^{-CExt \cdot LaiLowTr_{tl,t}}\right) \cdot \pi \cdot RdsTr_{tl,t}^2 \quad (117)$$

$$TotArLowTr = \sum_t NTr_{tl,t} \cdot ArMid_{tl,t} \quad (118)$$

For shrubs in lower layer:

$$ArLowSrb_{sl,s} = ParLow \cdot \left(1 - e^{-CExt \cdot LaiLowSrb_{sl,s}}\right) \cdot \pi \cdot RdsSrb_{sl,s}^2 \quad (119)$$

$$TotArLowSrb = \sum_s NSrb_{sl,s} \cdot ArLow_{sl,s} \quad (120)$$

For herbs in lower layer:

$$ArLowHrb_{hl,s} = ParLow \cdot \left(1 - e^{-CExt \cdot LaiLowHrb_{sl,s}}\right) \cdot \pi \cdot RdsHrb_{hl,h}^2 \quad (121)$$

$$TotArLowHrb = \sum_h NHrb_{hl,h} \cdot ArLow_{hl,h} \quad (122)$$

#### 4.3.7 Fraction absorbed radiation at the soilsurface

The fraction absorbed radiation at the soilsurface (FRdn [0-1]) is required to determine the germination environment for seedlings. It is defined as the ratio of radiation not absorbed by the vegetation and the amount of incoming radiation at the top of the canopy

$$NotAr = \frac{\left((ParLow \cdot PlotSize) - TotArLowTr - TotArLowSrb\right)}{PlotSize} \quad (123)$$

$$FRdn = \frac{NotAr}{Par} \quad (124)$$

#### 4.3.8 Net primary production

Net primary production of trees, shrubs and herbs [NppTr, NppSrb, NppHrb [kg DM / individual / month] production of biomass by photosynthesis. It depends on a species-specific radiation use efficiency and the amount of radiation absorbed by the individual plant. As individual plants can have their canopies in different layers, their Npp depends on the amount of absorbed radiation in either the lower, middle or upper layer.

Photosynthesis occurs only if the temperature exceeds a minimum value (CMnTmpPht [°C]).

$$\begin{aligned} NppTr_{TrTI,t} &= CRueTr_t \cdot \left( ArLow_{TrTI,t} + ArMid_{TrTI,t} + ArUpp_{TrTI,t} \right) \\ NppTr_{TrSI,t} &= CRueTr_t \cdot \left( ArLow_{TrSI,t} + ArMid_{TrSI,t} \right) \\ NppTr_{TrHI,t} &= CRueTr_t \cdot \left( ArLow_{TrHI,t} \right) \end{aligned} \quad (125)$$

$$NppSrb_{SrbSI,s} = CRueSrb_s \cdot \left( ArLow_{SrbHI,s} + ArMid_{SrbHI,s} \right)$$

$$NppSrb_{SrbHI,s} = CRueSrb_s \cdot \left( ArLow_{SrbHI,s} \right)$$

$$NppHrb_{HrbHI,h} = CRueHrb_h \cdot \left( ArLow_{HrbHI,h} \right)$$

(CRueTr, CRueSrb, CRueHrb)

### 4.3.9 Rate of change of new biomass

The rate of change of new biomass of trees, shrubs and herbs ( $WnwTr$ ,  $WnwSrb$ ,  $WnwHrb$  [kg DM/individual/month]) is the amount of  $Npp$  converted into new structural biomass, excluding reserves. Reserves are also expressed as dry mass per individual, and have first priority. The amount of  $Npp$  that is available for growth of new biomass thus depends on the level of the reserves based on the following rules:

- (1) at the begin of the growing season there is a flush of new foliage for deciduous plant species. Also if the amount of foliage becomes very little during the growing season, *e.g.* due to grazing, new foliage can be extracted from the reserves
- (2) if the level of reserves exceeds the maximum level, then all  $Npp$  is converted into structural biomass
- (3) if the level of reserves is less than the maximum level, then priority is given to refilling the reserves. Note that the maximum reserve level is not a constant but changes with the amount required for flushing biomass, according to Eqns. (34).

$$\begin{aligned}
 RWnwTr_{il,t} &= \begin{cases} \min(WrsTr_{il,t}, VlmCnTr_{il,t} \cdot OptDnsFlTr_{il,t} / CSlaTr_t) & WflTr_{il,t} < \varepsilon \\ NppTr_{il,t} & WrsTr_{il,t} \geq MxWrsTr_{il,t} \\ \min(NppTr_{il,t}, NppTr_{il,t} - (MxWrsTr_{il,t} - WrsTr_{il,t})) & WrsTr_{il,t} < MxWrsTr_{il,t} \end{cases} \\
 RWnwSrb_{sl,s} &= \begin{cases} \min(WrsSrb_{sl,s}, VlmCnSrb_{sl,s} \cdot OptDnsFlSrb_{sl,s} / CSlaSrb_s) & WflSrb_{sl,s} < \varepsilon \\ NppSrb_{sl,s} & WrsSrb_{sl,s} \geq MxWrsSrb_{sl,s} \\ \min(NppSrb_{sl,s}, NppSrb_{sl,s} - (MxWrsSrb_{sl,s} - WrsSrb_{sl,s})) & WrsSrb_{sl,s} < MxWrsSrb_{sl,s} \end{cases} \quad (126) \\
 RWnwHrb_{hl,h} &= \begin{cases} \min(WrsHrb_{hl,h}, VlmCnHrb_{hl,h} \cdot OptDnsFlHrb_{hl,h} / CSlaHrb_h) & WflHrb_{hl,h} < \varepsilon \\ NppHrb_{hl,h} & WrsHrb_{hl,h} \geq MxWrsHrb_{hl,h} \\ \min(NppHrb_{hl,h}, NppHrb_{hl,h} - (MxWrsHrb_{hl,h} - WrsHrb_{hl,h})) & WrsHrb_{hl,h} < MxWrsHrb_{hl,h} \end{cases}
 \end{aligned}$$

### 4.3.10 Growth rate of reserves

Growth of reserves of trees, shrubs and herbs ( $GWrsTr$ ,  $GWrsSrb$ ,  $GWrsHrb$  [kg DM / individual / month]) is  $Npp$  minus the growth of new structural biomass.

$$\begin{aligned}
 GWrsTr_{il,t} &= NppTr_{il,t} - RWnwTr_{il,t} \\
 GWrsSrb_{sl,s} &= NppSrb_{sl,s} - RWnwSrb_{sl,s} \\
 GWrsHrb_{hl,h} &= NppHrb_{hl,h} - RWnwHrb_{hl,h}
 \end{aligned} \quad (127)$$

### 4.3.11 Rate of change of crown radius

$RRdsTr$ ,  $RRdsSrb$ ,  $RRdsHrb$  [m/month] is the monthly increase of the crown radius of trees, shrubs and herbs. In FORSPACE, the crown radius of an individual plant is chosen to as a state variable, whereas the projected surface of the crown is considered a derived variable. The required rate of change of crown radius for the increase in surface of trees, shrubs and herbs is the increase in projected crown surface that is required if the plant were to expand by its maximum rate of surface increase. If there is a lack of space, the actual increase in surface, and thus radius, will be less.

For trees and shrubs the available data from the Forest Reserve Program allows estimating the maximum rate of change in projected crown surface ( $MxRSrfTr$ ,  $MxRSrfSrb$  [ $m^2/month$ ]). For herbs on the other hand, the data is available on the lateral rate of change. This information is converted into  $MxRSrfHrb$  [ $m^2/month$ ].

The required change of the crown radius for the calculation of growth of foliage is based on five steps:

- (1) first the required increase in surface is determined if the plant were to expand by its maximum rate of surface increase (Eqn. (128)). For herbs the maximum rate of increase in surface is calculated based on maximum rate of change in radius (Eqns. not presented here). For shrubs and trees  $MxRSrf$  is a parameter.
- (2) the maximum increase in crown radius is the difference between the actual and the maximum crown radius of the species (Eqn. (129)). Thus checking that the actual radius does not exceed the species-specific maximum radius.
- (3) to achieve the maximum radius the required rate of change in crown radius is the minimum of the increase in radius to attain the maximum increase in surface (1), and the increase allowed to attain the maximum radius of the species (2) (Eqn. (130)).
- (4) it is checked if the total increase in surface of all individuals in a layer does not exceed the total space in the plot. Therefore an intermediate integration is performed based on (3) (Eqns. not presented) to obtain  $RSrfTr$ ,  $RSrfSrb$ ,  $RSrfHrb$  [ $m^2/month$ ].
- (5) if such an overshoot occurs then the rate of change of crown radius is corrected proportional to the surface an individual contributes to the total vegetation surface in the plot (Eqns. not presented) to obtain the rate of increase in radius.

$$RqrRRdsSrfTr_{il,t} = \sqrt{\frac{\pi \cdot RdsTr_{il,t}^2 + MxRSrfTr_t \cdot \left(1 - \frac{RdsTr_{il,t}}{MxRdsTr_t}\right)}{\pi}} - RdsTr_{il,t} \quad (128)$$

$$RqrRRdsSrfSrb_{sl,s} = \sqrt{\frac{\pi \cdot RdsSrb_{sl,s}^2 + MxRSrfSrb_s \cdot \left(1 - \frac{RdsSrb_{sl,s}}{MxRdsSrb_s}\right)}{\pi}} - RdsSrb_{sl,s}$$

$$RqrRRdsSrfHrb_{hl,h} = \sqrt{\frac{\pi \cdot RdsHrb_{hl,h}^2 + MxRSrfHrb_h}{\pi}} - RdsHrb_{hl,h}$$

( $MxRSrfTr$ ,  $MxRSrfSrb$ ,  $MxRSrfHrb$ )



$$\begin{aligned}
MxRqrRRdsTr_{il,t} &= CMxRdsTr_{il,t} - RdsTr_{il,t} \\
MxRqrRRdsSrb_{sl,s} &= CMxRdsSrb_{sl,s} - RdsSrb_{sl,s} \\
MxRqrRRdsHrb_{hl,h} &= CMxRdsHrb_{hl,h} - RdsHrb_{hl,h}
\end{aligned} \tag{129}$$

(CMxRdsTr, CMxRdsSrb, CMxRdsHrb)

$$\begin{aligned}
RqrRRdsTr_{il,t} &= \min(RqrRRdsSrfTr_{il,t}, MxRqrRRdsTr_{il,t}) \\
RqrRRdsSrb_{sl,s} &= \min(RqrRRdsSrfSrb_{sl,s}, MxRqrRRdsSrb_{sl,s}) \\
RqrRRdsHrb_{hl,h} &= \min(RqrRRdsSrfHrb_{hl,h}, MxRqrRRdsHrb_{hl,h})
\end{aligned} \tag{130}$$

$$\begin{aligned}
RRdsTr_{il,t} &= \sqrt{\frac{\pi \cdot RdsTr_{il,t}^2 + RSrfTr_{il,t}}{\pi}} - RdsTr_{il,t} \\
RRdsSrb_{sl,s} &= \sqrt{\frac{\pi \cdot RdsSrb_{sl,s}^2 + RSrfSrb_{sl,s}}{\pi}} - RdsSrb_{sl,s} \\
RRdsHrb_{hl,h} &= \sqrt{\frac{\pi \cdot RdsHrb_{hl,h}^2 + RSrfHrb_{hl,h}}{\pi}} - RdsHrb_{hl,h}
\end{aligned} \tag{131}$$

#### 4.3.12 Rate of change of crown length

The rate of change of the length of the crown (RLngCnTr, RLngCnSrb, RLngCnHrb [m/month]) is calculated to determine the amount of foliage that is required to maintain a constant foliage density in the growing crown (see Eqn. (133)).

$$\begin{aligned}
RLngCnTr_{il,t} &= RHghCnTr_{il,t} - RBseCnTr_{il,t} - RdcLngCnGrzTr_{il,t} \\
RLngCnSrb_{sl,s} &= RHghCnSrb_{sl,s} - RBseCnSrb_{sl,s} - RdcLngCnGrzSrb_{sl,s} \\
RLngCnHrb_{hl,h} &= RHghCnHrb_{hl,h} - RBseCnHrb_{hl,h} - RdcLngCnGrzHrb_{hl,h}
\end{aligned} \tag{132}$$

#### 4.3.13 Growth rate of foliage

The growth rate of foliage of trees, shrubs and herbs (GWflTr, GWflSrb, GWflHrb [kg DM / individual / month]) is the amount of new weight allocated to foliage. The allocation to foliage has priority above the other plant component. Thus, it is first subtracted from the new weight, and the remaining new weight is distributed over the roots, sapwood and branches (see below).

For deciduous species, at the beginning of the growing season all new biomass (Wnw [kg/individual]) is allocated to growth of foliage. Otherwise, first the 'required growth rate' is calculated as the growth rate of the foliage to attain:

- (1) rate of change of the crown length (Eqn.(133))
  - (2) radius increase (Eqn. (134))
  - (3) optimal foliage density (Eqn. (135)). The optimal foliage density latter depends on the anticipated increase in volume of the crown. Therefore an intermediate integration for the new crown volume (ItmVlmCn) is performed based on the rates of change of crown length and radius (Eqns. not presented here)
- If there is insufficient productivity to meet all these demands, then priority is given to increase in height, next to attain the optimal foliage density, and finally to lateral growth.

$$RqrGWflLngCnTr_{il,t} = \frac{RLngCnTr_{il,t} \cdot \pi \cdot RdsTr_{il,t}^2 \cdot DnsFlTr_{il,t}}{CSlaTr_t} \quad (133)$$

$$RqrGWflLngCnSrb_{sl,s} = \frac{RLngCnSrb_{sl,s} \cdot \pi \cdot RdsSrb_{sl,s}^2 \cdot DnsFlSrb_{sl,s}}{CSlaSrb_s}$$

$$RqrGWflLngCnHrb_{hl,h} = \frac{RLngCnHrb_{hl,h} \cdot \pi \cdot RdsHrb_{hl,h}^2 \cdot DnsFlHrb_{hl,h}}{CSlaHrb_h}$$

$$RqrGWflRdsTr_{il,t} = \left( (RdsTr_{il,t} + RRdsTr_{il,t})^2 - RdsTr_{il,t}^2 \right) \cdot \pi \cdot \left( LngCnTr_{il,t} + RLngCnTr_{il,t} \right) \cdot \frac{DnsFlTr_{il,t}}{CSlaTr_t}$$

$$RqrGWflRdsSrb_{sl,s} = \left( (RdsSrb_{sl,s} + RRdsSrb_{sl,s})^2 - RdsSrb_{sl,s}^2 \right) \cdot \pi \cdot \left( LngCnSrb_{sl,s} + RLngCnSrb_{sl,s} \right) \cdot \frac{DnsFlSrb_{sl,s}}{CSlaSrb_s} \quad (134)$$

$$RqrGWflRdsHrb_{hl,h} = \left( (RdsHrb_{hl,h} + RRdsHrb_{hl,h})^2 - RdsHrb_{hl,h}^2 \right) \cdot \pi \cdot \left( LngCnHrb_{hl,h} + RLngCnHrb_{hl,h} \right) \cdot \frac{DnsFlHrb_{hl,h}}{CSlaHrb_h}$$

$$RqrGWflOptDnsTr_{il,t} = \frac{(CDnsFlTr_{il,t} - DnsFlTr_{il,t}) \cdot ItmVlmCnTr_{il,t}}{CSlaTr_t}$$

$$RqrGWflOptDnsSrb_{sl,s} = \frac{(CDnsFlSrb_{sl,s} - DnsFlSrb_{sl,s}) \cdot ItmVlmCnSrb_{sl,s}}{CSlaSrb_s} \quad (135)$$

$$RqrGWflOptDnsHrb_{hl,h} = \frac{(CDnsFlHrb_{hl,h} - DnsFlHrb_{hl,h}) \cdot ItmVlmCnHrb_{hl,h}}{CSlaHrb_h}$$

$$\begin{aligned}
GWflTr_{il,t} &= \min \left( 0.8 \cdot RWnwTr_{il,t}, \right. \\
&\quad \left. RqrGWflLngCnTr_{il,t} + RqrGWflRdsTr_{il,t} + RqrGWflOptDnsTr_{il,t} \right) \\
GWflSrb_{sl,s} &= \min \left( 0.8 \cdot RWnwSrb_{sl,s}, \right. \\
&\quad \left. RqrGWflLngCnSrb_{sl,s} + RqrGWflRdsSrb_{sl,s} + RqrGWflOptDnsSrb_{sl,s} \right) \\
GWflHrb_{hl,h} &= \min \left( 0.8 \cdot RWnwHrb_{hl,h}, \right. \\
&\quad \left. RqrGWflLngCnHrb_{hl,h} + RqrGWflRdsHrb_{hl,h} + RqrGWflOptDnsHrb_{hl,h} \right)
\end{aligned} \tag{136}$$

#### 4.3.14 Growth rate of branches

The growth rate of foliage of trees, shrubs and herbs (**GWbrTr**, **GWbrSrb**, **GWbrHrb** [kg DM/individual/month]) is the amount of new weight allocated to foliage. The same allometric relationship that defines the initial biomass of the different plant components is used. As only sapwood is alive and hence can grow, the fraction of branches to sapwood is calculated from the optimal ratio between branches and stem (**OptRatioWbrWstTr**, **OptRatioWbrWstSrb** Eqn. (10))

The following calculations are performed to determine the growth rate of branches:

- (1) weight of new branches plus sapwood (Eqn. (137))
- (2) weight of new shoot (above-ground biomass) (Eqn. (138))
- (3) optimal ratio of weight branches to stem (Eqn. (10))
- (4) fraction of branches of new weight (Eqn. (139))
- (5) allocation of above-ground Npp to branches (Eqn. (140))
- (6) growth rate of branches (Eqn. (141))

$$\begin{aligned}
WnwbrstTr_{il,t} &= (RWnwTr_{il,t} - GWflTr_{il,t}) \cdot (1 - AlcWrtTr_{il,t}) \\
WnwbrstSrb_{sl,s} &= (RWnwSrb_{sl,s} - GWflSrb_{sl,s}) \cdot (1 - AlcWrtSrb_{sl,s})
\end{aligned} \tag{137}$$

$$\begin{aligned}
WshTr_{il,t} &= WflTr_{il,t} + WbrTr_{il,t} + WstTr_{il,t} + WnwbrstTr_{il,t} \\
WshSrb_{sl,s} &= WflSrb_{sl,s} + WbrSrb_{sl,s} + WstSrb_{sl,s} + WnwbrstSrb_{sl,s}
\end{aligned} \tag{138}$$

$$\begin{aligned}
FWbrWnwTr_{il,t} &= \frac{\frac{WbrTr_{il,t}}{OptRatioWbrWstTr_{il,t}} - WstTr_{il,t} - WnwbrstTr_{il,t}}{\frac{WnwbrstTr_{il,t}}{OptRatioWbrWstTr_{il,t}} - WnwbrstTr_{il,t}} \\
FWbrWnwSrb_{sl,s} &= \frac{\frac{WbrSrb_{sl,s}}{OptRatioWbrWstSrb_{sl,s}} - WstSrb_{sl,s} - WnwbrstSrb_{sl,s}}{\frac{WnwbrstSrb_{sl,s}}{OptRatioWbrWstSrb_{sl,s}} - WnwBrStSrb_{sl,s}}
\end{aligned} \tag{139}$$

$$\begin{aligned}
AlcWbrTr_{il,t} &= (1 - AlcWrtTr_{il,t}) \cdot FWbrWnwTr_{il,t} \\
AlcWbrSrb_{sl,s} &= (1 - AlcWrtSrb_{sl,s}) \cdot FWbrWnwSrb_{sl,s}
\end{aligned} \tag{140}$$

$$\begin{aligned}
GWbrTr_{il,t} &= AlcWbrTr_{il,t} \cdot (RWnwTr_{il,t} - GWflTr_{il,t}) \\
GWbrSrb_{sl,s} &= AlcWbrSrb_{sl,s} \cdot (RWnwSrb_{sl,s} - GWflSrb_{sl,s}) \\
GWbrHrb_{hl,h} &= AlcWbrHrb_{hl,h} \cdot (RWnwHrb_{hl,h} - GWflHrb_{hl,h})
\end{aligned} \tag{141}$$

#### 4.3.15 Growth of sapwood

The growth rate of sapwood of trees and shrubs ( $GWswTr$ ,  $GWswSrb$  [kg DM/individual/month]) is the amount of new weight allocated to sapwood. It is the amount of new weight allocated neither to the roots nor to the branches, nor to the foliage.

$$\begin{aligned}
AlcWswTr_{il,t} &= (1 - AlcWrtTr_{il,t}) \cdot (1 - FWbrWnwTr_{il,t}) \\
AlcWswSrb_{sl,s} &= (1 - AlcWrtSrb_{sl,s}) \cdot (1 - FWbrWnwSrb_{sl,s})
\end{aligned} \tag{142}$$

$$\begin{aligned}
GWswTr_{il,t} &= AlcWswTr_{il,t} \cdot (RWnwTr_{il,t} - GWflTr_{il,t}) \\
GWswSrb_{sl,s} &= AlcWswSrb_{sl,s} \cdot (RWnwSrb_{sl,s} - GWflSrb_{sl,s})
\end{aligned} \tag{143}$$

#### 4.3.16 Growth of heartwood

The growth rate of heartwood of trees and shrubs ( $GWhwTr$ ,  $GWhwSrb$  [kg DM/individual/month]) is the amount of sapwood to heartwood. The rate of conversion depends on the longevity of the sapwood.

$$\begin{aligned}
GWhwTr_{il,t} &= \frac{1}{CLgnSwTr_{il,t}} \cdot WswTr_{il,t} \\
GWhwSrb_{sl,s} &= \frac{1}{CLgnSwSrb_{sl,s}} \cdot WswSrb_{sl,s}
\end{aligned} \tag{144}$$

( $CLgnSwTr$ ,  $CLgnSwSrb$ )

#### 4.3.17 Growth rate of stalks of herbs

The growth rate of stalks of herbs ( $GWstHrb$  [kg DM/individual/month]) is a fixed fraction of the amount of new weight after the growth of foliage has been subtracted.

$$GWstHrb_{hl,h} = AlcWstHrb_{hl,h} \cdot (RWnwHrb_{hl,h} - GWflHrb_{hl,h}) \tag{145}$$

#### 4.3.18 Growth rate of roots

The growth rate of roots of trees, shrubs and herbs ( $GWrtTr$ ,  $GWrtSrb$ ,  $GWrtHrb$  [kg DM/individual/month]) is a fixed fraction of the amount of new weight after the growth of foliage has been subtracted.

$$\begin{aligned}GWrtTr_{il,t} &= AlcWrtTr_{il,t} \cdot (RWnwTr_{il,t} - GWflTr_{il,t}) \\GWrtSrb_{sl,s} &= AlcWrtSrb_{sl,s} \cdot (RWnwSrb_{sl,s} - GWflSrb_{sl,s}) \\GWrtHrb_{hl,h} &= AlcWrtHrb_{hl,h} \cdot (RWnwHrb_{hl,h} - GWflHrb_{hl,h})\end{aligned}\quad (146)$$

#### 4.3.19 Turnover of foliage

The turnover of foliage of trees, shrubs and herbs ( $TWflTr$ ,  $TWflSrb$ ,  $TWflHrb$  [kg DM/individual/month]) is the loss of foliage from the plant into the litter pool. For deciduous plants all foliage is lost at the end of the growing season (at month  $EndSsn + 1$ ). For evergreen species, a constant turnover of foliage outside the growing season is assumed.

$$\begin{aligned}TWflTr_{il,t} &= CTrnWflTr_{il,t} \cdot WflTr_{il,t} \\TWflSrb_{sl,s} &= CTrnWflSrb_{sl,s} \cdot WflSrb_{sl,s} \\TWflHrb_{hl,h} &= CTrnWflHrb_{hl,h} \cdot WflHrb_{hl,h}\end{aligned}\quad (147)$$

$(CTrnWflTr, CTrnWflSrb, CTrnWflHrb)$

#### 4.3.20 Turnover of branches

The turnover of branches of trees, shrubs and herbs ( $TWbrTr$ ,  $TWbrSrb$ ,  $TWbrHrb$  [kg DM/individual/month]) is the loss of branches from the plant into the litter pool. A constant turnover of branches outside the growing season is assumed.

$$\begin{aligned}TWbrTr_{il,t} &= CTrnWbrTr_{il,t} \cdot WbrTr_{il,t} \\TWbrSrb_{sl,s} &= CTrnWbrSrb_{sl,s} \cdot WbrSrb_{sl,s} \\TWbrHrb_{hl,h} &= CTrnWbrHrb_{hl,h} \cdot WbrHrb_{hl,h}\end{aligned}\quad (148)$$

$(CTrnWbrTr, CTrnWbrSrb, CTrnWbrHrb)$

#### 4.3.21 Turnover of stalks

The turnover of stalks of herbs ( $TWstHrb$  [kg DM/individual/month]) is the loss of stalks from the herbs into the litter pool. For deciduous plants, all stalks are lost after the end of the growing season

For herb species that are not evergreen but with woody stalks and branches such as *Ericaceae* it is assumed that there is a constant turnover outside the growing season.

$$TWstHrb_{hl,h} = CTrnWst_h \cdot WstHrb_{hl,h} \quad (149)$$

(CTrnWstHrb)

#### 4.3.22 Turnover of roots

The turnover of roots of trees, shrubs and herbs (TWrtTr, TWrtSrb, TWrtHrb [kg DM/individual/month]) is the loss of roots from the plants into the litter pool. A constant turnover throughout the year is assumed.

$$TWrtTr_{tl,t} = CTrnWrtTr_{tl,t} \cdot WbrTr_{tl,t}$$

$$TWrtSrb_{sl,s} = CTrnWrtSrb_{sl,s} \cdot WbrSrb_{sl,s} \quad (150)$$

$$TWrtHrb_{hl,h} = CTrnWrtHrb_{hl,h} \cdot WbrHrb_{hl,h}$$

(CTrnWrtTr, CTrnWrtSrb, CTrnWrtHrb)

#### 4.3.23 Germination

The germination of seeds of trees, shrubs and herbs (IsGrmTr, IsGrmSrb, IsGrmHrb [yes/no]) indicates if seeds can germinate in the plot or not. It is determined based on the following set of rules:

- (1) germination only occurs during the first month of the growing season
- (2) the same species does not already occur in the herb layer, in case of woody species only
- (3) there should be sufficient free space available for the seedling to get its initial dimensions
- (4) there must be sufficient light available on the soil
- (5) the litter layer should not be too deep
- (6) the fermentation layer should not be too thin, in case of herbs and grasses

If these constraints are met then the number of germinating seeds depends on the probability of germination on the soiltype of the plot, and the fraction of the produced seeds that are viable. No stochasticity is assumed, thus the probability of germination is taken as a fraction of seeds that can germinate on a given soiltype.

$$\begin{aligned}
IsGrmTr_{il,t} &= \begin{cases} Mnt = BgnSsn \\ NTr_{TrHl,t} = 0 \\ CvrHl \leq CMxCvrGrmTr_{il,t} \\ FRdn > CMnFRdnGrmTr_{il,t} \\ HghLt2 < CMxHghLtGrmTr_{il,t} \end{cases} \\
IsGrmSrb_{sl,s} &= \begin{cases} Mnt = BgnSsn \\ NSrb_{SrbHl,s} = 0 \\ CvrHl \leq CMxCvrGrmSrb_{sl,s} \\ FRdn > CMnFRdnGrmTr_{il,t} \\ HghLt1 + HghLt2 < CMxHghLtGrmSrb_{sl,s} \end{cases} \\
IsGrmHrb_{hl,h} &= \begin{cases} Mnt = BgnSsn \\ CvrHl \leq CMxCvrGrmHrb_{hl,h} \\ FRdn > CMnFRdnGrmHrb_{hl,h} \\ HghLt2 < CMxHghLt2GrmHrb_{hl,h} \\ HghLt3 > CMnHghLt3GrmHrb_{hl,h} \end{cases} \quad (151)
\end{aligned}$$

(CMxCvrGrmTr, CMxCvrGrmSrb, CMxCvrGrmHrb,  
CMnFRdnGrmTr, CMnFRdnGrmSrb, CMnFRdnGrmHrb,  
CMxHghLtGrmTr, CMxHghLtGrmSrb, CMxHghLtGrmHrb)

If IsGrm is true then:

$$\begin{aligned}
NGrmTr_t &= CPGrmTr_t \cdot NsdTr_t \cdot CFGrmSdTr_t \\
NGrmSrb_s &= CPGrmSrb_s \cdot NsdSrb_s \cdot CFGrmSdSrb_s \\
NGrmHrb_h &= CPGrmHrb_h \cdot NsdHrb_h \cdot CFGrmSdHrb_h
\end{aligned} \quad (152)$$

(CPGrmTr, CPGrmSrb, CPGrmHrb,  
CFGrmSdTr, CFGrmSdSrb, CFGrmSdHrb)

#### 4.3.24 Production of seeds

The production of seeds of trees, shrubs and herbs (PrdNsdTr, PrdNsdSrb, PrdNsdHrb [# /plot]) is based on 4 classes of seed production, *i.e.* 0-10%, 10-40%, 40-70% and 70-100% of the maximum seedproduction. Each of these classes have their own frequency distribution. *E.g.* for a mast tree may produce every 5 year 70-100% of its maximum number of seeds. The frequency of the 4 production classes are determined by the species-specific parameters CF0\_10MxPrdNSd, CF10\_40MxPrdNSd, CF40\_70MxPrdNSd,

CF70\_100MxPrdNSd. For woody species, the maximum seedproduction is scaled by the actual crown volume relative to the maximum crown volume that the species can obtain if its maximum dimensions are reached.

Seed production is a stochastic process. This is simulated in FORSPACE by drawing 2 values from a random distribution. The first random number determines the class of seed production based on its frequency of occurrence, whilst the second random number determines the number of seeds from that class. The stochastic procedure is simplified in Eqn. (153) by  $r$  to avoid cumbersome equations.

It is assumed that only adult individuals produce seeds, thus only trees in the treelayer, shrubs in the shrublayer and herbs in the herblayer.

$$\begin{aligned}
 PrdNsdTr_t &= CMxPrdNSdTr_t \cdot \frac{VlmTr_{TrTL,t}}{MxVlmTr_{TrTL,t}} \cdot r \\
 PrdNsdSrb_s &= CMxPrdNSdSrb_{st} \cdot \frac{VlmSrb_{SrbSL,s}}{MxVlmSrb_{SrbSL,s}} \cdot r \\
 PrdNsdHrb_h &= CMxPrdNSdHrb_h \cdot r
 \end{aligned} \tag{153}$$

(CMxPrdNSdTr, CMxPrdNSdSrb, CMxPrdNSdHrb)

#### 4.3.25 Dispersion

Dispersion of seeds from trees, shrubs and herbs is the spread of produced seeds in the surroundings of a mother plant. It depends on the number of seeds produced per plant and the range of dispersion. A Gaussian distribution is assumed to spread the seeds to neighbouring plots. Thus, for each species it is determined how many seeds a plot receives from neighboring plots.

In principle each seed can be spread over the landscape individually. However, to avoid very long computation times the total seedproduction is lumped in about 1000 packages.

$$\begin{aligned}
 RNsdDspTr_t &= \text{ibngauss} \left( PrdNsdTr_{TrTL,t} \cdot NTr_t, CRngTr_t \right) \\
 RNsdDspSrb_s &= \text{ibngauss} \left( PrdNsdSrb_{SrbSL,s} \cdot NTr_t, CRngSrb_s \right) \\
 RNsdDspHrb_h &= \text{ibngauss} \left( PrdNsdHrb_{HrbHL,h} \cdot NTr_t, CRngHrb_h \right)
 \end{aligned} \tag{154}$$

(CRngTr, CRngSrb, CRngHrb)

#### 4.3.26 Turnover of seeds

The turnover of seeds of trees, shrubs and herbs (TNsdTr, TNsdSrb, TNsdHrb [#/#plot/month]) is the loss of seeds. A constant turnover throughout the year is assumed. The number of seeds is set to zero in case of fire in a plot.



$$\begin{aligned}
TNsdTr_{t,t} &= \begin{cases} NsdTr_t & , IsFrHl \\ CTrnNsdTr_t \cdot NsdTr_t & \end{cases} \\
TNsdSrb_{sl,s} &= \begin{cases} NsdSrb_s & , IsFrHl \\ CTrnNsdSrb_s \cdot NsdSrb_s & \end{cases} \\
TNsdHrb_{hl,h} &= \begin{cases} NsdHrb_h & , IsFrHl \\ CTrnNsdHrb_h \cdot NsdHrb_h & \end{cases}
\end{aligned} \tag{155}$$

(CTrnWsdTr,CTrnWsdSrb,CTrnWsdHrb)

#### 4.3.27 Rate of change in litter layers

There are three litter layers with rapidly, intermediate and slowly decomposing material, indicated by 1, 2 and 3 respectively. Furthermore, a dead wood pool is distinguished that contains dead trees from the tree layer. There are two fluxes: the outgoing litter and deadwood due to fire or decomposition (**OutWlt,OutWdw** [kg DOM/plot/month]), and the incoming material due to litter fall from trees, shrubs and herbs (**InWlt,InWltTr,InWltSrb, InWltHrb** [kg DOM/plot/month]).

For the outgoing material, each litter class has its own decomposition coefficient. Furthermore, it is assumed that by fire 50% of the litterclass-1 and dead-wood material is removed, whereas litterclass-2 and 3 are unaffected. Other assumptions on the effects of fire on the amount of litter and deadwood can, however, also be formulated and their long-term impact evaluated.

$$\begin{aligned}
OutWlt_{L1} &= \begin{cases} CDcmLt_{L1} \cdot Wlt_{L1} + \\ 0.5 \cdot Wlt_{L1} & , IsFrHl \end{cases} \\
OutWlt_{L2} &= CDcmLt_{L2} \cdot Wlt_{L2} \\
OutWlt_{L3} &= CDcmLt_{L3} \cdot Wlt_{L3} \\
OutWdw &= \begin{cases} CDcmDw \cdot Wdw + \\ 0.5 \cdot Wdw & , IsFrHl \end{cases}
\end{aligned} \tag{156}$$

(CDcmLt)

Incoming material in litter layer 1 includes the rapidly decomposing material of trees, shrubs and herbs. Thus excluding stems of shrubs and trees in the shrub- and tree layer.

$$\begin{aligned}
InWltTr_{Lt1} &= \sum_{il,t} \left( \begin{aligned} & \left\{ \begin{aligned} & \text{from herb layer :} \\ & (WflTr_{il,t} + WbrTr_{il,t} + WstTr_{il,t} + WrtTr_{il,t} + WrsTr_{il,t}) \cdot \\ & \min(NTr_{il,t}, NMrtThnTr_{il,t} + NMrtRDbhTr_{il,t} + NMrtAge_{il,t}) + \\ & (TWflTr_{il,t} + TWbrTr_{il,t} + TWrtTr_{il,t}) \cdot (NTr_{il,t} - NMrtTr_{il,t}) \end{aligned} \right. \\ & + \\ & \left\{ \begin{aligned} & \text{from tree – and shrub layer :} \\ & (WflTr_{il,t} + WbrTr_{il,t} + WrtTr_{il,t} + WrsTr_{il,t}) \cdot \\ & \min(NTr_{il,t}, NMrtThnTr_{il,t} + NMrtRDbhTr_{il,t} + NMrtAgeTr_{il,t}) + \\ & (TWflTr_{il,t} + TWbrTr_{il,t} + TWrtTr_{il,t}) \cdot (NTr_{il,t} - NMrtTr_{il,t}) \end{aligned} \right. \end{aligned} \right) \\
InWltSrb_{Lt1} &= \sum_{sl,s} \left( \begin{aligned} & \left\{ \begin{aligned} & \text{from herb layer :} \\ & (WflSrb_{sl,s} + WbrSrb_{sl,s} + WstSrb_{sl,s} + WrtSrb_{sl,s} + WrsSrb_{sl,s}) \cdot \\ & \min(NSrb_{sl,s}, NMrtThnSrb_{sl,s} + NMrtRDbhSrb_{sl,s} + NMrtAgeSrb_{sl,s}) + \\ & (TWflSrb_{sl,s} + TWbrSrb_{sl,s} + TWrtSrb_{sl,s}) \cdot (NSrb_{sl,s} - NMrtSrb_{sl,s}) \end{aligned} \right. \\ & + \\ & \left\{ \begin{aligned} & \text{from shrub layer :} \\ & (WflSrb_{sl,s} + WbrSrb_{sl,s} + WrtSrb_{sl,s} + WrsSrb_{sl,s}) \cdot \\ & \min(NSrb_{sl,s}, NMrtThnSrb_{sl,s} + NMrtRDbhSrb_{sl,s} + NMrtAgeSrb_{sl,s}) + \\ & (TWflSrb_{sl,s} + TWbrSrb_{sl,s} + TWrtSrb_{sl,s}) \cdot (NSrb_{sl,s} - NMrtSrb_{sl,s}) \end{aligned} \right. \end{aligned} \right) \quad (157) \\
InWltHrb_{Lt1} &= \sum_{hl,h} \left( \begin{aligned} & (WflHrb_{hl,h} + WbrHrb_{hl,h} + WstHrb_{hl,h} + WrtHrb_{hl,h} + WrsHrb_{hl,h}) \cdot \\ & \min(NHrb_{hl,h}, NMrtThnHrb_{hl,h} + NMrtAgeHrb_{hl,h}) + \\ & (TWflHrb_{hl,h} + TWbrHrb_{hl,h} + TWrtHrb_{hl,h}) \cdot (NHrb_{hl,h} - NMrtHrb_{hl,h}) \end{aligned} \right) \\
InWlt_{Lt1} &= InWltTr_{Lt1} + InWltSrb_{Lt1} + InWltHrb_{Lt1} \quad (158)
\end{aligned}$$

Incoming material in litter layer 2 includes the stems of shrubs and trees in the shrub layer.

$$InWltTr_{Lt2} = \sum_{il,t} \left( \begin{array}{l} \text{from shrub layer :} \\ (WhwTr_{il,t} + WswTr_{il,t}) \cdot \\ \min(NTr_{il,t}, NMrtThnTr_{il,t} + NMrtRDbhTr_{il,t} + NMrtAgeTr_{il,t}) \end{array} \right) \quad (159)$$

$$InWltSrb_{Lt2} = \sum_{sl,s} \left( \begin{array}{l} \text{from shrub layer :} \\ (WhwSrb_{sl,s} + WswSrb_{sl,s}) \cdot \\ \min(NSrb_{sl,s}, NMrtThnSrb_{sl,s} + NMrtRDbhSrb_{sl,s} + NMrtAgeSrb_{sl,s}) \end{array} \right)$$

$$InWlt_{Lt2} = \begin{cases} InWltTr_{Lt2} + InWltSrb_{Lt2} + OutWlt_{Lt1} - \\ 0.5 \cdot Wlt_{Lt2} \end{cases} , IsFrHl \quad (160)$$

Incoming material in litter layer 3 includes the decomposed material from the second litter class and the dead wood pool.

$$InWlt_{Lt3} = \begin{cases} OutWlt_{Lt2} + OutWdw - \\ 0.5 \cdot Wdw \end{cases} , IsFrHl \quad (161)$$

Incoming material in dead wood pool includes the stems of trees from the tree layer.

$$InWdw = \sum_{il,t} \left( \begin{array}{l} \text{from tree layer :} \\ (WhwTr_{il,t} + WswTr_{il,t}) \cdot \\ \min(NTr_{il,t}, NMrtThnTr_{il,t} + NMrtRDbhTr_{il,t} + NMrtAgeTr_{il,t}) \end{array} \right) , IsFrHl \wedge \quad (162)$$

$$0.5 \cdot FldTl \quad FlmHl > MnBseCnSl \wedge$$

$$FlmSl > MnBseCnTl$$



## 5 Integration

### 5.1 Herbivores

#### 5.1.1 Weight

Weight of herbivore per age group (adults, juveniles) ( $WghPerGroup$  [kg/population]) is the biomass of the entire population.

For adults the weight of the next time step ( $t+1$ ) is based on:

- (1) the old weight plus the rate of change in weight (Eqn.(87))
- (2) the weight of the juveniles entering the adult cohort at the end of pregnancy (1-year after birth)
- (3) the loss of weight due to mortality of individual animals (Eqn. (82))

For juveniles the new weight is based on:

- (1) the number of new born, and their initial birth weight
- (2) the old weight plus the rate of change in weight (Eqn.(87))
- (3) the loss of weight of the juveniles entering the adult cohort at the end of pregnancy (1-year after birth)
- (4) the loss of weight due to mortality of individual animals (Eqn. (82))

$$\begin{aligned}
 WghPerGroup_{b,Ad}(t+1) &= WghPerGroup_{b,Ad}(t) + RWgh_{b,Ad}(t) \\
 &\quad + WghPerGroup_{b,Jv}(t) \quad , Mnt = CEndPrg_b \\
 &\quad - NMrt_{b,Ad}(t) \cdot WghInd_{b,Ad}(t) \\
 WghPerGroup_{b,Jv}(t+1) &= CBrtWghIndJv_b \cdot NBrt_b(t) \quad (163) \\
 &\quad + WghPerGroup_{b,Jv}(t) + RWgh_{b,Jv}(t) \\
 &\quad - WghPerGroup_{b,Jv}(t) \quad , Mnt = CEndPrg_b \\
 &\quad - NMrt_{b,Jv}(t) \cdot WghInd_{b,Jv}(t) \\
 &\quad (CBrtWghIndJv, CEndPrg)
 \end{aligned}$$

#### 5.1.2 Number

##### *per age class*

The number of adult animals per age class of the next time step ( $NPerAge$  [#/population]) is the number of animals present in a given age reduced by mortality. Mortality (Eqn. (82)) is applied from the maximum age of the species downward to younger age classes until all dead animals are accounted for. The annual shift in age classes occurs at the end of pregnancy. At that moment, the juveniles become the adults of the second-year age class.

$$\begin{aligned}
NPerAge_{b,a}(t+1) &= NPerAge_{b,a}(t) - NMrt_{b,Ad}(t) \\
&\quad - NPerAge_{b,a}(t) + NPerAge_{b,a-1}(t), Mnt = CEndPrg_b \\
NPerAge_{b,2}(t+1) &= NPerAge_{b,2}(t) - NMrt_{b,Ad}(t)(remaining) \\
&\quad - NPerAge_{b,2}(t) + NPerGroup_{b,Jv}(t), Mnt = CEndPrg_b
\end{aligned} \tag{164}$$

(CEndPrg)

### **per group**

The number of adult animals per group class of the next time step (NPerGroup [#/population]) are the number of adults and juveniles. All individuals of a group have the same weight. For adults the number per group is the sum over age classes. For juveniles it is the number of juveniles reduced by mortality. At the end of pregnancy, it is the number of newborn.

$$NPerGroup_{b,Ad}(t+1) = \sum_{a=2}^{a=Mx} NPerAge_{b,a}(t+1) \tag{165}$$

$$NPerGroup_{b,Jv}(t+1) = \begin{cases} NPerGroup_{b,Jv}(t+1) - NMrt_{b,Jv}(t+1) \\ NBr_t(t+1) \end{cases}, Mnt = CEndPrg_b \tag{166}$$

## **5.1.3 Number of reproducing herbivores**

Not all age classes are reproducing. Reproduction starts at a given age and ends before the maximum age, depending on the species. Whether a given age class reproduces is indicated by Rpr [0,1]. Thus, the number of reproducing herbivores (NRpr [#/population]) Is the sum of the product of Rpr times the number of adults per age class.

$$NRpr_b(t+1) = \sum_a Rpr_{b,a} \cdot NPerAge_{b,a}(t+1) \tag{167}$$

## **5.2 Plants**

### **5.2.1 Number**

The number of trees, shrubs and herbs of the next time step (NTr,NSrb, NHrb [#plot]), is the number present reduced by mortality (Eqn. (102)). Subsequently, the number of individuals per species group and layer (NTrPerLayer, NSrbPerlayer, NHrbPerLayer, Eqn. (28)) are derived, as well as the total of trees, shrubs and herbs per layer (NTI, NSI, NHI Eqn. (29)).

$$\begin{aligned}
NTr_{il,t}(t+1) &= NTr_{il,t}(t) - NMrtTr_{il,t}(t) \\
NSrb_{sl,s}(t+1) &= NSrb_{sl,s}(t) - NMrtSrb_{sl,s}(t) \\
NHrb_{hl,s}(t+1) &= NHrb_{hl,s}(t) - NMrtHrb_{hl,s}(t)
\end{aligned}
\tag{168}$$

### 5.2.2 Weight of foliage

The weight of foliage of trees, shrubs and herbs for the next time step (**WflTr, WflSrb, WflHrb** [kg DM/individual]) is the current weight of foliage increased by the growth of foliage (Eqn. (136)) and reduced by both turnover (Eqn. (147)) and grazing (Eqn. (73)).

$$\begin{aligned}
WflTr_{il,t}(t+1) &= WflTr_{il,t}(t) + GWflTr_{il,t}(t) - TWflTr_{il,t}(t) - GrzWflTr_{il,t}(t) \\
WflSrb_{sl,s}(t+1) &= WflSrb_{sl,s}(t) + GWflSrb_{sl,s}(t) - TWflSrb_{sl,s}(t) - GrzWflSrb_{sl,s}(t) \\
WflHrb_{hl,s}(t+1) &= WflHrb_{hl,s}(t) + GWflHrb_{hl,s}(t) - TWflHrb_{hl,s}(t) - GrzWflHrb_{hl,s}(t)
\end{aligned}
\tag{169}$$

### 5.2.3 Weight of branches

The weight of branches of trees, shrubs and herbs for the next time step (**WbrTr, WbrSrb, WbrHrb** [kg DM/individual]) is the current weight of branches increased by the growth of branches (Eqn.(141)) and reduced by both turnover (Eqn.(148)) and grazing (Eqn.(74)).

$$\begin{aligned}
WbrTr_{il,t}(t+1) &= WbrTr_{il,t}(t) + GWbrTr_{il,t}(t) - TWbrTr_{il,t}(t) - GrzWbrTr_{il,t}(t) \\
WbrSrb_{sl,s}(t+1) &= WbrSrb_{sl,s}(t) + GWbrSrb_{sl,s}(t) - TWbrSrb_{sl,s}(t) - GrzWbrSrb_{sl,s}(t) \\
WbrHrb_{hl,s}(t+1) &= WbrHrb_{hl,s}(t) + GWbrHrb_{hl,s}(t) - TWbrHrb_{hl,s}(t) - GrzWbrHrb_{hl,s}(t)
\end{aligned}
\tag{170}$$

#### ***weight of new branches***

The weight of new branches of trees, shrubs and herbs for the next time step (**WnwbrTr, WnwbrSrb, WnwbrHrb** [kg DM/individual]) is the calculated similarly to that of branches, however, it is reset each year at the begin of the growing season.

$$\begin{aligned}
WnwbrTr_{il,t}(t+1) &= WnwbrTr_{il,t}(t) + GWnwbrTr_{il,t}(t) - TWnwbrTr_{il,t}(t) - GrzWnwbrTr_{il,t}(t) \\
WnwbrSrb_{sl,s}(t+1) &= WnwbrSrb_{sl,s}(t) + GWnwbrSrb_{sl,s}(t) - TWnwbrSrb_{sl,s}(t) - GrzWnwbrSrb_{sl,s}(t) \\
WnwbrHrb_{hl,s}(t+1) &= WnwbrHrb_{hl,s}(t) + GWnwbrHrb_{hl,s}(t) - TWnwbrHrb_{hl,s}(t) - GrzWnwbrHrb_{hl,s}(t)
\end{aligned}
\tag{171}$$

### 5.2.4 Weight of sapwood

The weight of sapwood of trees and shrubs for the next time step (**WswTr, WswSrb** [kg DM/individual]) is the current weight of sapwood increased by the growth of sapwood (Eqn.(143)) and reduced by turnover into heartwood (Eqn. (144)).

$$\begin{aligned}
W_{sw}Tr_{il,t}(t+1) &= W_{sw}Tr_{il,t}(t) + GW_{sw}Tr_{il,t}(t) - GWhwTr_{il,t}(t) \\
W_{sw}Srb_{sl,s}(t+1) &= W_{sw}Srb_{sl,s}(t) + GW_{sw}Srb_{sl,s}(t) - GWhwSrb_{sl,s}(t)
\end{aligned} \tag{172}$$

### 5.2.5 Weight of heartwood

The weight of heartwood of trees and shrubs for the next time step (**WhwTr, WhwSrb** [kg DM/individual]) is the current weight of heartwood increased by the growth of heartwood (Eqn.(144)).

$$\begin{aligned}
WhwTr_{il,t}(t+1) &= WhwTr_{il,t}(t) + GWhwTr_{il,t}(t) \\
WhwSrb_{sl,s}(t+1) &= WhwSrb_{sl,s}(t) + GWhwSrb_{sl,s}(t)
\end{aligned} \tag{173}$$

### 5.2.6 Weight of stem

The weight of the stem of trees and shrubs for the next time step (**WstTr, WstSrb** [kg DM/individual]) is the sum of the sapwood and heartwood of this time step. The weight of the stalk of herbs for the next time step (**WstHrb** [kg DM/individual]) is the current weight of the stalks increased by the growth of the stalks (Eqn. (145)) and reduced by the turnover (Eqn. (149)).

$$WstTr_{il,t}(t+1) = W_{sw}Tr_{il,t}(t+1) + WhwTr_{il,t}(t+1) \tag{174}$$

$$WstSrb_{sl,s}(t+1) = W_{sw}Srb_{sl,s}(t+1) + WhwSrb_{sl,s}(t+1)$$

$$WstHrb_{hl,s}(t+1) = WstHrb_{hl,s}(t) + GWstHrb_{hl,s}(t) - TWstHrb_{hl,s}(t) \tag{175}$$

### 5.2.7 Weight of roots

The weight of roots of trees, shrubs and herbs for the next time step (**WrtTr, WrtSrb, WrtHrb** [kg DM/individual]) is the current weight of roots increased by the growth of roots (Eqn.(146)) and reduced by turnover (Eqn.(150)). In case of herbs the weight of roots can also be reduced by grazing (Eqn.(74)).

$$WrtTr_{il,t}(t+1) = WrtTr_{il,t}(t) + GWrtTr_{il,t}(t) - TWrtTr_{il,t}(t) \tag{176}$$

$$WrtSrb_{sl,s}(t+1) = WrtSrb_{sl,s}(t) + GWrtSrb_{sl,s}(t) - TWrtSrb_{sl,s}(t)$$

$$WrtHrb_{hl,s}(t+1) = WrtHrb_{hl,h}(t) + GWrtHrb_{hl,s}(t) - TWrtHrb_{hl,h}(t) - GrzWrtHrb_{hl,h}(t)$$

### 5.2.8 Weight of reserves

The weight of reserves of trees, shrubs and herbs for the next time step (**WrsTr, WrsSrb, WrsHrb** [kg DM/individual]) is the current weight of roots increased by the growth of reserves (Eqn.(127)).

It is assumed that there is neither turnover of reserves nor loss by grazing.



$$\begin{aligned}
WrsTr_{il,t}(t+1) &= WrsTr_{il,t}(t) + GWrsTr_{il,t}(t) \\
WrsSrb_{sl,s}(t+1) &= WrsSrb_{sl,s}(t) + GWrsSrb_{sl,s}(t) \\
WrsHrb_{hl,h}(t+1) &= WrsHrb_{hl,h}(t) + GWrsHrb_{hl,h}(t)
\end{aligned} \tag{177}$$

### 5.2.9 Number of seeds

The number of seeds from trees, shrubs and herbs in the next time step (**NsdTr**, **NsdSrb**, **NsdHrb** [# / plot]) is the current number increased by the incoming seeds by dispersion (Eqn. (154)) and decreased by turnover (Eqn. (155)) and germination (Eqn. (152)). In case of large seeds from trees, *i.e.* acorns and beechnuts, there is also a reduction due to grazing (Eqn. (72)).

$$\begin{aligned}
NsdTr_t(t+1) &= NsdTr_t(t) + RNsdDspTr_t(t) - TNsdTr_t(t) - NGrmTr_t(t) - \frac{GrzSdTr_t(t)}{CWsdTr_t} \\
NsdSrb_s(t+1) &= NsdSrb_s(t) + RNsdDspSrb_s(t) - TNsdSrb_s(t) - NGrmSrb_s(t) \\
NsdHrb_h(t+1) &= NsdHrb_h(t) + RNsdDspHrb_h(t) - TNsdHrb_h(t) - NGrmHrb_h(t)
\end{aligned} \tag{178}$$

(CWsdTr)

### 5.2.10 Height

The height in the next time step of individual trees, shrubs and herbs (**HghTrPerLayer**, **HghSrbPerLayer**, **HghHrbPerLayer** [m]) is the current height increased by the rate of height growth (Eqn. (104)) and can be reduced by grazing (Eqn. (88)). The reduction in height by grazing occurs if the top of the plant is less than the maximum height of grazing of the herbivore(s) visiting the plot (Eqn. (90)). Hence, it is never applied to trees in the tree layer. The height is constrained by the minimum height of grazing (Eqn. (89)) and the maximum height of the species on the given soil type.

$$\begin{aligned}
HghTrPerLayer_{TrHL,t}(t+1) &= HghTrPerLayer_{TrHL,t}(t) + RHghTr_{TrHL,t}(t) - RdcLngCnGrzTr_{TrHL,t}(t) \\
HghTrPerLayer_{TrSL,t}(t+1) &= HghTrPerLayer_{TrSL,t}(t) + RHghTr_{TrSL,t}(t) - RdcLngCnGrzTr_{TrSL,t}(t) \\
HghTrPerLayer_{TrTL,t}(t+1) &= HghTrPerLayer_{TrTL,t}(t) + RHghTr_{TrTL,t}(t) \\
HghSrbPerLayer_{SrbHL,s}(t+1) &= HghSrbPerLayer_{SrbHL,s}(t) + RHghSrb_{SrbHL,s}(t) - RdcLngCnGrzSrb_{SrbHL,s}(t) \\
HghSrbPerLayer_{SrbSL,s}(t+1) &= HghSrbPerLayer_{SrbSL,s}(t) + RHghSrb_{SrbSL,s}(t) - RdcLngCnGrzSrb_{SrbSL,s}(t) \\
HghHrbPerLayer_{HrbHL,h}(t+1) &= HghHrbPerLayer_{HrbHL,h}(t) + RHghHrb_{HrbHL,h}(t) - RdcLngCnGrzHrb_{HrbHL,h}(t)
\end{aligned} \tag{179}$$

### 5.2.11 Crown base

The crown base in the next time step of individual trees, shrubs and herbs (**BseCnTr**, **BseCnSrb**, **BseCnHrb** [m]) is the current crown based increased by the rate of increase of the crown base (Eqn. (105)) and can be increased by grazing (Eqn. (88)). The increase in crown base due to by grazing occurs if the top of the plant is exceeds

the maximum height of grazing of the herbivore(s) visiting the plot (Eqn. (90) and the current crown base is less than this value. Hence, it is never applied to trees in the herb layer. The crown base is constrained by zero (ground level) and the actual height of the plant.

Thus, the reduction of the length of the crown by grazing is applied either on the plants' height or on the plants' crown base

$$\begin{aligned}
 BseCnTr_{TrHL,t}(t+1) &= BseCnTr_{TrHL,t}(t) + RBseCnTr_{TrHL,t}(t) \\
 BseCnTr_{TrSL,t}(t+1) &= BseCnTr_{TrSL,t}(t) + RBseCnTr_{TrSL,t}(t) + RdcLngCnGrzTr_{TrSL,t}(t) \\
 BseCnTr_{TrTL,t}(t+1) &= BseCnTr_{TrTL,t}(t) + RBseCnTr_{TrTL,t}(t) + RdcLngCnGrzTr_{TrTL,t}(t) \\
 BseCnSrb_{SrbHL,s}(t+1) &= BseCnSrb_{SrbHL,s}(t) + RBseCnSrb_{SrbHL,s}(t) \\
 BseCnSrb_{SrbSL,s}(t+1) &= BseCnSrb_{SrbSL,s}(t) + RBseCnSrb_{SrbSL,s}(t) + RdcLngCnGrzSrb_{SrbSL,s}(t) \\
 BseCnHrb_{HrbHL,h}(t+1) &= BseCnHrb_{HrbHL,h}(t) + RBseCnHrb_{HrbHL,h}(t)
 \end{aligned} \tag{180}$$

### 5.2.12 Radius of the crown

The radius of the crown of trees, shrubs and herbs in the next time step (**RdsTr**, **RdsSrb**, **RdsHrb** [m]) is the current radius increased with the rate of change of the radius (Eqn. (131)).

$$\begin{aligned}
 RdsTr_{tl,t}(t+1) &= RdsTr_{tl,t}(t) + RRdsTr_{tl,t}(t) \\
 RdsSrb_{sl,s}(t+1) &= RdsSrb_{sl,s}(t) + RRdsSrb_{sl,s}(t) \\
 RdsHrb_{hl,h}(t+1) &= RdsHrb_{hl,h}(t) + RRdsHrb_{hl,h}(t)
 \end{aligned} \tag{181}$$

### 5.2.13 Litter

The weight of litter per litter layer, and dead wood in the next time step (**Wlt**, **Wdw** [kg DM/plot]) is the current weight increase with in incoming flux of litter and dead wood (Eqn. (158),(160),(161),(162)) and reduced by the outgoing flux (Eqn. (156)).

$$\begin{aligned}
 Wlt_l(t+1) &= Wlt_l(t) + InWlt_l(t) - OutWlt_l(t) \\
 Wdw(t+1) &= Wdw(t) + InWdw(t) - OutWdw(t)
 \end{aligned} \tag{182}$$

### 5.2.14 Shifts from one layer to the other

A shift of a cohort of a plant species occurs if cover for the same species in the higher layer equals zero *and* the height attains the maximum height of the current layer. If these conditions are met then all state variables are attributed to the cohort of the species of the higher layer and the state variables of the layer that is left are reset to zero. The state variables include: biomass of foliage, branches, sapwood and heartwood for trees and shrubs and of stems for herbs, roots and reserves; radius of the crown; height; age; number of individuals; crown base and length (Table 11).

### 5.2.15 Germination

In case of germination in the herb layer of the plot (Eqn. (151)), then for the newly established individuals are initialised based on the following rules:

- (1) the age is set at zero
  - (2) the height is set at the initial height ( $C_{IniHgh}$ )
  - (3) the initial crown base is set at zero. Hence, the initial crown length equals the height
  - (4) the crown radius is initialised at the initial crown radius ( $C_{IniRds}$ )
  - (5) the initial cover per layer is calculated based on crown radius and number of germinated seeds
  - (6) the new numbers are accounted for, and the new number of individuals per layer are calculated (Eqn. (27))
  - (7) the weight of plants components are initialised according to Eqn. (8) to Eqn. (22)
- For herbs, also germination in a plot is possible that is already occupied with individuals of the same species. If germination conditions are suitable, then the state variables of that species is updated based proportionally to the initial conditions and the relative contribution of the newly established seedlings.



## 6 Derived variables

Derived variables are variables that can be calculated based on other state variables, while the state variables are independent from the derived variables. *E.g.* crown length is a derived variable from height and crown base, and accumulated plot biomass depends on the biomass of the individuals on the plot. In the following the calculations required for all derived variables are explained

### 6.1 Herbivores

There are no derived variables for herbivores.

### 6.2 Plants

#### 6.2.1 Age

The age of a cohort of trees and shrubs ( $Age_{Tr}$ ,  $Age_{Srb}$  [year]) is increased by one at the beginning of the growing season. The initial age is based on the plant's height (Eqn. (7)).

#### 6.2.2 Numbers

The number of individuals per species group and layer ( $N_{TrPerLayer}$ ,  $N_{SrbPerLayer}$ ,  $N_{HrbPerLayer}$  [# / plot] Eqn. (28)) are derived from the number of trees, shrubs and herbs ( $N_{Tr}$ ,  $N_{Srb}$ ,  $N_{Hrb}$  [# / plot]), as well as the total of trees, shrubs and herbs per layer ( $N_{TI}$ ,  $N_{SI}$ ,  $N_{HI}$  [# / plot] Eqn. (29))

#### 6.2.3 Average weight

The average individual weight of an individual plant in a given layer ( $AvrWgh_{IndTI}$ ,  $AvrWgh_{IndSrb}$ ,  $AvrWgh_{IndHrb}$  [kg / individual]) is calculated from the total weight accumulated over all plants ( $Wgh_{TI}$ ,  $Wgh_{SI}$ ,  $Wgh_{HI}$  [kg / plot]) and the total number of plants per layer ( $N_{TI}$ ,  $N_{SI}$ ,  $N_{HI}$  [# / plot]).

#### 6.2.4 Maximum number

The maximum number of individuals ( $MxN_{TI}$ ,  $MxN_{SI}$ ,  $MxN_{HI}$  [# / plot]) is based on the self-thinning rule Eqn. (94).

### 6.2.5 Coverage

The coverage of trees, shrubs and herbs per layer (**CvrTrPerLayer**, **CvrSrbPerLayer**, **CvrHrbPerLayer** [fraction]) is calculated based on the radius of the crown and the number of individuals per plot. The cumulative cover over all plants (trees plus shrubs plus herbs) is subsequently calculated (**CvrTl**, **CvrSl**, **CvrHl**).

$$\begin{aligned}
 CvrTrPerLayer_{it,t} &= \pi \cdot RdsTr_{it,t}^2 \cdot \frac{NTr_{it,t}}{PlotSize} \\
 CvrSrbPerLayer_{sl,s} &= \pi \cdot RdsSrb_{sl,s}^2 \cdot \frac{NSrb_{sl,s}}{PlotSize} \\
 CvrHrbPerLayer_{hl,h} &= \pi \cdot RdsHrb_{hl,h} \cdot \frac{NHrb_{hl,h}}{PlotSize}
 \end{aligned} \tag{183}$$

### 6.2.6 Maximum height

**MxHghTl**, **MxHghSl** and **MxHghHl** [m] indicate the maximum plant heights of a plot.

### 6.2.7 Minimal crown base

The minimum crown base (**MnBseCnTr**, **MnBseCnSrb** [m]) is the lowest crown base of any individual in either the tree- or shrub layer

### 6.2.8 Crown length

The length of a crown (**LngCnHrb**, **LngCnSrb**, **LngCnTr** [m]) is the difference between the height and the crown base.

### 6.2.9 Annual net primary production

Annual net primary production (**ANppTr**, **ANppSrb**, **ANppHrb** [kg DM/individual/month]) is the annual accumulated net primary production per individual and layer (Eqn. (125)).

$$\begin{aligned}
 ANppTr_{it,t} &= \sum_{Mnt=1}^{Mnt=12} NppTr_{it,t} \\
 ANppSrb_{sl,s} &= \sum_{Mnt=1}^{Mnt=12} NppSrb_{sl,s} \\
 ANppHrb_{sl,s} &= \sum_{Mnt=1}^{Mnt=12} NppHrb_{hl,h}
 \end{aligned} \tag{184}$$

### 6.2.10 Total annual net primary production

Total annual net primary production ( $TotANppTr$ ,  $TotANppSrb$ ,  $TotANppHrb$  [kg DM/plot/month]) is the annual accumulated net primary production of all individuals per layer.

$$\begin{aligned} TotANppTr_{it,t} &= \sum_{Mnt=1}^{Mnt=12} NTr_{it,t} \cdot NppTr_{it,t} \\ ANppSrb_{st,s} &= \sum_{Mnt=1}^{Mnt=12} NSrb_{st,s} \cdot NppSrb_{st,s} \\ ANppHrb_{st,s} &= \sum_{Mnt=1}^{Mnt=12} NHrb_{ht,h} \cdot NppHrb_{ht,h} \end{aligned} \quad (185)$$

### 6.2.11 Maximum weight of reserves

The maximum weight of the reserves ( $MxWrsTr$ ,  $MxWrsSrb$ ,  $MxWrsHrb$  [kg DM/individual]) is the amount of dry matter that is required for flushing of new foliage in spring (Eqn. (34)).

### 6.2.12 Crown volume

The volume of the crown of an individual plant ( $VlmCnHrb$ ,  $VlmCnSrb$ ,  $VlmCnTr$  [m<sup>3</sup>]) is determined from the length and radius of the crown, assuming a cylindrical crown (Eqn. (38)).

### 6.2.13 Density of foliage

The density of the foliage of trees, shrubs and herbs ( $DnsFlTr$ ,  $DnsFlSrb$ ,  $DnsFlHrb$  [m<sup>2</sup> foliage/m<sup>3</sup> crown]), is the surface of foliage per volume of the crown (Eqn.(39)).

### 6.2.14 Leaf area index

The leaf area index [m<sup>2</sup> foliage / m<sup>2</sup> soil] is calculated per individual and layer ( $LaiTrPerLayer$ ,  $LaiSrbPerLayer$ ,  $LaiHrbPerLayer$  Eqn. (40)); per cohort and layer ( $LaiTr$ ,  $LaiSrb$ ,  $LaiHrb$  Eqn.(41)); per layer ( $LaiTl$ ,  $LaiSl$ ,  $LaiHl$  Eqn.(42) ) and per plot ( $TotLai$  Eqn. (43)).

### 6.2.15 Stem volume

The volume of the stem [m<sup>3</sup>] is calculated per individual and layer ( $VlmIndTr$ ,  $VlmIndSrb$  [m<sup>3</sup>/individual]) (Eqn. (23)) and per cohort and plot ( $VlmTr$ ,  $VlmSrb$  [m<sup>3</sup>/plot] Eqn. (30)). The annual rate of change of stem volume ( $AGVlmTr$ ,

**AGVImSrb** [m<sup>3</sup>/plot/year]) (*i.e.* current annual increment per plot). Is the annual cumulative of stem growth.

$$AGVImTr_{il,t} = \sum_1^{12} \frac{GW_{sw}Tr_{il,t}}{CDnsWdTr_{il,t}} \cdot NTr_{il,t}$$

$$AGVImSrb_{sl,s} = \sum_1^{12} \frac{GW_{sw}Srb_{sl,s}}{CDnsWdSrb_s} \cdot NSrb_{sl,s}$$
(186)

### 6.2.16 Basal area

The basal of trees and shrubs (**BslTr, BslSrb** [m<sup>2</sup>/plot]) is the area of the stems of all individuals of a plot (Eqn. (45)). The total basal area (**TotBslTr, TotBslSrb** [m<sup>2</sup>/plot]) is the basal area accumulated over all tree and shrub species and layers (Eqn. (46)), whereas **Bsl** is the total basal area over all woody plants present on a plot (Eqn. (47)).

### 6.2.17 Height of litter layers

The height of the litter layers (**HghLt** [m]) is determined from the weight of the litter and its density (Eqn. (48)).

### 6.2.18 Total weight

The total weight per plant component for herbs ([kg DM/plot]) is calculated from the 'number' of herbs per plot and their weight.

$$TotWfHrb_{hl,h} = NHrb_{hl,h} \cdot WfHrb_{hl,h}$$

$$TotWbrHrb_{hl,h} = NHrb_{hl,h} \cdot WbrHrb_{hl,h}$$

$$TotWnwbrHrb_{hl,h} = NHrb_{hl,h} \cdot WnwbrHrb_{hl,h}$$

$$TotWstHrb_{hl,h} = NHrb_{hl,h} \cdot WstHrb_{hl,h}$$

$$TotWrtHrb_{hl,h} = NHrb_{hl,h} \cdot WrtHrb_{hl,h}$$

$$TotWrsHrb_{hl,h} = NHrb_{hl,h} \cdot WrsHrb_{hl,h}$$
(187)

### 6.2.19 New 'number' of herbs

The 'number' of herb on a plot (**NHrb** [m<sup>2</sup>/plot]) is defined as the number of square metres a cohort occupies on a plot. For consistency with trees and shrubs, also the number of herbs per layer is calculated (cf. Eqn. (28)).

$$NHrb_{hl,h} = CvrHrbPerLayer_{hl,h} \cdot PlotSize$$
(188)

$$NHrbPerLayer_{hl} = \sum_h NHrb_{hl,h}$$
(189)



### 6.2.20 New weight of herbs

The weight of the plant components of herbs [kg DM/m<sup>2</sup>] is expressed per metre square. Thus, the weights must be the corrected based on the new 'number' of herbs.

$$\begin{aligned}WflHrb_{hl,h} &= TotWflHrb_{hl,h} / NHrb_{hl,h} \\WbrHrb_{hl,h} &= TotBrHrb_{hl,h} / NHrb_{hl,h} \\WnwbrHrb_{hl,h} &= TotWnwbrHrb_{hl,h} / NHrb_{hl,h} \\WstHrb_{hl,h} &= TotWstHrb_{hl,h} / NHrb_{hl,h} \\WrtHrb_{hl,h} &= TotWrtHrb_{hl,h} / NHrb_{hl,h} \\WrsHrb_{hl,h} &= TotWrsHrb_{hl,h} / NHrb_{hl,h}\end{aligned}\tag{190}$$

### 6.2.21 New radius of herbs

The radius of herbs (RdsHrb [m]) is calculated based on the coverage and the new 'number' of herbs.

$$RdsHrb_{hl,h} = \sqrt{\frac{CvrHrbPerLayer_{hl,h} \cdot PlotSize / NHrb_{hl,h}}{\pi}}\tag{191}$$



## 7 Fire

*Jelmer Dam, Koen Kramer & Janneke van Goethem*

Fire is an important aspect in forest dynamics. Although it is usually not directly controlled by a forest manager, there are strong interactions with the prevailing management regime such as the forestry practice and *e.g.* the occurrence of grazing by large herbivores.

In FORSPACE a relatively simple fire model is used. It includes the build-up of fuel load, the occurrence of a fire depending on the fuel load and other conditions, the rate of spread of fire within the plot, which determines the intensity of the fire. The fire intensity on its turn determines the height of the flame in the herb layer. The fire may be propagated vertically to the shrub and tree layer depending on the structure of the forest and the actual flame length. The impact of a fire on the vegetation includes the mortality of the plants and the removal of the burned vegetation. The fire may also be propagated horizontally to adjacent plots if there is sufficient fuel load in these plots. Here an outline of the approach is presented, whilst details can be found in Dam (1998) and Van Goethem (2000).

### 7.1 Fuel load

The built-up of fuel load in the herblayer is the total weight of stem and foliage of all plants occurring in the herb layer, weighted by the efficiency of combustion of the plant material. Also a half of the coarse litter layer (litter layer 1) and of the dead wood is considered as

$$\begin{aligned} FldTr_{hi} &= WstTr_{hi} \cdot NTr_{hi} \cdot CEffCmbWstTr + WflTr_{hi} \cdot NTr_{hi} \cdot CEffCmbWflTr \\ FldSrb_{hi} &= WstSrb_{hi} \cdot NSrb_{hi} \cdot CEffCmbWstSrb + WflSrb_{hi} \cdot NSrb_{hi} \cdot CEffCmbWflSrb \\ FldHrb_{hi} &= WstHrb_{hi} \cdot NHrb_{hi} \cdot CEffCmbWstHrb + WflHrb_{hi} \cdot NHrb_{hi} \cdot CEffCmbWflHrb \end{aligned} \quad (192)$$

$$Fld_{hi} = FldTr_{hi} + FldSrb_{hi} + FldHrb_{hi} + 0.5Wlt1 + 0.5Wdw \quad (193)$$

### 7.2 Occurrence

In FORSPACE, the ignition of a fire is a stochastic process, that can be set at a certain frequency. *E.g.* with a probability of 0.001 per plot per year. However, if an ignited plot actually burns also depends on a number of factors. The most important is if there is sufficient fuel load present to sustain the fire. Also the total cover of all plants in the herb layers should exceed a minimal value, and the period of the year should be such that a forest fire is likely.

### 7.3 Rate of spread

Rate of spread (RSpr, [m/min]) of a fire is the speed at which a fire moves through the forest. This is strongly affected by the wind speed. As windspeed is not an input variable in FORSPACE, a simple stochastic distribution of wind speed is considered, and can vary between 1 and 10 m s<sup>-1</sup>. In the Netherlands the average rate of spread is considered to lie between 0 and 15 m min<sup>-1</sup> (Dam, 1998). Three values of rate of spread are defined in the model: 5, 10 and 15 m min<sup>-1</sup>, based on:

$$\begin{aligned}
 RSpr &= 5, 0 \leq WindSpeed \leq 3 \\
 RSpr &= 5, 3 < WindSpeed \leq 6 \\
 RSpr &= 5, WindSpeed \geq 6
 \end{aligned}
 \tag{194}$$

### 7.4 Intensity

The intensity of the fire indicates how much heat is transferred by the burning material to its surroundings. Thereby affecting if these surroundings are burned themselves as well. The fire intensity is calculated based on the rate of spread of the fire, an intensity coefficient, the heat of combustion of the plant material, and the fuel load.

The heat of combustion is the heat released per unit mass by flaming combustion and is set at 18700 kJ kg<sup>-1</sup> (van Wagner, 1972, Albini, 1976). The intensity coefficient is set at 60 (Byram, 1959 in Johnson, 1992).

$$\begin{aligned}
 I_{HI} &= RSpr / (IC \cdot HComb \cdot Fld_{HI}) \\
 I_{SI} &= RSpr / (IC \cdot HComb \cdot (Fld_{HI} + Fld_{SI})) \\
 I_{TI} &= RSpr / (IC \cdot HComb \cdot (Fld_{HI} + Fld_{SI} + Fld_{TI}))
 \end{aligned}
 \tag{195}$$

### 7.5 Flame height

The height of the flame in the herb layer determines whether the fire is transferred to the shrub and tree layer of the forest. The height of the flame in the herb layer is based on the intensity of the fire and an operational flame coefficient. A fire is transferred from the herb to the above laying layers if the flame height reaches the base of the crown in either the shrub layer or tree layer.

$$\begin{aligned}
 Flm_{HI} &= I_{HI} / CFlm^{0.46} \\
 Flm_{SI} &= MxHgh_{SI}, Flm_{HI} > MnBseCn_{SI} \\
 Flm_{TI} &= MxHgh_{TI}, Flm_{SI} > MnBseCn_{TI}
 \end{aligned}
 \tag{196}$$

## 7.6 Mortality

The plants in the herb layer are considered to die completely if a fire occurs. A fraction of the trees and shrubs that have their crown in the shrub- or tree layer may die due to a fire in the herb layer. Some plant species are more sensitive to fire than other species. A larger percentage of the more sensitive species, *eg* beech, will be killed compared to species that are not so sensitive to fire, *eg* pine.

If the fire moves from the herb layer into the shrub layer the fire consumes all the plants in the shrub layer, and only a certain percentage of the trees with their crown in the treelayer are killed. If the fire is also transferred to the treelayer, then all trees die due to crown burning.

The effect of a fire on the vegetation is the removal of the plant material. A fraction of the stem is transferred into the dead wood pool for trees that are killed by the fire.

## 7.7 Burned area

The propagation of a fire over the landscape depends on the fuel load of the plots adjacent to the plot that burns. In PCRaster, a 'clump' is defined as adjacent plots, optionally including diagonally positioned plots, that meet certain similar characteristics. In this case, the clumping of plots is based on the fact whether they contain a fuel load exceeding the minimal value required for a forest fire.

A clump is considered the fire area if an ignition occurs in any plot within this clump. If this occurs, and the conditions are met (see section *Occurrence*) then the whole clump is set on fire.



## **8 Initialisation of a realistic landscape**

### **8.1 General**

The aim of this chapter is to show how actual initial values are determined of state variables for herbivores and plants. A critical issue for the initialisation of the vegetation at a landscape scale is that as little as possible information should be required to run the model. For FORSPACE this includes for plant species the initial cover and initial height per species and per plot only. All other state variables for plants are derived from these features, *i.e.* for woody plants expressed as characteristics per individual and for herbs per unit area (m<sup>2</sup>).

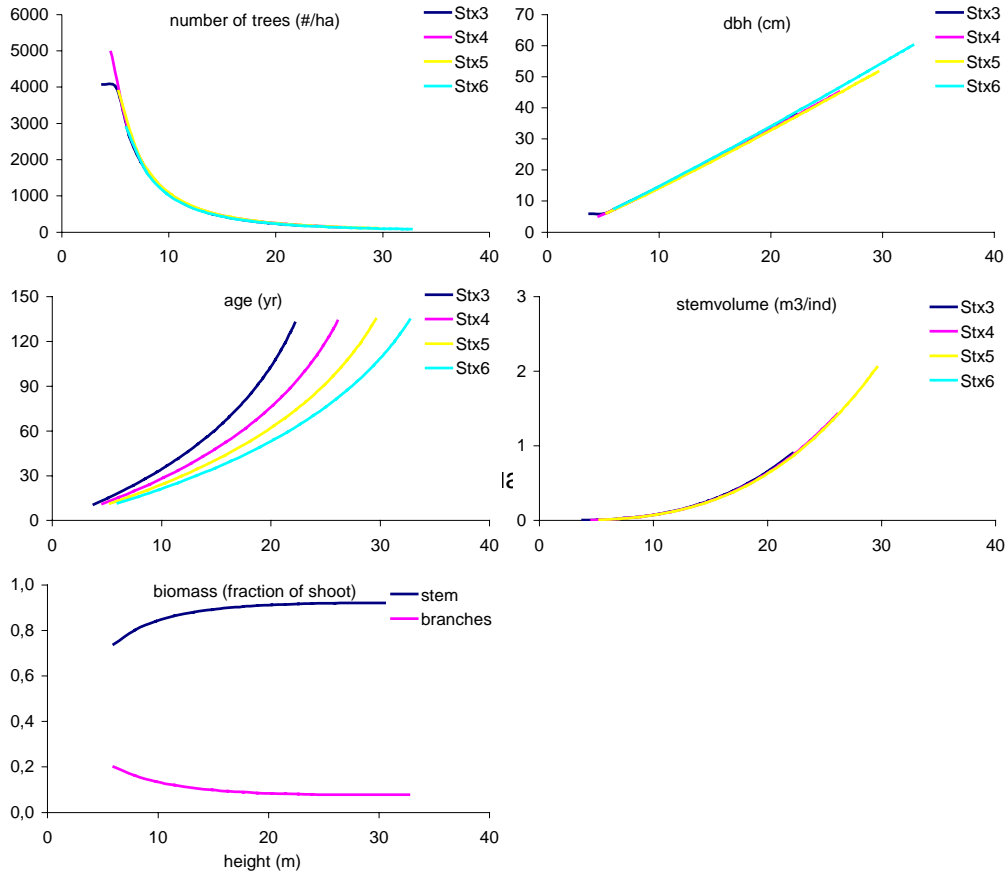
### **8.2 Herbivores**

The initialisation of the herbivores includes the number of adult animals in the research area only. The initial body weight is determined based on an average adult body-weight.

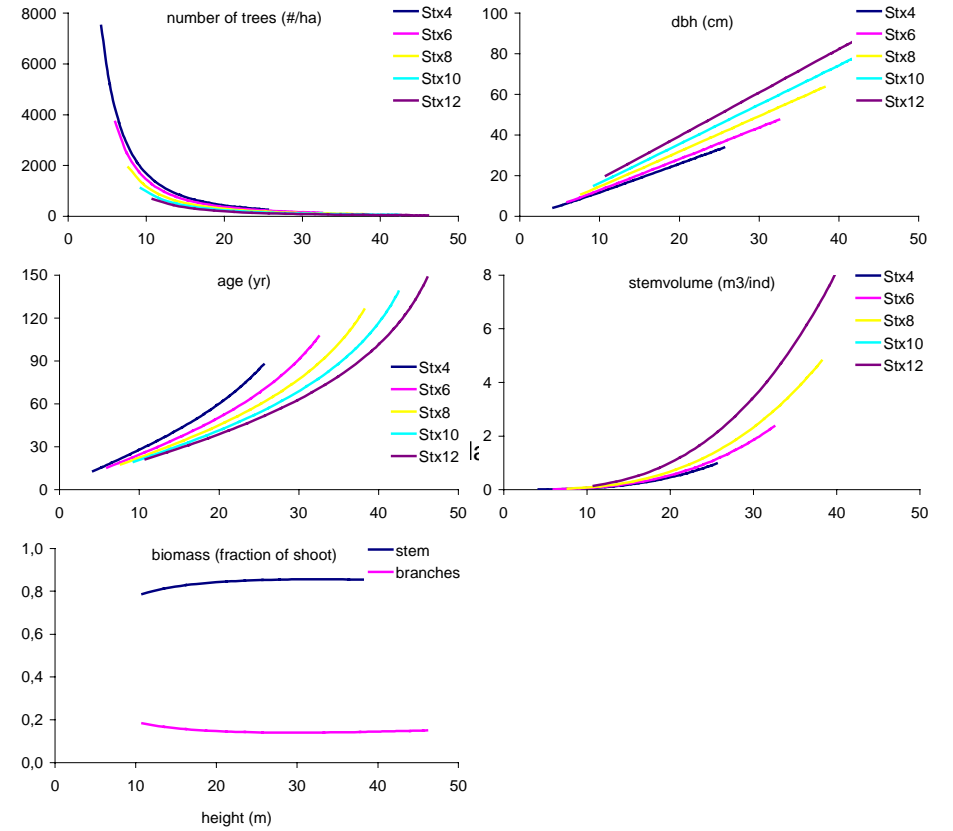
### **8.3 Woody species**

Initial simulation runs with FORSPACE showed that the output is very sensitive to initial values of the state variables. The characteristics of woody species that are initialized based on initial height and cover include: age (Eqn. (7)), number of trees (Eqn. (26)), dbh (Eqn. (24)) and stemvolume (Eqn. (23)). These features all depend on the site index of the plot. The biomass of tree components is determined by Eqn. (8) - (21). For both the initial weight of the branches and the stem, optimal ratios between these components and the above-ground dry-matter are assumed (Eqns. (15) and (17), respectively). For the roots a fixed ratio with shoot weight is used (Eqn. (21)). For the initial weight of the foliage an optimal foliage density is assumed (Eqn. (32)) based on the initial crown volume Eqn. (37). The latter is determined from the initial crown radius (Eqn. (31)) and crown length. The initial cover of a species in a plot reduces the number of trees only, not its physical dimensions.

### Betula initial values



### Fagus initial values





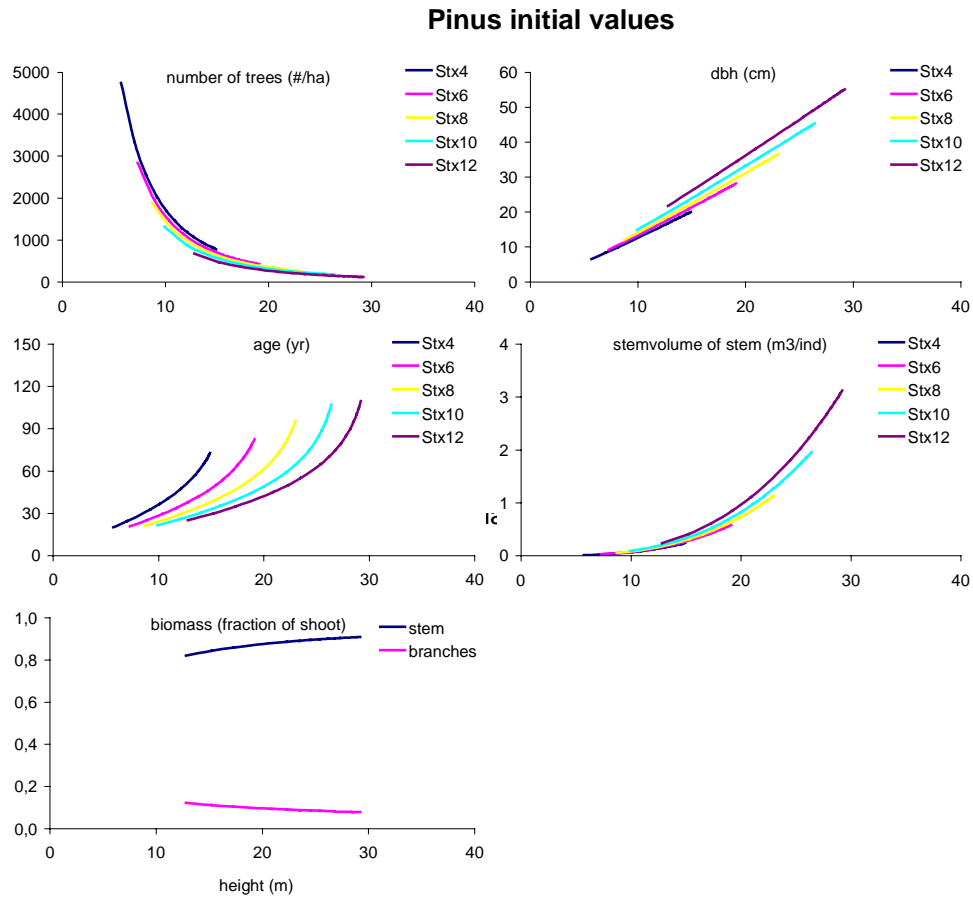


Figure 13: Initial values that are dependent on site index for pine of tree density, diameter at breast height (dbh), age, stem volume of individual tree, and the fraction of stem and branches of the shoot, as a function of tree height.

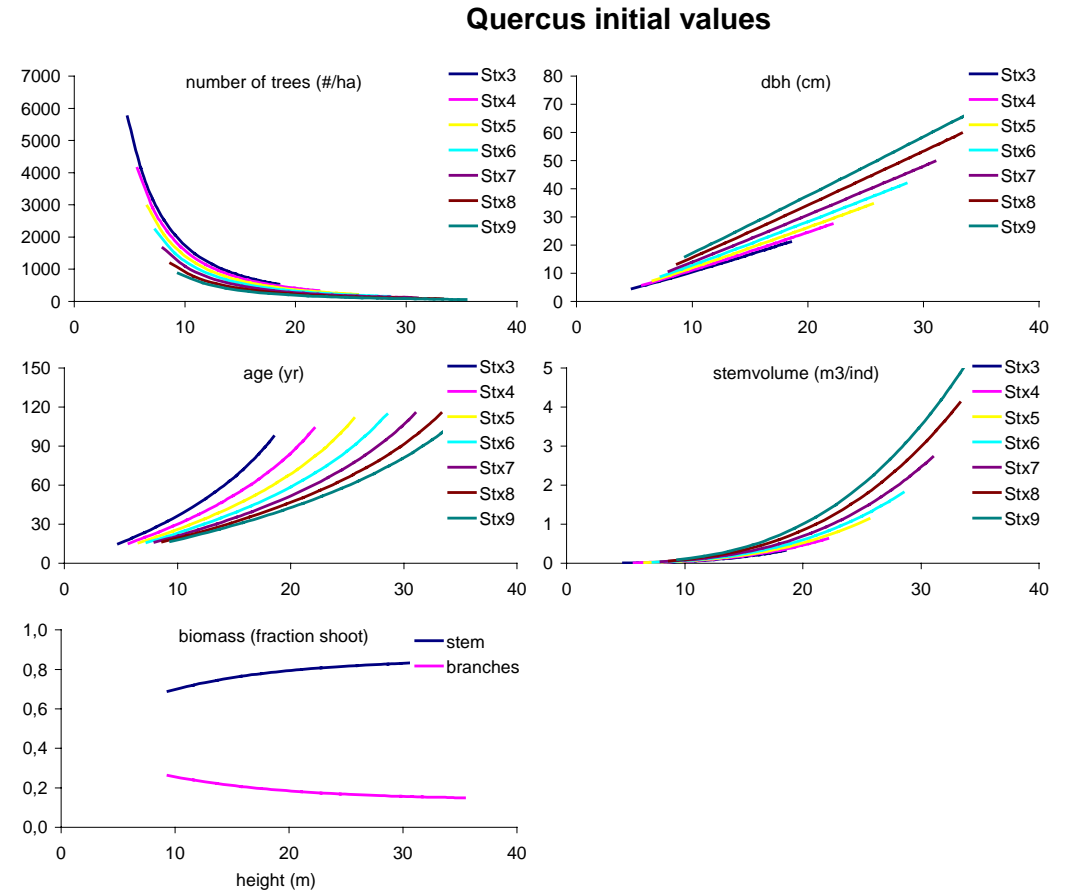


Figure 14: Initial values that are dependent on site index for oak of tree density, diameter at breast height, individual tree, and the fraction of stem and branches of the shoot, as a function of tree height.

The state variables that depend on the site index were calibrated based on the growth and yield tables presented in Jansen *et al.* (1996). These values closely match the data on which they are calibrated in all situations ( $r^2$  (individual stem volume) > 0.95). The calibration was done for all site indices that are presented in Jansen *et al.* (1996). There was an interpolation performed between the presented site indices, but no extrapolation was done outside the range of site indices of which data is available. For a given site index, a range from the growth and yield table was selected for the calibration. The selection of the range was based on the following criteria: the tree height should exceed 8 m (*i.e.* trees in the tree layer as defined in FORSPACE) and the tree density should be less than 5000 tree per hectare (for many tree species the upper limit in Jansen *et al.* (1996)). To avoid a too strong effect of the asymptotic value of the height to age relationship, the range was reduced such to attain the highest  $r^2$ . Also the values that are presented as uncertain in Jansen *et al.* (1996) were disregarded.

Figure I1-4 present for birch, beech, pine and oak the initial values that depend on the site index of the plot. It shows that with increasing tree height, there is an exponential decrease of tree density; an virtually linear increase of dbh; a lower age at which the maximum height is attained; and an exponential increase of stem volume. The general effect of site index on initial values of these state variables is that at a given tree height there are more, thinner and older trees at low site index (nutrient poor, dry soil) compared to a better site index. Furthermore, there are only small differences between site indices for the fraction of both stem and branches of the total above-ground biomass. Therefore the results of only 1 site index is presented in figures I1-4 (biomass, fraction of shoot) per species. More specifically, figure I1-4 show that for birch the differences between the sites indices are negligible for the initial number of trees, their dbh, and stemvolume. For beech, pine and oak there is a clear effect of site index on these tree characteristics.

## 8.4 Herbs

The initial values of the state variables of herbs and grasses include the biomass of the different plant components. For foliage an optimal density per  $m^2$  is assumed. Both the initial weight of the stalk or stems of the herbs depend on the optimal amount of foliage using fixed ratio's. The weight of the roots is considered to be the same as the weight of the stalks or stem. No figures are presented for the initial values for herbs.

## 9 Model dynamics

The aim of this chapter is to illustrate the dynamics of animals and plants and simulated by FORSPACE under different scenarios.

An example of the dynamics of the energy balance of red deer is presented for both a female adult and a juvenile, and its consequences for the individual body weight and the number of adults and juveniles in the red deer population.

For the model dynamics of trees, different tree composition and different soil conditions (arenosol and podsol) are evaluated. In the simulation runs we show results of monospecies stands (section *Monospecies*), of mixed stands (section *Mixed species*). In all situations we are dealing with 4 different tree species: *Betula spec*, *Fagus sylvatica*, *Pinus sylvestris*, *Quercus robur*. In the monospecies runs, a forest stand of a certain age is simulated, illustrating the growth of the stand and reduction in number of trees during the simulation period. In the simulation runs with two or more species present we aim to illustrate the competition between the species considered. At the start of the simulation all trees have the same height which makes the analysis of the results more transparent.

For the model dynamics of herbs and grasses (jointly referred to as herbs), the time evolution of the weight of the different plant organs and the change in cover is presented. Also how the change in cover of a species is affected both by the presence of other herb-species in the plot, and by the effect of light availability on the herb layer. The latter mimics the effect of the closure of an open patch in the forest on the herb vegetation.

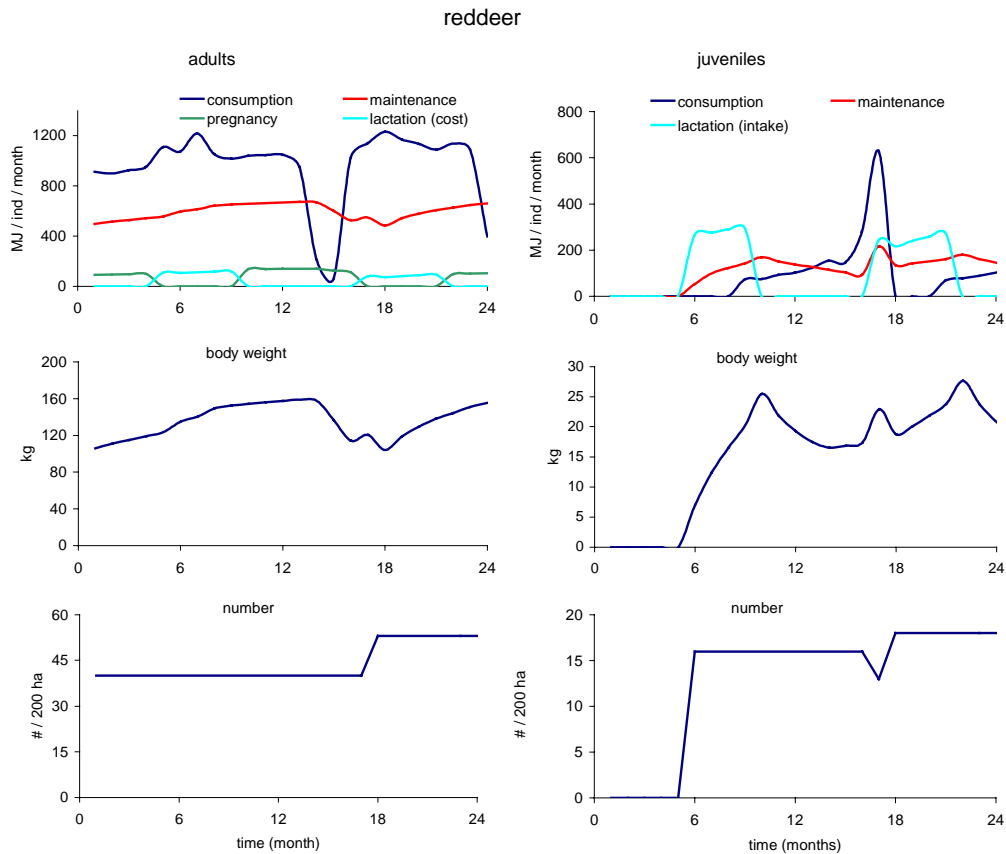
Furthermore some of the spatial aspects of the model are presented. Especially dispersal of seeds is a very important aspect of forest dynamics. To show this feature of FORSPACE, a 200-ha large part of the Imbos of which the vegetation is known in detail, is used.

### 9.1 Herbivores

The energy input of herbivores comes from the consumption of the vegetation. This energy is in the first place required to meet the costs for maintenance and movement and in case of female animals also for pregnancy and lactation. If there is energy remaining, this can be used to gain body weight. If not, the animal losses weight. The number of animals in a given are changes by birth and mortality. The rate at which this occurs depends on the reproductive capacity of the species but also on the individual body weight.

Figure MD-herbivore-1 shows an example of the energy balance of an adult female red deer for a 24-month period at a 200-ha section of the Imbos. The energy intake by consumption shows a large drop during late winter and late spring, the costs for maintenance are also reduced during this period because this depends on the body weight (Eqn. (84)). Nevertheless the costs for maintenance are much higher than the costs for pregnancy and lactation. For a juvenile animal (either male or female) the gains in energy comes during its first month from lactation and later from grazing.

Juveniles shift to the 2nd-year adult cohort just before the new young are born, which causes the drastic reduction in consumption at the start of lactation of the 2nd simulation year. The net balance between energy uptake and energy requirements determine the body weight of both adults and juveniles. This gives a decline in body weight during winter, but for juveniles it appears that the shift from lactation to grazing in the end of the summer also causes a reduction in average weight. The number of both adults and juveniles is the net results of birth and mortality. It can be seen that the death of 3 juveniles makes food available such that the surviving animals can increase in weight again.



*Figure MD-herbivore-1. Development during a 24-month period of the energy balance, the body weight and the number of individuals of both adults and juvenile red deer. The simulation was performed on a 200-ha large section of the Imbos.*

## 9.2 Trees

### 9.2.1 Monospecies

The aim of this section is to present the dynamics of FORSPACE for monoculture of birch, beech, pine and oak. The dynamics in the number of individuals, height, diameter at breast height (dbh), annual growth in volume (=current annual increment), basal area and standing volume are presented. Hundred initially identical plots are simulated over a period of 300 years. At the start of the simulation each plot is fully covered by individuals of one species, all being 9m tall. The output is the average of the variable considered over all plots, including plots that are not occupied anymore by the species. For this simulation experiment the regeneration is switches off, hence spatial variability between plots occurs due to mortality only. This heterogeneity is presented by the interval  $X \pm 2 \cdot \sigma$ , in which  $X$  is the variable considered and  $\sigma$  the standard deviation over all plots. The  $\pm 2 \cdot \sigma$  values are presented as thinner lines as the X-lines. The entire experimental setup is performed both for a relatively poor and dry sandy soil, represented by arenosol, and a somewhat richer and better watered soil, represented by podsol. No other species are considered in these simulation experiments.

#### ***Numbers of individuals***

In Fig MD.Tree.1 the trends in the number of individuals is shown varying tree species and soil type. For all species some similar trends are to be recognized. On the other hand, a species might be exceptional. This will be clarified below, starting with the similarities.

For all species, the simulated initial number of trees is lower on more nutrient rich soils, directly caused by parametrisations of the used equations (see Chapter *Initialisation*). The initialization procedure as well as the parametrization is based on the growth and yield table (Jansen *et al*, 1996) and so the initial numbers should be comparable. The simulated initial numbers of individuals being 9 m tall, is between 2500 and 3500 per ha, which is in broad outlines comparable with the Dutch growth and yield table. Differences between simulation and yield tables occur for beech and oak as the yield table indicates that the differences between soils is not as big as the simulation suggests.

Another general trend which can be drawn from this figure is that the reduction in number is more pronounced in poor soils, resulting from a stronger competition between individuals in this situation: more individuals at the start and a less productive system. This general conclusion can also be drawn from the yield table.

The maximum age a species can get is a factor which also causes differences in steepness of the trend. Oak lives a longer time than beech and pine (second best) and than birch, which has the shortest life span. In model parametrization the maximum age is supposed not to be soil type dependend.

The very strong reduction in numbers of birch on both soils, followed by a stable period is not a quite satisfying pattern compared to the yield table, which might be caused by the parameter that determines the onset of age related mortality (see Eqn. (99)). The variation between plots concerning the numbers of individuals is more pronounced for pine than for any other species.

### ***Height development***

In Fig MD.Tree.2 present the average height over all plots in the area for a species. Height development follows the growth and yield tables closely (Jansen *et al*, 1996) as the calibration of the equation used in FORSPACE (Eqn. (104)) is based on this data.

The reduction in height after a certain simulation time suggests that trees can shrink in the model. This is not the case. The reduction is because the average height is determined over all plots. Thus also plots without trees, i.e. with zero height, are taken into account resulting in the tendency as described.

### ***Diameter at breast height***

Fig MD.Tree.3 presents the development of the average diameter at breast height (dbh). One general conclusion from these graphs is that the dbh on the podsol increases faster compared to the arenosol. This results partly from a higher productivity at the better soils, expressed in FORSPACE by a higher value of the parameter Radiation Use Efficiency (RUE). Another explaining aspect is the number of individuals present, which is higher on the arenosol. At a given production level, the more individuals are present the less energy each individual will get, resulting in a slower dbh increment.

Given the whole set of parameter values and process descriptions, one can conclude that beech has the most rapid dbh-development on podsols, but oak can reach the largest diameter as it lives longer. On arenosols, oak, beech and pine are comparable concerning the dbh-development in time. But again, oak attains the largest dbh-values because of its longer life span. Note that oak decline on podsols starts earlier compared to arenols. The larger the trees are, the stronger they compete.

Concerning growth and mortality only, birch is a species with lower competitive ability, because of the fact that age-related mortality starts earlier than the other species.

Dbh-development in this simulation experiment, as given in Fig MD.Tree.3, could in principle be compared with values from growth and yield tables, but differences in simulated number of individuals compared to numbers in the tables make the figures on dbh difficult to compare.

As explained in the previous section 'Height development', the suggested reduction in dbh in the graphs is also caused by the method of calculating the average value over all plots, also plots that do not contain trees anymore.

### ***Annual growth of volume***

In Fig MD.Tree.4 presents the simulated annual volume increments of the 4 tree species. The radiation use efficiency (RUE) is calibrated on the yield class for the site, thus this figure shows the accuracy of the calibration. Table MD.1 shows the yields classes of the 4 species for the arenosol and podsol. It can be concluded that the simulated yield closely matches the observed values.

Table MD.1: Relation soil type and yield classes (maximum annual increment  $m^3 yr^{-1}$ ) for the species concerned

	arenosol	podsol
<i>Betula</i>	5	6
<i>Fagus</i>	4	10
<i>Pinus</i>	6	8
<i>Quercus</i>	5	8

### ***Volumes***

Fig MD.Tree.5 shows the standing volume per species for the arenosol and podsol, based on the number of trees present and their dbh. The richer podsol has a larger standing volume, but also a larger variability. This is due to the fact that the reduction in numbers is larger at the podsol than at the arenosol, so that the presence or absence of fewer and bigger trees result in larger spatial heterogeneity. Consequently, although there is relatively little variability between the plots in the number of trees (Fig MD-tree-1), their height (MD-tree-2) and dbh (Fig MD-tree-3), the product of these resulting in the volume, show a much larger spatial heterogeneity. This variability increases with age because trees get bigger in time.

### ***Basal area***

Fig MD.Tree.6 presents the results for the basal area and show a similar pattern as the standing volume.

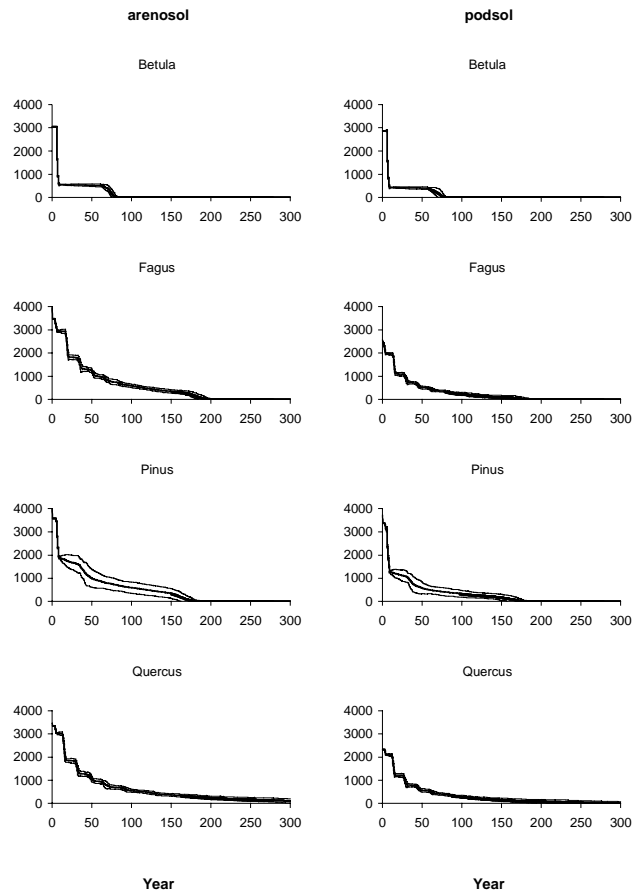
### ***Dead wood***

Fig MD.Tree.7 show the FORSPACE output for dead wood. Dead wood is an important feature for the evaluation of the natural quality of the forest. The absolute values are tentative because of the homogeneous initial conditions and the absence of regeneration. The figure shows that the at the podsol more deadwood is produced, with a larger spatial variability. The age related mortality of the trees result in a marked increase of the amount of dead wood in the forest, that decays over a period of several decades.

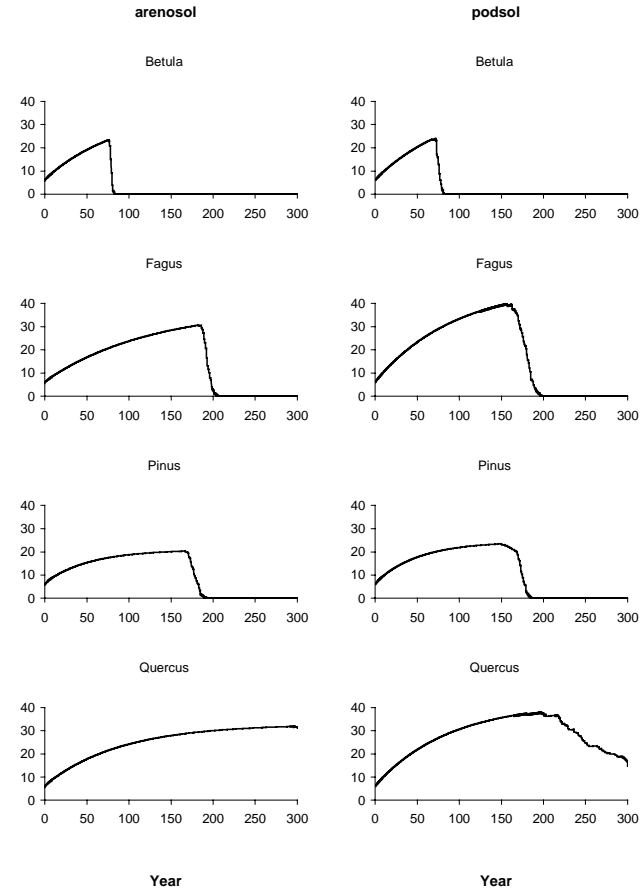
### ***Depth of litter***

Fig MD.Tree.8 show the depth of the three litter layers that are considered in FORSPACE. These layers are roughly comparable to the litter, fermentation and raw humus horizon of the forest, but called litter layer 1,2, and 3, respectively in FORSPACE. The figure shows a rapid build-up of the litter layers, and attain after a build-up period a dynamic steady-state between input and decomposition. FORSPACE predicts a larger depth of the litter layers for the richer podsol than the arenosol due to the larger input of foliage, branches, stems and roots. The parameters determining the decomposition rates are the same for both soils. A future improvement of FORSPACE may contain differences in litter quality and thereby different turnover rates between different soils

### Number of individuals (ha-1)



### Height (m)



*Fig MD.Tree.1 Simulated trends in number of individuals in monocultures of *Betula pendula*, *Fagus sylvatica*, *Pinus sylvestris*, *Quercus robur* in a plot of 400 m<sup>2</sup> on a poor soil (arenosol) and a relatively rich soil (podsol). The expressed values are the averages over 100 plots. Numbers are expressed per ha.*

*Fig MD.Tree.2 Simulated trends in height (m) of monocultures of *Betula pendula*, *Fagus sylvatica*, *Pinus sylvestris*, *Quercus robur* in a plot of 400 m<sup>2</sup> on a poor soil (arenosol) and a relatively rich soil (podsol). The expressed values are the averages over 100 plots.*



## DBH (cm)

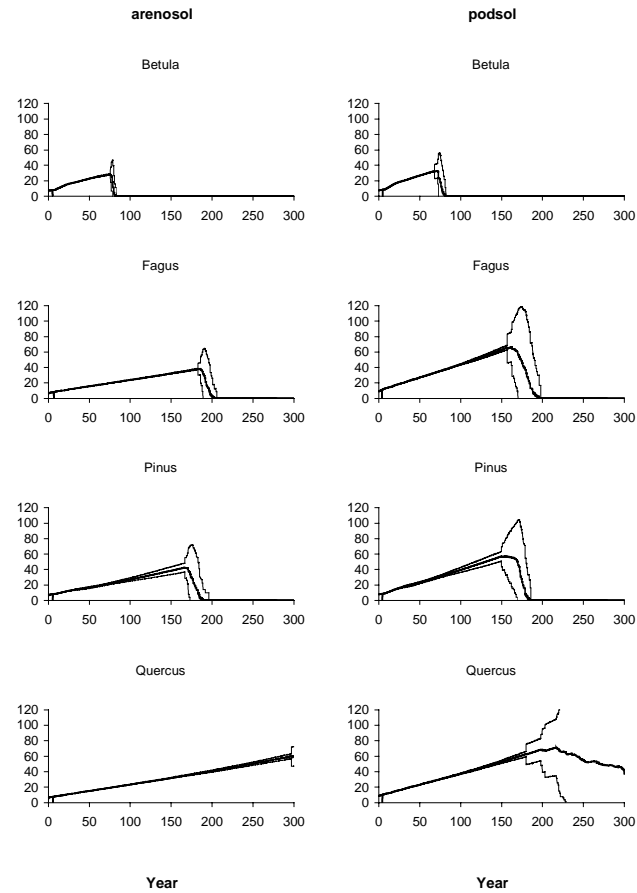


Fig MD.Tree.3 Simulated trends in diameter at breast height (dbh, cm) of monocultures of *Betula pendula*, *Fagus sylvatica*, *Pinus sylvestris*, *Quercus robur* in a plot of 400 m<sup>2</sup> on a poor soil (arenosol) and a relatively rich soil (podsol). The expressed values are the averages over 100 plots.

## Annual growth of Volume (m<sup>3</sup> ha<sup>-1</sup> yr<sup>-1</sup>)

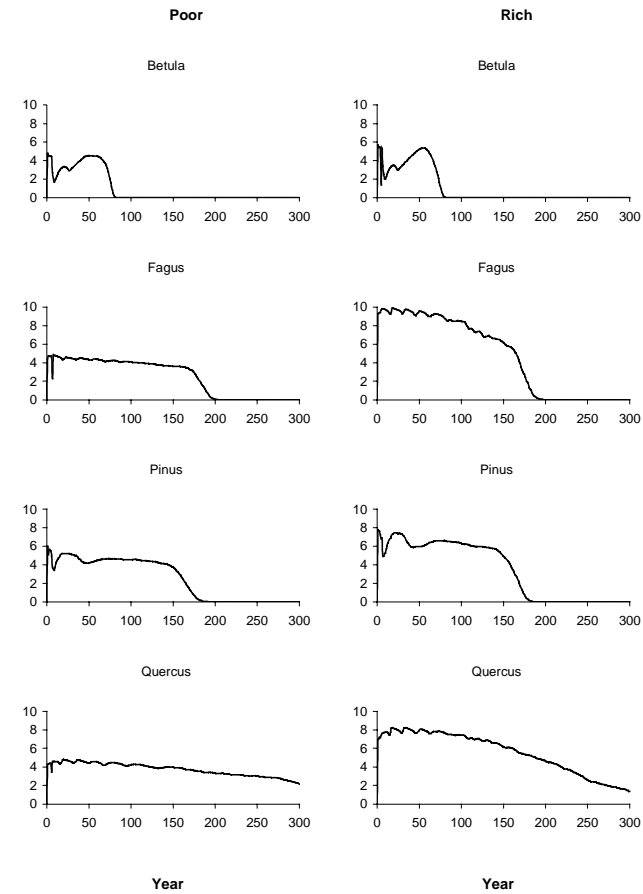


Fig MD.Tree.4 Simulated trends in annual increment of volume (m<sup>3</sup> ha<sup>-1</sup>) of monocultures of *Betula pendula*, *Fagus sylvatica*, *Pinus sylvestris*, *Quercus robur* in a plot of 400 m<sup>2</sup> on a poor soil (arenosol) and a relatively rich soil (podsol). The expressed values are the averages over 100 plots.

### Standing volume (m3 ha-1)

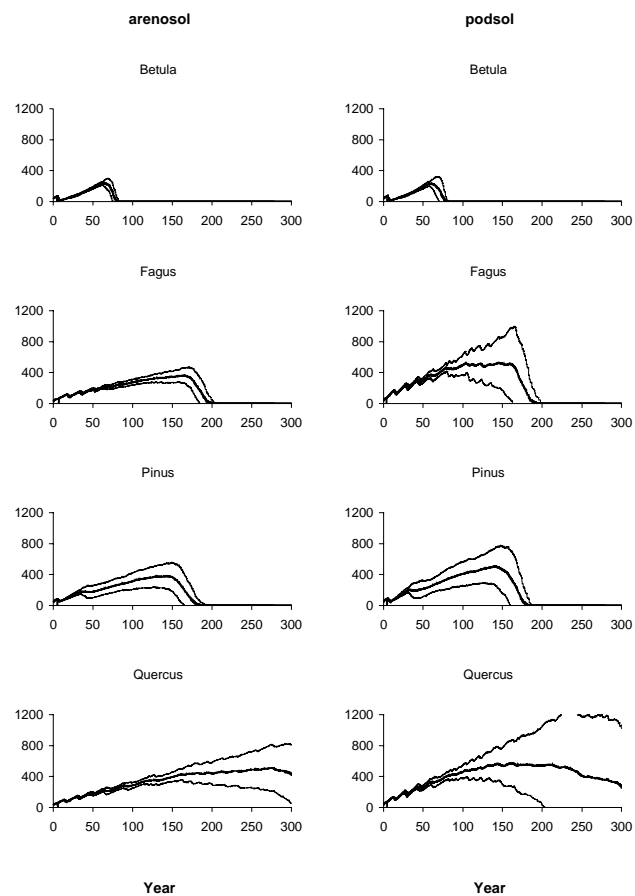


Fig MD.Tree.5 Simulated trends in standing volume of monocultures (m3 ha-1) of *Betula pendula*, *Fagus sylvatica*, *Pinus sylvestris*, *Quercus robur* in a plot of 400 m2 on a poor soil (arenosol) and a relatively rich soil (podsol). The expressed values are the averages over 100 plots.

### Basal area (m2 ha-1)

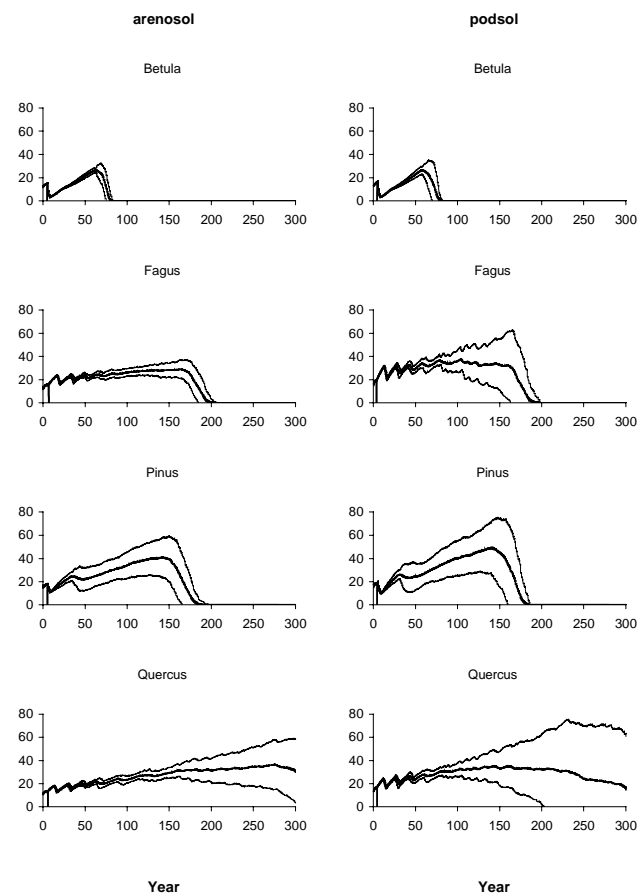


Fig MD.Tree.6 Simulated trends in basal area (m2 ha-1) of monocultures of *Betula pendula*, *Fagus sylvatica*, *Pinus sylvestris*, *Quercus robur* in a plot of 400 m2 on a poor soil (arenosol) and a relatively rich soil (podsol). The expressed values are the averages over 100 plots.

## Dead wood (kg m<sup>-2</sup>)

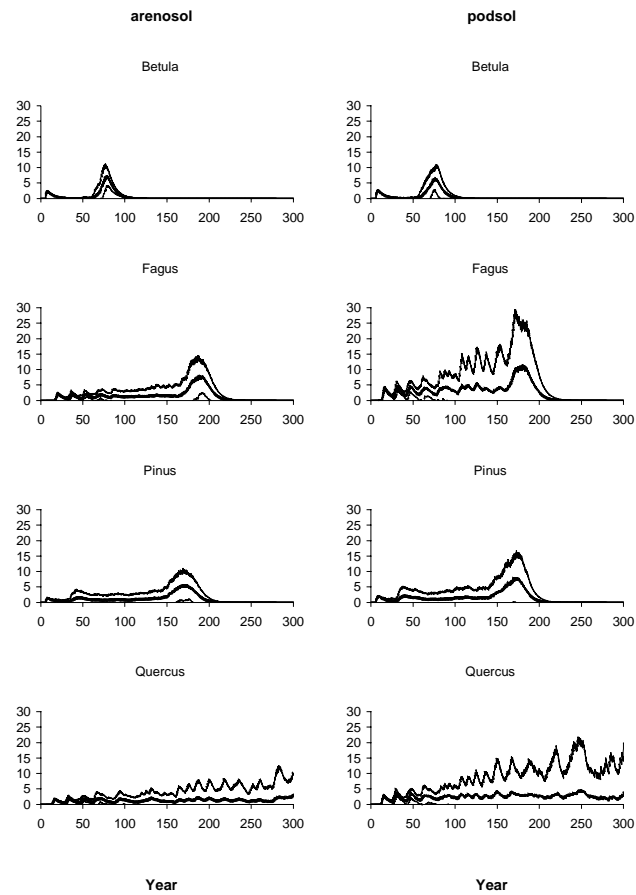


Fig MD.Tree.7 Simulated trends in the amount of dead wood of monocultures of *Betula pendula*, *Fagus sylvatica*, *Pinus sylvestris*, *Quercus robur* in a plot of 400 m<sup>2</sup> on a poor soil (arenosol) and a relatively rich soil (podsol). The expressed values are the averages over 100 plots.

## Depth of Litter (m)

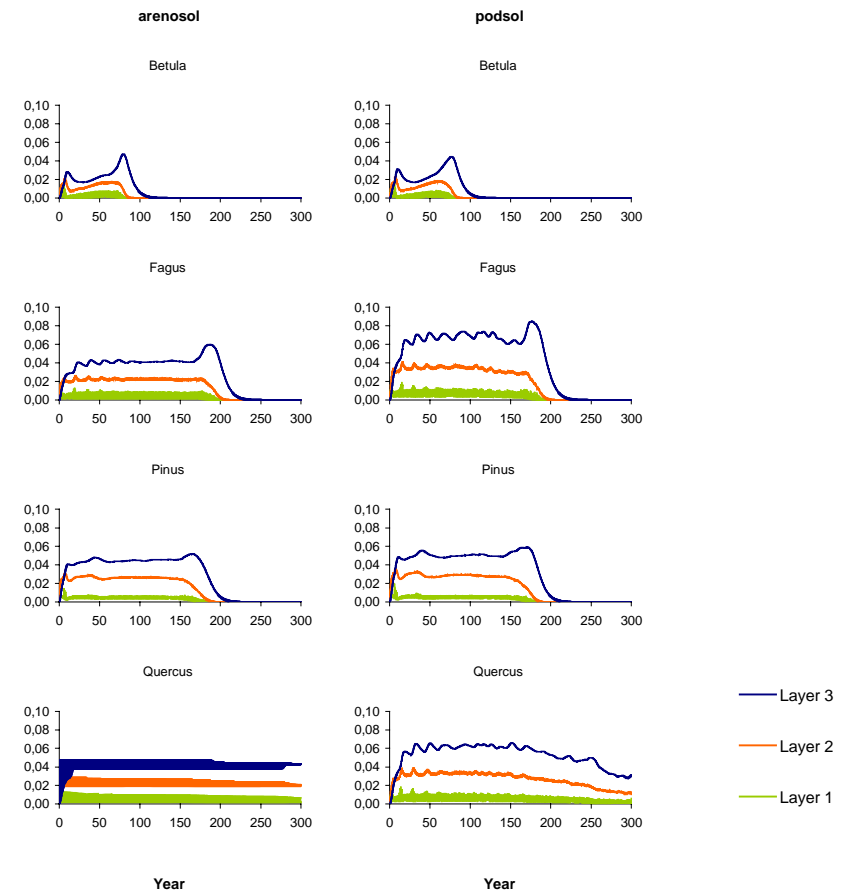


Fig MD.Tree.8 Simulated trends in development of the litter layers of monocultures of *Betula pendula*, *Fagus sylvatica*, *Pinus sylvestris*, *Quercus robur* in a plot of 400 m<sup>2</sup> on a poor soil (arenosol) and a relatively rich soil (podsol). The expressed values are the averages over 100 plots.

### 9.2.2 Mixed species

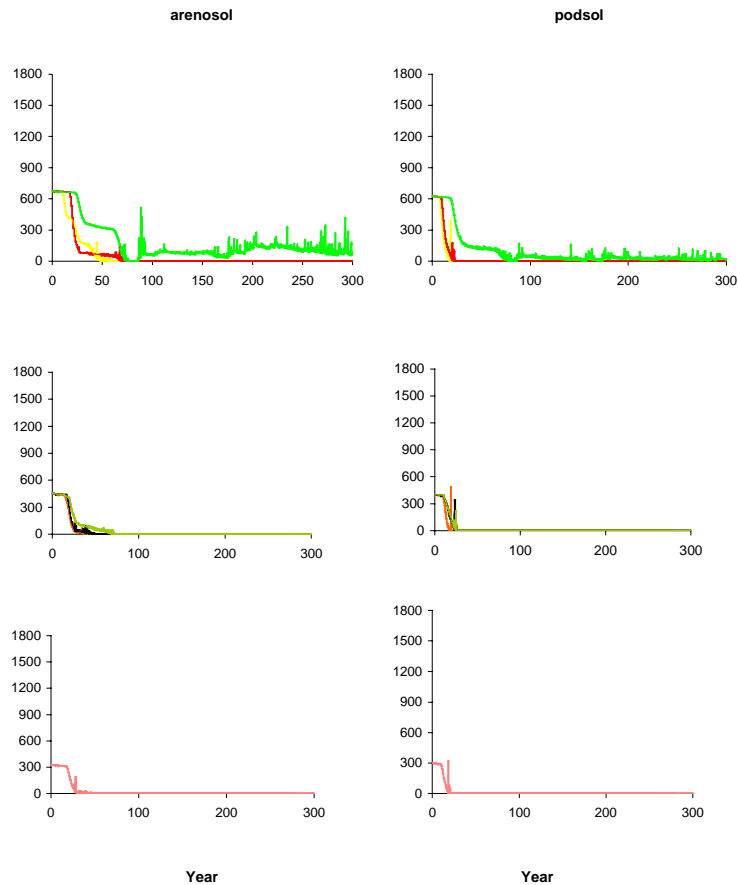
The aim of this section is to show the results of FORSPACE if tree species compete with each other in standardized conditions. These conditions allow to analyse the performance of the model with as few as possible factors that cause differences in the results.

The standardized conditions are that a species covers initially 50, 33 or 25% of a plot, and that all trees are 9m tall. The mixtures include 2, 3 and 4 species for all combinations between birch, beech, pine and oak, with a total cover of 100%. The simulation run starts with 100 identical 20x20m plots, with a simulation period of 300 years. Spatial heterogeneity occurs due to stochasticity in mortality and dispersal, and thus establishment of new seedlings. The results of the simulation experiments are presented as average values of number of trees per hectare, diameter at breast height and basal area per species over all 100 plots, including those at which the species is absent. In relevant cases the spatial heterogeneity is presented by the interval  $X \pm 2 \cdot \sigma$ , in which  $X$  is the variable considered and  $\sigma$  the standard deviation over all plots. The  $\pm 2 \cdot \sigma$  values are presented as thinner lines with the same color as the  $X$ -lines. The entire experimental setup is performed both for a relatively poor and dry sandy soil, represented by arenosol, and a somewhat richer and better watered soil, represented by podsol. No other species are considered in these simulation experiments.

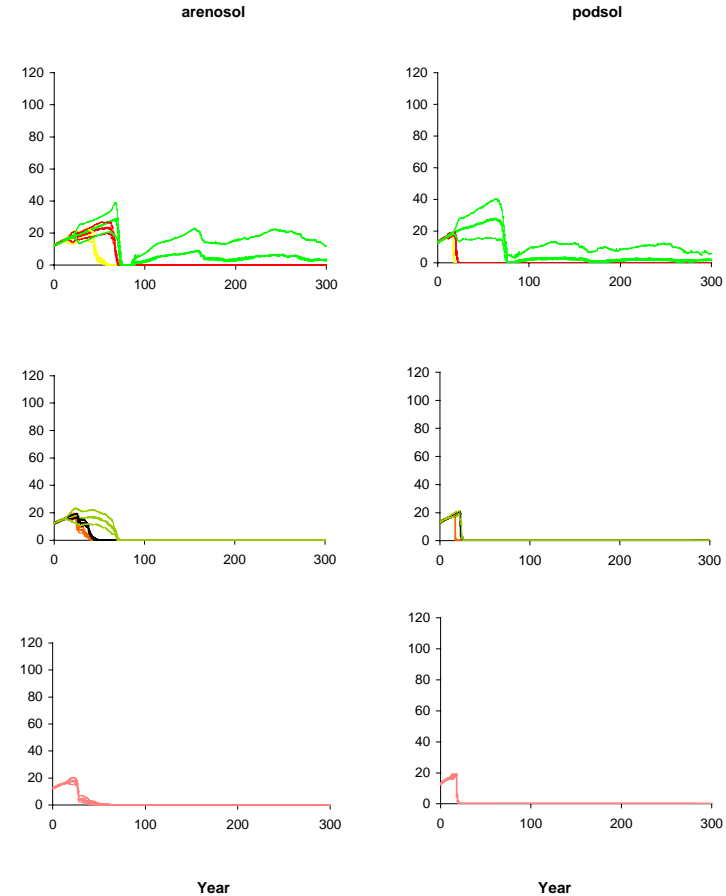
#### ***Dynamics of *Betula pendula* in competition with other tree species***

Figures MD-tree 9 to 11 show that FORSPACE predicts that birch may only survive in a situation where it competes with pine only. The relative competitive ability of birch compared to the other species is higher at the arenosol than the podsol because the differences in soil quality between arenosol and podsol are less for birch than for the other species (see Table MD.1). Birch is outcompeted if either beech or oak are present independent of the initial conditions, even though the first generation of birch may last for several decades. The presence of birch collapses after approximately 80 years due to age related mortality, but it is able to have 2<sup>nd</sup> and 3<sup>rd</sup> generations under pine due to the relatively low maximal LAI of 3 for pine. Under either beech or pine no new establishment of birch seedlings is possible due to low light conditions.

## Number of Individuals of Betula



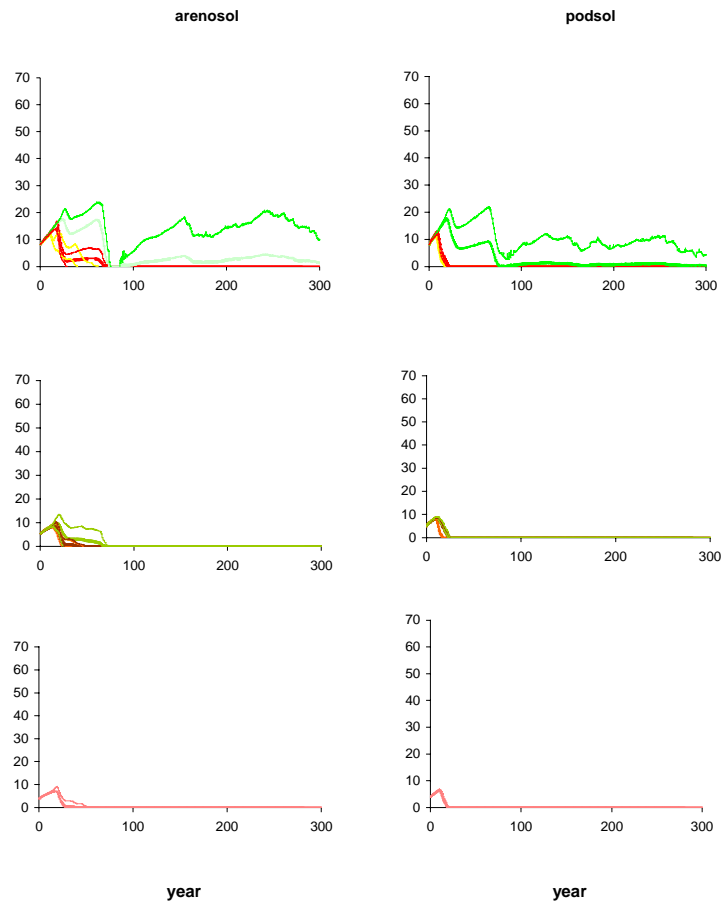
## DBH of Betula



*Fig MD.Tree.9. Simulated trends in the number of individuals ( $\# \text{ ha}^{-1}$ , average over 100 plots) of birch in mixture with beech, pine, and oak. The mixtures include all combinations of 2, 3 and 4 species. The simulation experiment is performed both on a relatively pool sandy soil (arenosol) and a relatively rich sandy soil (podzol). (see Fig 20 for legend)*

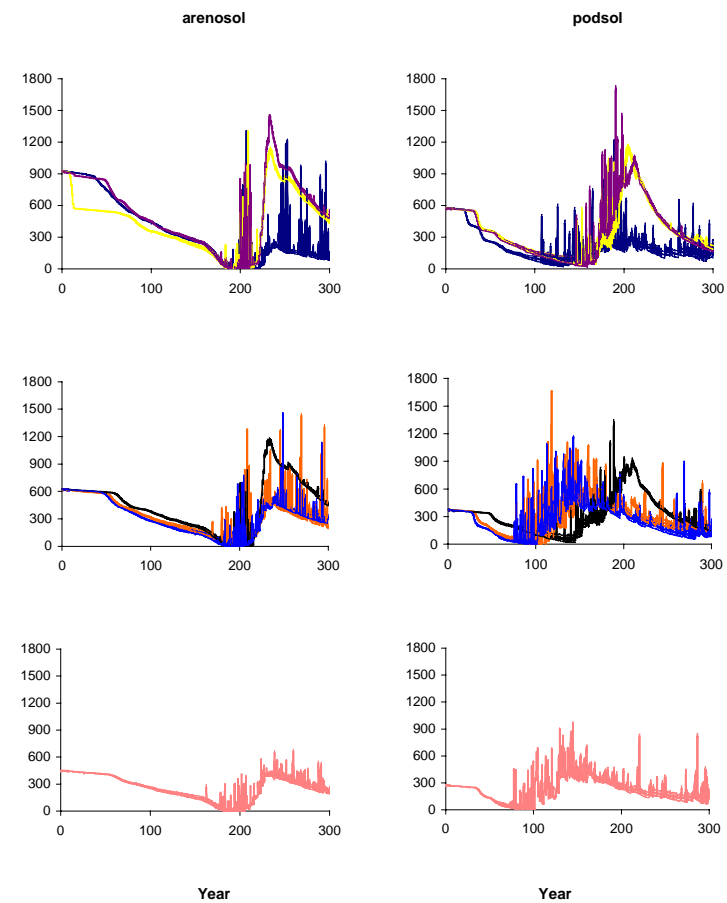
*Fig MD.Tree.10. Simulated trends in diameter at breast height (dbh, cm, average over 100 plots) of birch in mixture with beech, pine, and oak. The mixtures include all combinations of 2, 3 and 4 species. The simulation experiment is performed both on a relatively pool sandy soil (arenosol) and a relatively rich sandy soil (podzol). (see Fig 20 for legend)*

## Basal area (m<sup>2</sup> ha<sup>-1</sup>) of Betula



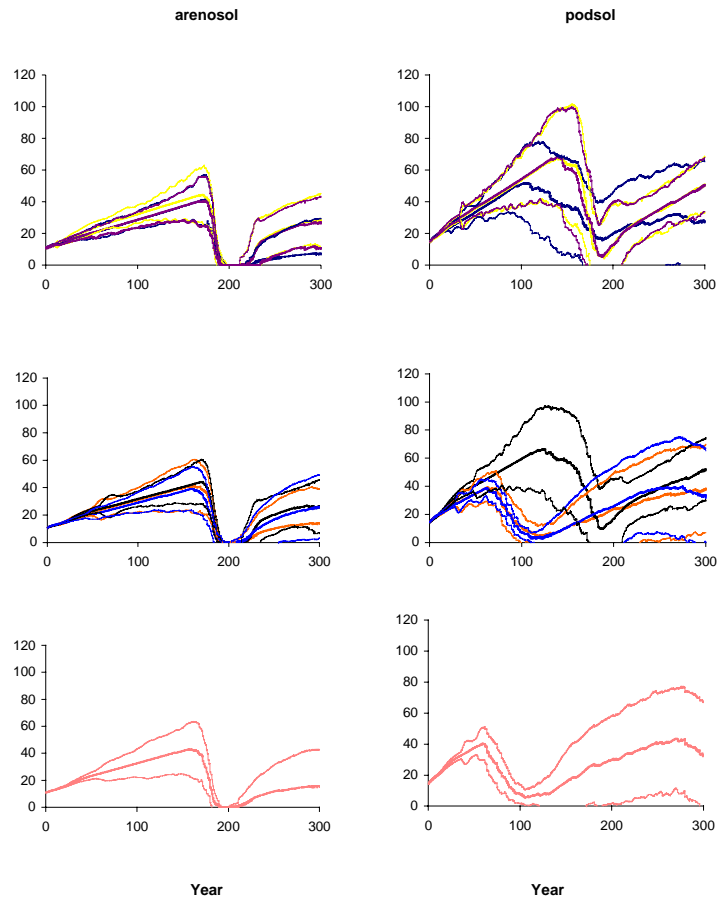
*Fig MD.Tree.11. Simulated trends in basal area (m<sup>2</sup> ha<sup>-1</sup>, average over 100 plots) of birch in mixture with beech, pine, and oak. The mixtures include all combinations of 2, 3 and 4 species. The simulation experiment is performed both on a relatively pool sandy soil (arenosol) and a relatively rich sandy soil (podzol). (see Fig 20 for legend)*

## Number of Individuals of Fagus



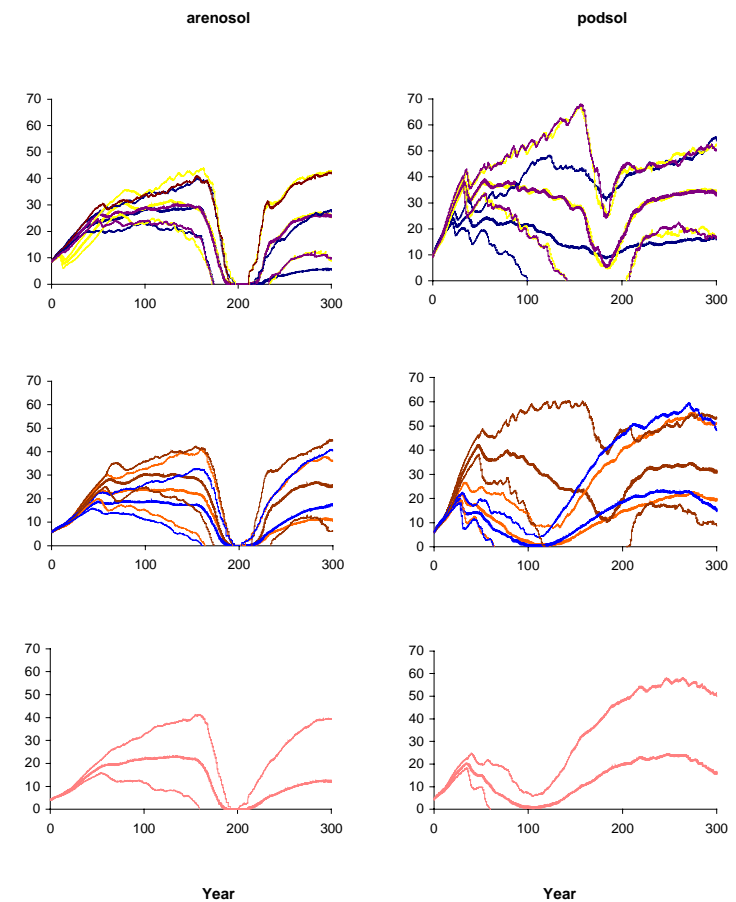
*Fig MD.Tree.12. Simulated trends in the number of individuals (# ha<sup>-1</sup>, average over 100 plots) of beech in mixture with birch, pine, and oak. The mixtures include all combinations of 2, 3 and 4 species. The simulation experiment is performed both on a relatively pool sandy soil (arenosol) and a relatively rich sandy soil (podzol). (see Fig 20 for legend)*

## DBH of Fagus



*Fig MD.Tree.13. Simulated trends in diameter at breast height (dbh, cm, average over 100 plots) of beech in mixture with birch, pine, and oak. The mixtures include all combinations of 2, 3 and 4 species. The simulation experiment is performed both on a relatively pool sandy soil (arenosol) and a relatively rich sandy soil (podzol). (see Fig 20 for legend)*

## Basal area (m<sup>2</sup> ha<sup>-1</sup>) of Fagus



*Fig MD.Tree.14. Simulated trends in basal area (m<sup>2</sup> ha<sup>-1</sup>, average over 100 plots) of beech in mixture with birch, pine, and oak. The mixtures include all combinations of 2, 3 and 4 species. The simulation experiment is performed both on a relatively pool sandy soil (arenosol) and a relatively rich sandy soil (podzol). (see Fig 20 for legend)*

## Number of Individuals of Pinus

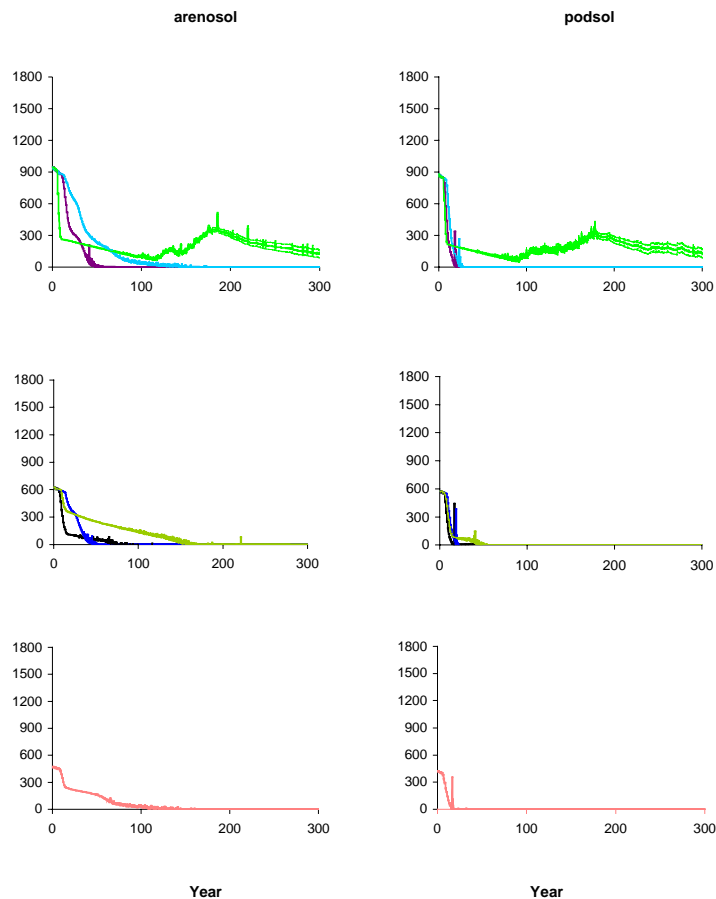


Fig MD.Tree.15. Simulated trends in the number of individuals ( $\# \text{ ha}^{-1}$ , average over 100 plots) of pine in mixture with birch, beech and oak. The mixtures include all combinations of 2, 3 and 4 species. The simulation experiment is performed both on a relatively pool sandy soil (arenosol) and a relatively rich sandy soil (podzol). (see Fig 20 for legend)

## DBH of Pinus

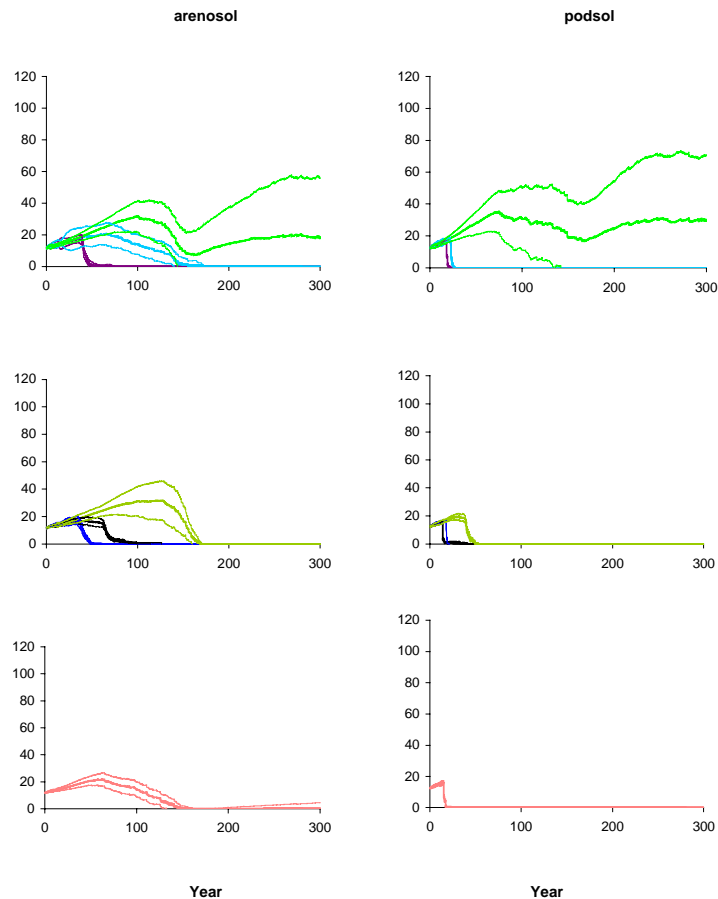
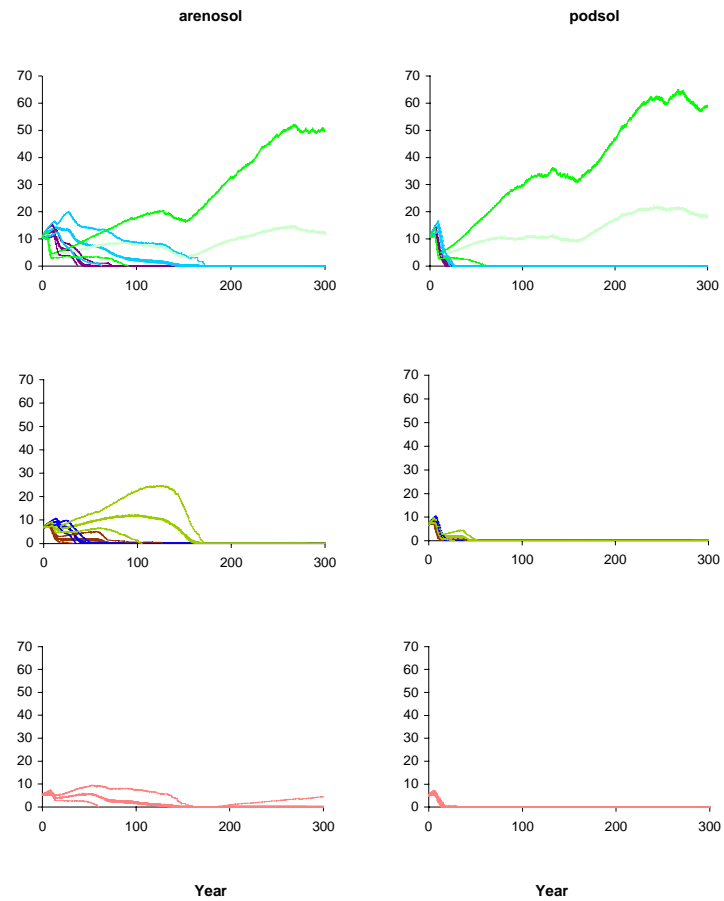


Fig MD.Tree.16. Simulated trends in diameter at breast height (dbh, cm, average over 100 plots) of pine in mixture with birch, beech and oak. The mixtures include all combinations of 2, 3 and 4 species. The simulation experiment is performed both on a relatively pool sandy soil (arenosol) and a relatively rich sandy soil (podzol). (see Fig 20 for legend)



### Basal area (m<sup>2</sup> ha<sup>-1</sup>) of Pinus



### Number of Individuals of Quercus

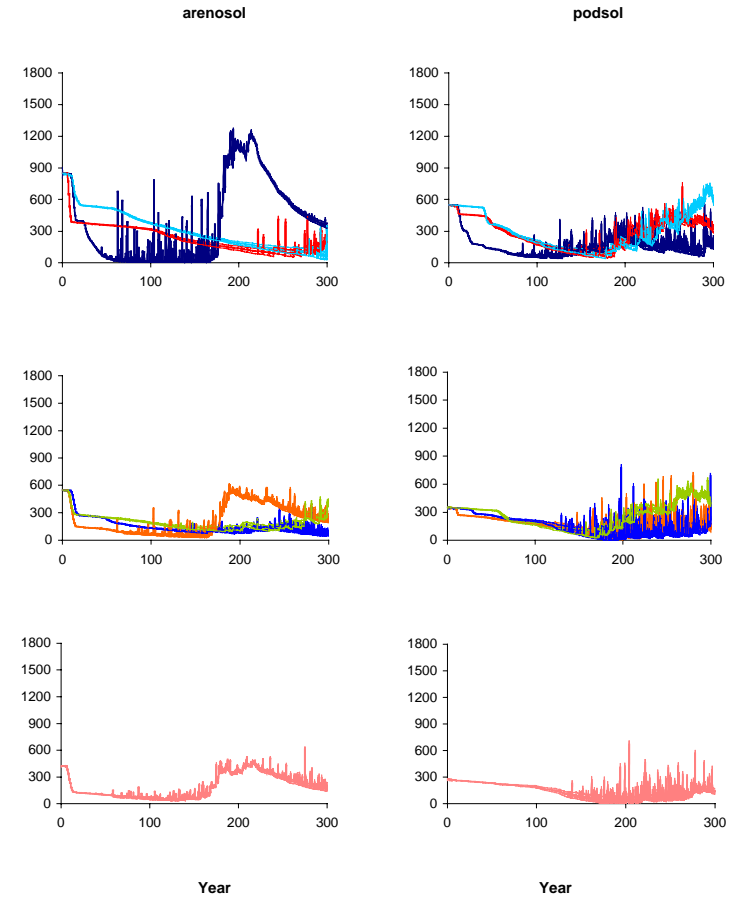


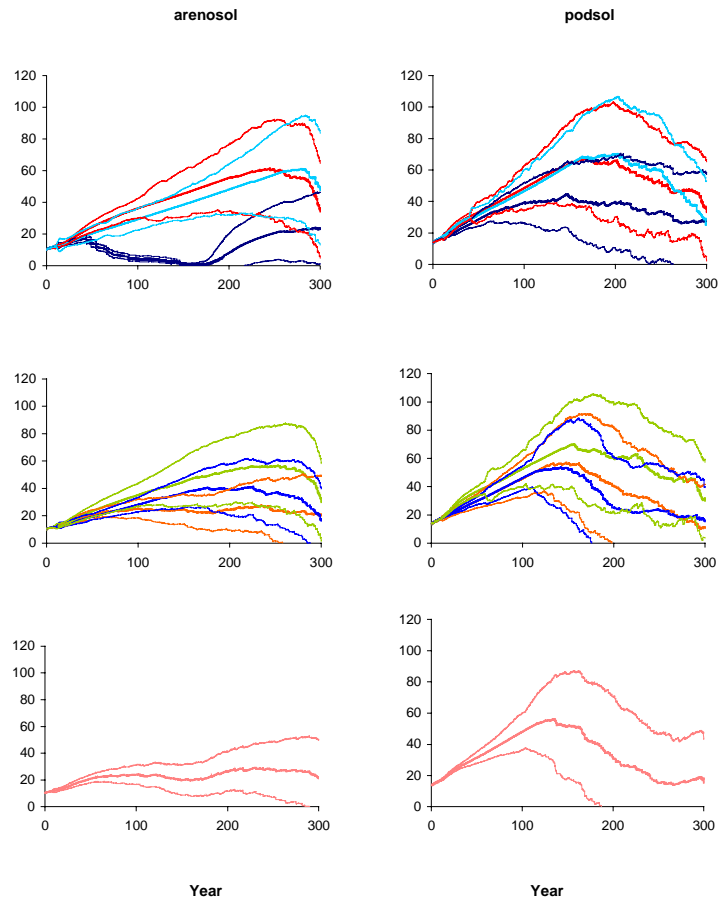
Fig MD.Tree.17. Simulated trends in basal area (m<sup>2</sup> ha<sup>-1</sup>, average over 100 plots) of pine in mixture with birch, beech and oak. The mixtures include all combinations of 2, 3 and 4 species. The simulation experiment is performed both on a relatively pool sandy soil (arenosol) and a relatively rich sandy soil (podzol). (see Fig 20 for legend)

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Fig MD.Tree.18. Simulated trends in the number of individuals (# ha<sup>-1</sup>, average over 100 plots) of oak mixture with birch, beech and pine. The mixtures include all combinations of 2, 3 and 4 species. The simulation experiment is performed both on a relatively pool sandy soil (arenosol) and a relatively rich sandy soil (podzol). (see Fig 20 for legend)

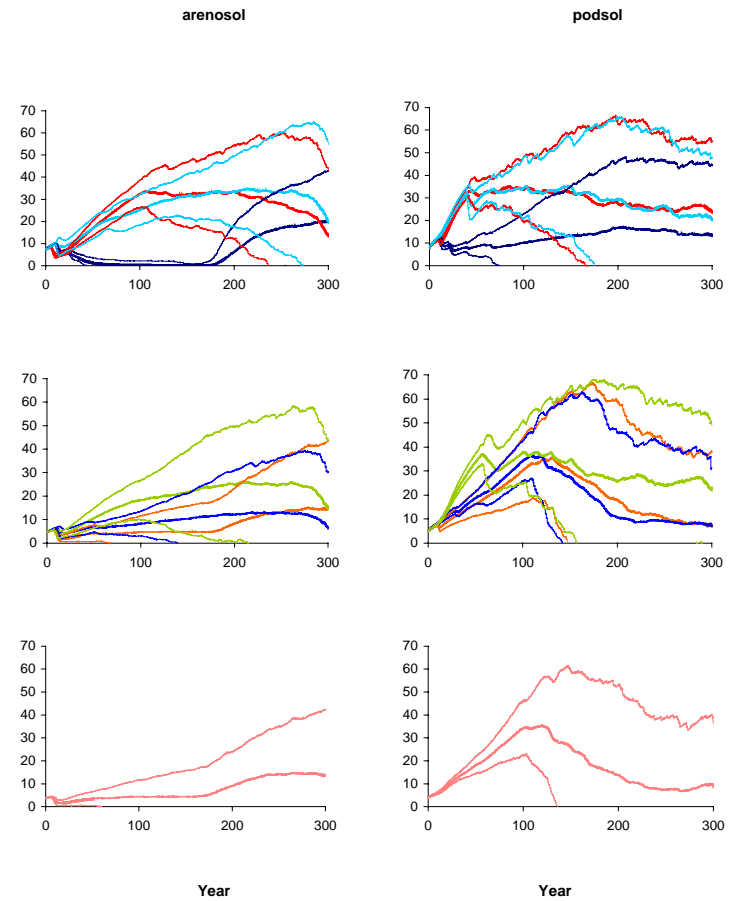
113

### DBH of Quercus



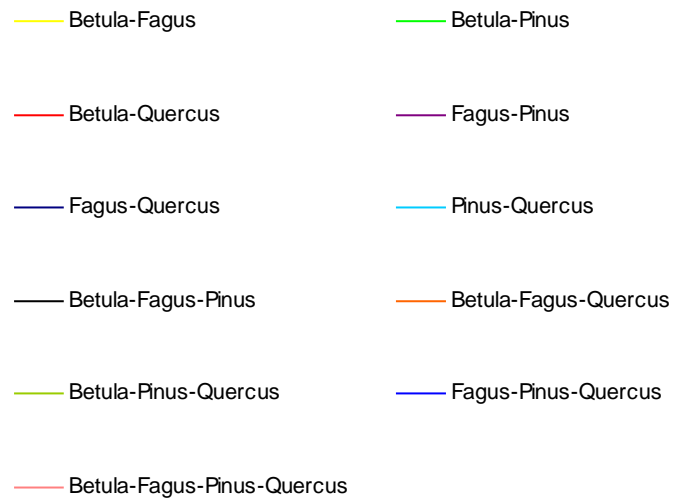
*Fig MD.Tree.19. Simulated trends in diameter at breast height (dbh, cm, average over 100 plots) of oak in mixture with birch, beech and pine. The mixtures include all combinations of 2, 3 and 4 species. The simulation experiment is performed both on a relatively pool sandy soil (arenosol) and a relatively rich sandy soil (podzol). (see Fig 20 for legend)*

### Basal area (m<sup>2</sup> ha<sup>-1</sup>) of Quercus



*Fig MD.Tree.20. Simulated trends in basal area (m<sup>2</sup> ha<sup>-1</sup>, average over 100 plots) of oak in mixture with birch, beech and pine. The mixtures include all combinations of 2, 3 and 4 species. The simulation experiment is performed both on a relatively pool sandy soil (arenosol) and a relatively rich sandy soil (podzol)*

*A3 part 1*



### ***Dynamics of Fagus sylvatica in competition with other tree species***

Figures MD-tree12-14 show the same output for beech as presented for birch. Beech is strong competitor to all species both at the arenosol and podsol. However, it is a much stronger competitor on the arenosol than at the podsol (see Table MD.1). Beech experiences most competition from oak, and there are little differences between birch and pine in their impact on beech. Although beech performs much better on the podsol, the relative impact of oak on beech compared to the other species is highest at this soil. Tree mortality of beech is higher on the podsol, which results in a much earlier 2<sup>nd</sup> generation of beech compared to the arenosol, and a higher variability between plots in dbh and basal area on the podsol.

### ***Dynamics of Pinus sylvestris in competition with other tree species***

Figures MD.Tree15-17 show the results for pine. For this species FORSPACE predicts that it will be present in the long run if beech and oak are absent, but that it dominant species in the presence of birch. Pine is a relatively strong competitor at the arenosol (see Table MD.1), but even at these poor sandy soils it is unable to have a 2<sup>nd</sup> generation in presence of either beech or oak. The differences between in soil quality between arenosol and podsol are relatively small (Table XX), and thus the differences in the number of trees, dbh and basal area between these soil. However, similar as beech the 2<sup>nd</sup> generation of pine is predicted to occur earlier at the better soil due to higher tree mortality.

### ***Dynamics of Quercus robur in competition with other tree species***

Figures MD-tree18-20 show the results for oak. Oak is little affected by the presence of either birch or pine at both the arenosol and the podsol. However, beech is a strong competitor for oak, and the prediction of FORSPACE is that this is even more so at the poor arenosol than at the richer podsol. This is not what could be expected under field conditions where oak appears to function better at dry sandy soils and beech at better watered and richer soils. This result could be due to the fact that under the standardized conditions both oak and beech are 9m tall. Beech may have a better height- and lateral growth and thereby suppress oak from the start of the simulation onwards. At the better soil oak may perform relatively better, although beech wins also under these conditions. If this is the case then the competitive outcome between beech and oak is much affected by their initial conditions and less by differences in site conditions.

The reason that oak has a strong increase at the arenosol when competing with beech only is due to the fact that the maximum age of oak is 450 years and that of beech 250. The age-related mortality of beech starts 90 year before its maximum age, thus enabling oak to increase in numbers, dbh and basal area.

### ***Dynamics of dead wood and litter***

Fig MD.Tree.21. show the dynamics of dead wood for the mixed species situation. The results are consistent with the monospecies situation in that: more dead wood is accumulated at the podsol than at the arenosol soil due to the higher productivity at the podsol whereas the decomposition rates are the same for both soils; there is a marked age effect which is caused by the fact that the starting age is for all individuals is the same; and there appear to be stronger fluctuations in amount of

dead wood at the podsol that at the arenosol also because of the higher productivity level of the podsol.

Fig MD.Tree.22 and MD.Tree.23 show the dynamics in the depth of litter layer 2 and 3 as calculated by FORSPACE. Litter layer 1 is not presented as this litter shows strong fluctuations, blurring the differences between the lines presented. Both litter layer 2 and 3 show that steady state conditions are quickly met, whereas litter layer 2 shows a stronger year-to-year variation than litter layer 3 because of the larger time constants for decomposition of layer 3. The strong decline in the depth of both litter layers is due to the fact that after the age-related mortality of many trees (most of this material is decomposed in litter layer 1) there is a build-up of above-ground biomass which reduces the litter input, whilst there is an ongoing decomposition of the material available. After ca. 50 years the previous steady-state are met again. These predicted dynamics of the model can be evaluated under field conditions.

### 9.3 Herbs

In the following paragraph the model dynamics for herbs are presented. This includes: the development in time of the weight of the different plant components; the change in cover per herb species and how this is affected by the presence of other herb-species in the plot; and the effect of light availability on the herb layer. The latter mimics the effects of the closure of an open patch in the forest on the herb vegetation.

#### 9.3.1 Weight of foliage, branches, stem and roots

Figure MD-herbs-1 shows the development over a 5-year period of the weight of foliage, branches (if relevant), stalks or stems, and roots of *Calluna*, *Deschampsia*, Grass, *Pteridium* and *Vaccinium*. The figures show that in FORSPACE the maximum amount of foliage is approximately the same for all species, and that Grass and *Pteridium* are deciduous species, whilst the other species are evergreen. Grass and *Deschampsia* have a higher fraction of stalks, which are not edible for herbivores, and less roots compared to *Calluna*, *Vaccinium* and *Pteridium*. The parameter values used in FORSPACE to characterize *Calluna* and *Vaccinium* are largely the same for the different plant features. These species differ mainly in their palatability for the different herbivore species.

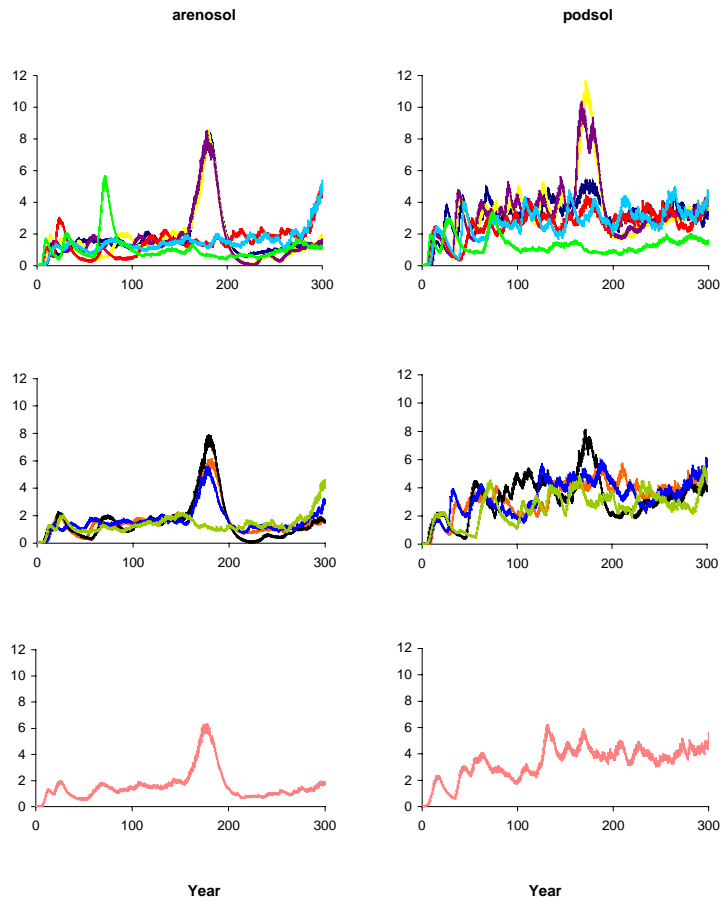
#### 9.3.2 Cover

Two mechanisms play a role for the change in cover of a herb or grass species: lateral expansion, *i.e.* lateral growth by plants that are present in the plot; and establishment of new seedlings of the same species, if the circumstances are favourable for germination.

Figure MD-herbs-2 shows that under full light conditions, the rate of lateral increase is highest for *Pteridium* and Grass, and lowest for *Deschampsia*. Lateral expansion occurs until the plot is fully covered. During this phase the change in cover of a species is not affected by the presence of another species. There will be competition for light during this phase, however this does not affect the rate of lateral expansion, because light is not limiting in this case. Competition for space with other species occurs if the plot is fully covered with vegetation, and other species are present. This competition for space is then for the plot area that is not occupied. This uncovered part of the plot area is generated by 'micro-disturbances'. By this mechanism, annually 5% of the vegetation in the herblayer is removed, mimicking the role of mice, rabbits and other animals that open the vegetation. This free coming space is invaded based on lateral expansion rate (and new establishment: see next paragraph). For the exercise represented in Figure MD-herbs-2, the relative expansion rates determine competitive outcome between species.

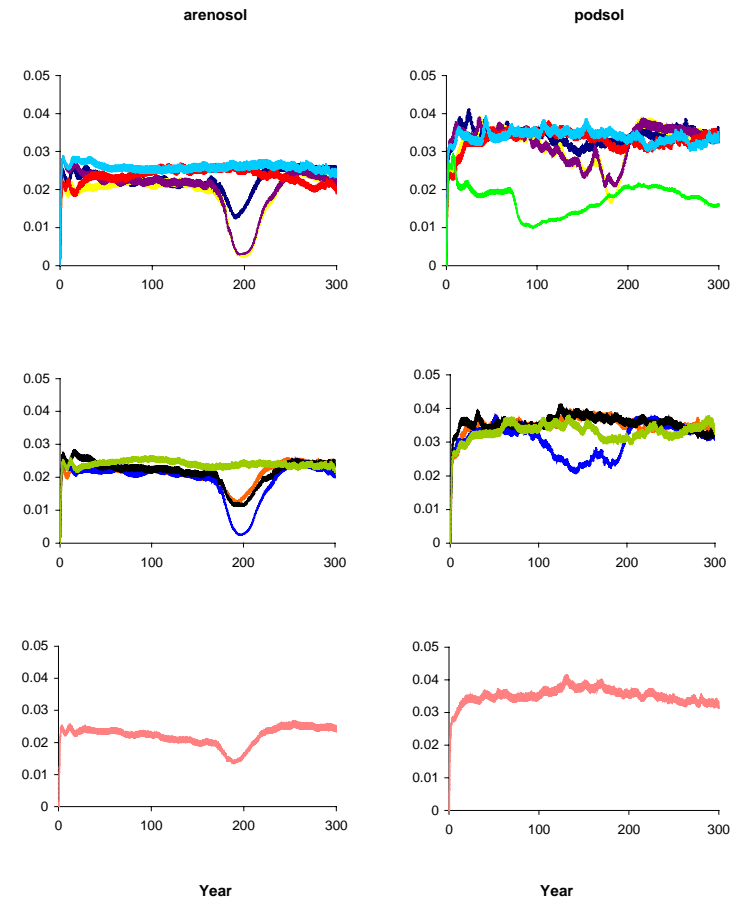
Figure MD-herbs-3 presents an example where both lateral expansion and new establishment determine the change in cover of herbs and grasses. If circumstances in the plot are favourable for germination for a given species, then also new germination occurs of seeds that are present in the plot. This has a drastic effect on the competitive outcome between two species if one of the competing species can germinate and the other species cannot. *E.g* the competition between *Deschampsia* and other species is affected the development of the fermentation layer. If fermentation layer is sufficiently developed then new establishment of *Deschampsia* possible and thereby its rapid expansion. Such situations will occur when a forest matures and the litter is partly decomposed into a fermentation layer.

### Dead wood (kg m<sup>-2</sup>)



*Fig MD.Tree.21. Simulated trends in dead wood (kg m<sup>-2</sup>, average over 100 plots) for all mixtures of birch, beech, pine and oak. The mixtures include all combinations of 2, 3 and 4 species. The simulation experiment is performed both on a relatively pool sandy soil (arenosol) and a relatively rich sandy soil (podzol)*

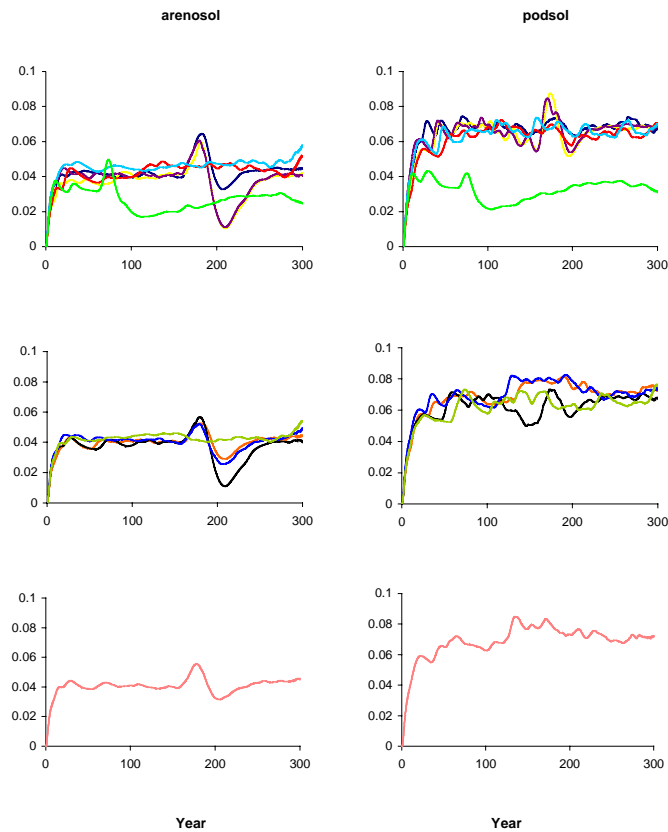
### Depth of Litter-layer 2



*Fig MD.Tree.22. Simulated trends in depth of litter layer 2(m, average over 100 plots) for all mixture of birch, beech, pine and oak. The mixtures include all combinations of 2, 3 and 4 species. The simulation experiment is performed both on a relatively pool sandy soil (arenosol) and a relatively rich sandy soil (podzol)*

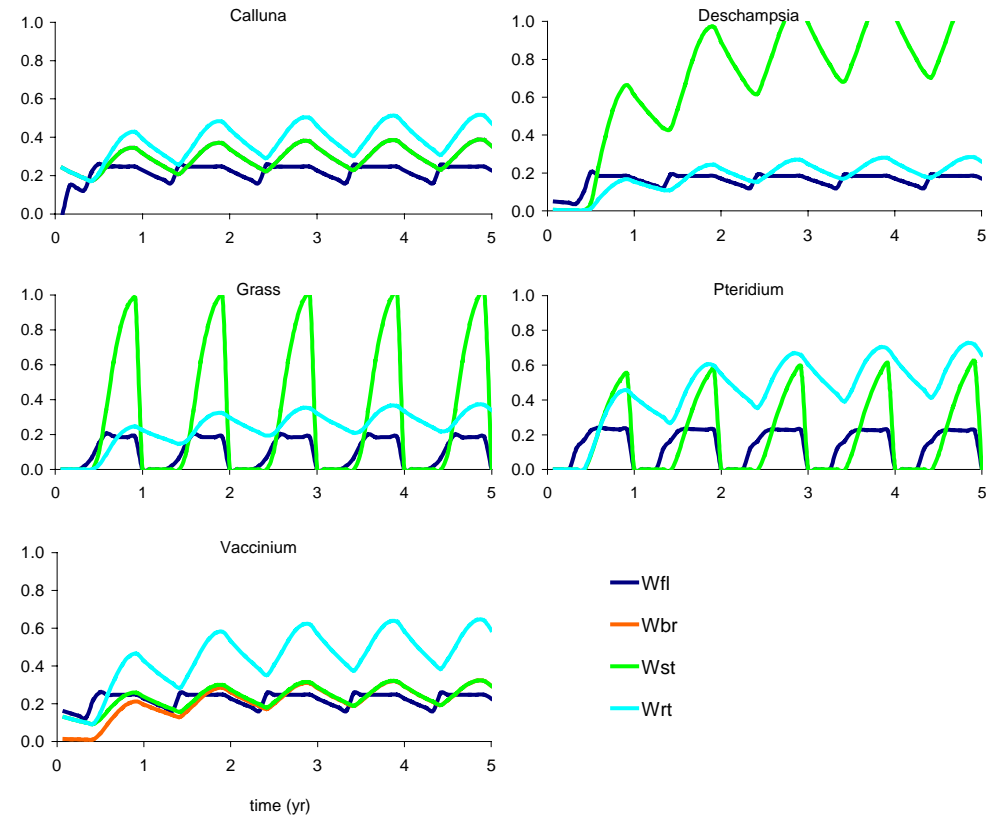


### Depth of Litter-layer 3



*Fig MD.Tree.23. Simulated trends in depth of litter layer 2(m, average over 100 plots) for all mixture of birch, beech, pine and oak. The mixtures include all combinations of 2, 3 and 4 species. The simulation experiment is performed both on a relatively pool sandy soil (arenosol) and a relatively rich sandy soil (podzol)*

### Weights (kg DM m<sup>-2</sup>)



*Figure MD-herbs-1. Development during a 5-year period of the weight of foliage, branches, stalks or stems and roots of Calluna, Deschampsia, Grass, Pteridium and Vaccinium.*

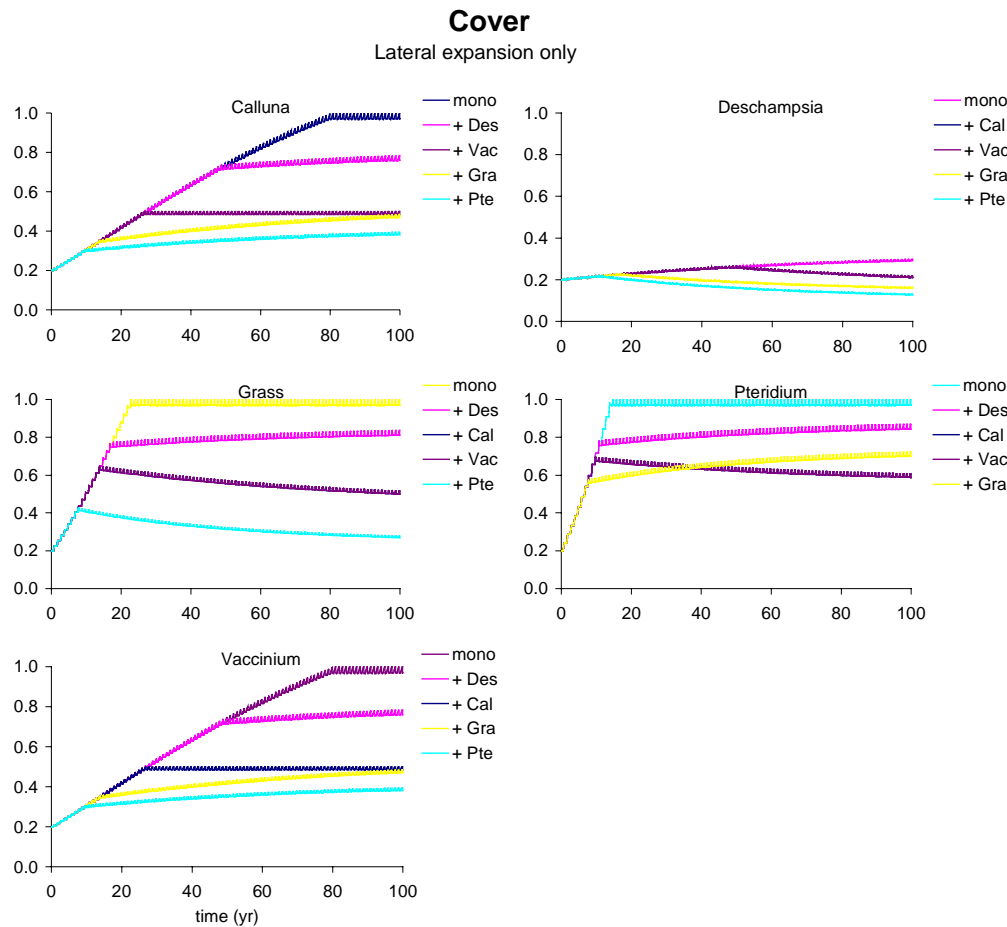


Figure MD-herbs-2. Change in cover during a 100 year period of Calluna, Deschampsia, Grass, Pteridium and Vaccinium, both in monoculture and in competition with one of the other herb species, if lateral expansion only is taken into account.

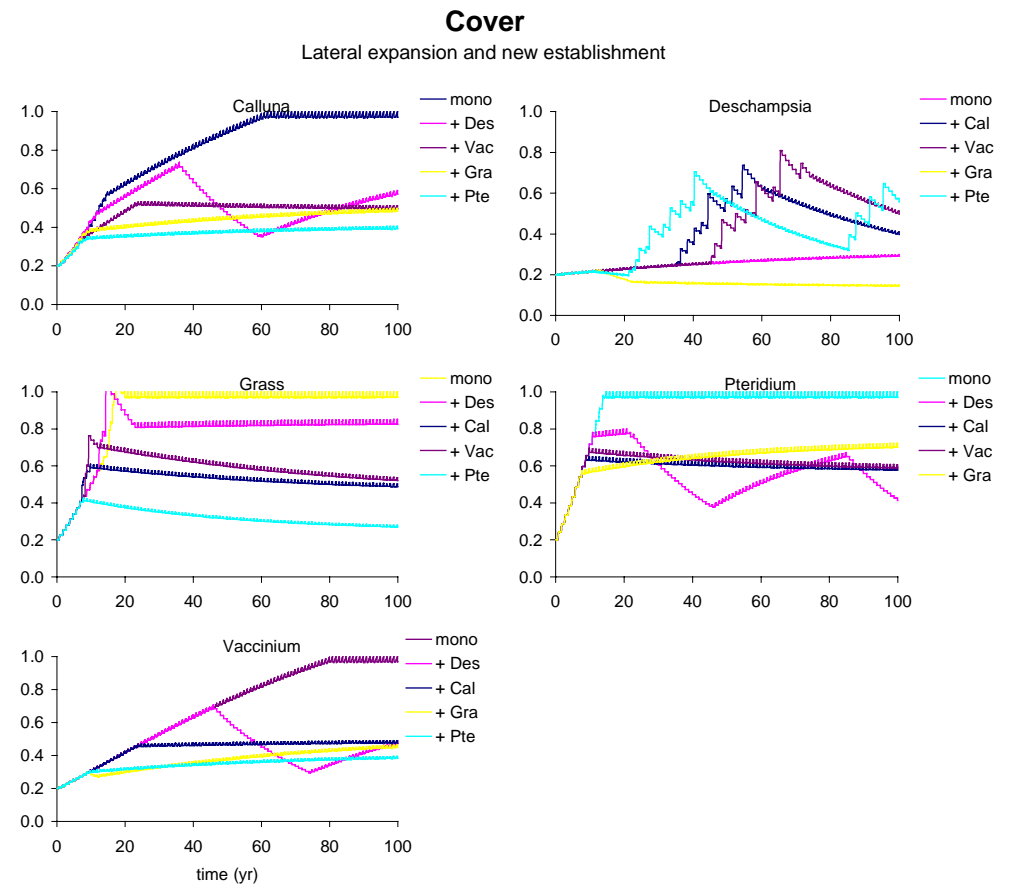


Figure MD-herbs-3. Change in cover during a 100 year period of Calluna, Deschampsia, Grass, Pteridium and Vaccinium, both in monoculture and in competition with one of the other herb species, if both lateral expansion and new establishment in the plot is taken into account.

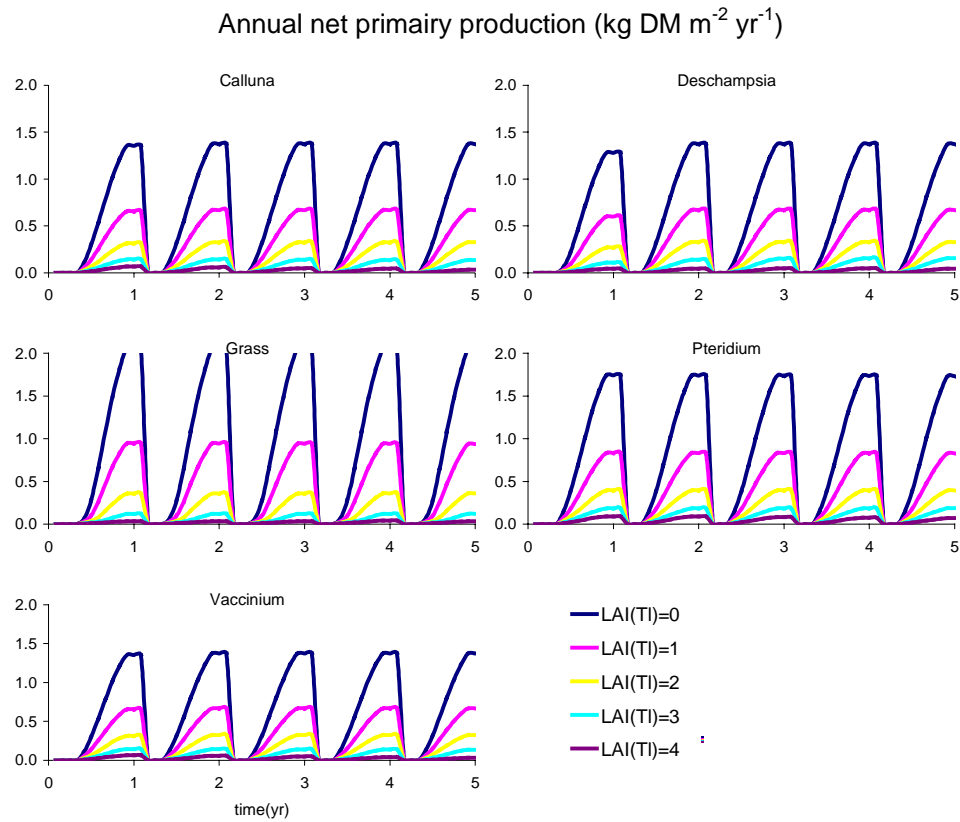


Figure MD-herbs-4. Effect of increasing LAI in the tree layer (LAI(TL)) on the annual net primary production of Calluna, Deschampsia, Grass, Pteridium and Vaccinium.

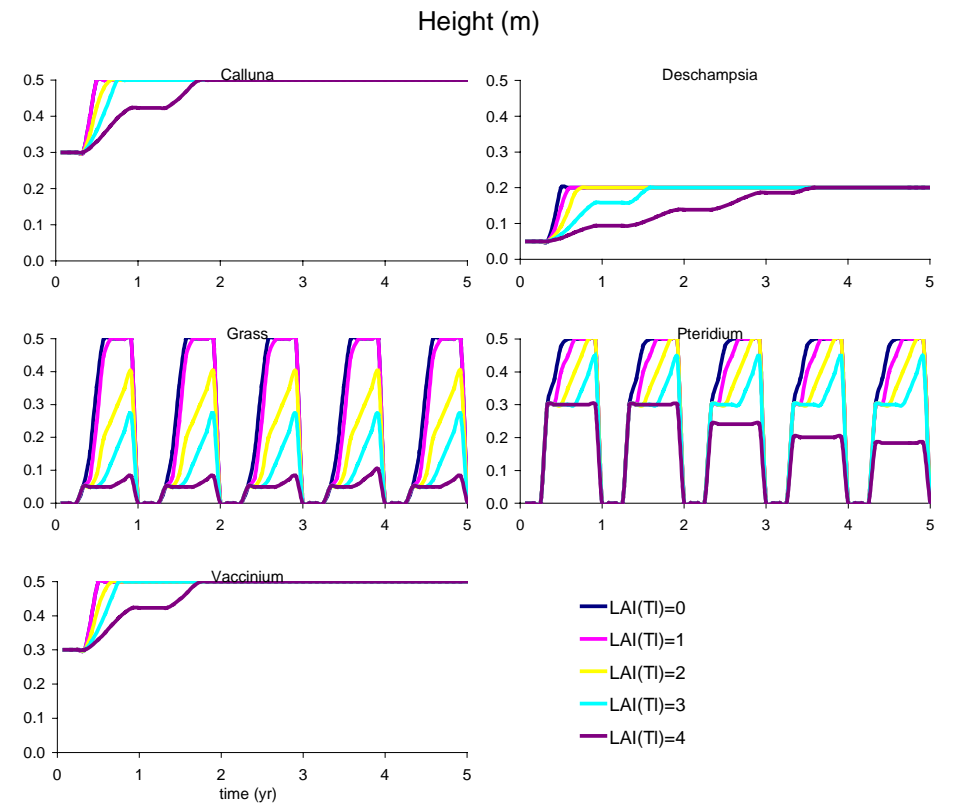


Figure MD-herbs-5. Effect of increasing LAI in the tree layer (LAI(TL)) on height of Calluna, Deschampsia, Grass, Pteridium and Vaccinium.

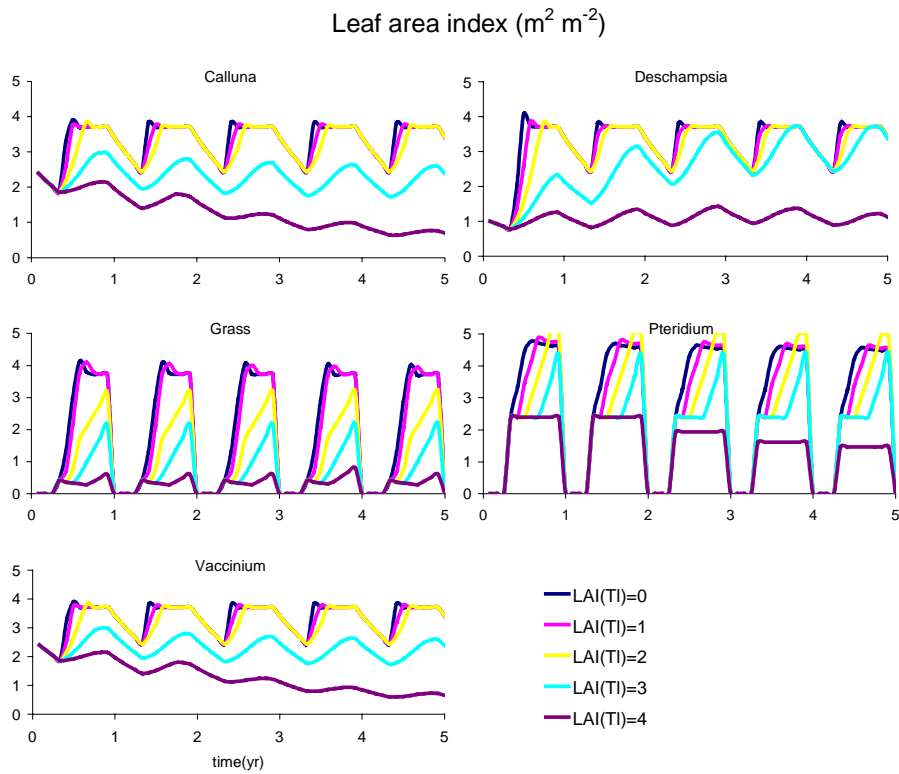


Figure MD-herbs-6. Effect of increasing LAI in the tree layer ( $LAI(TL)$ ) on LAI of Calluna, Deschampsia, Grass, Pteridium and Vaccinium.

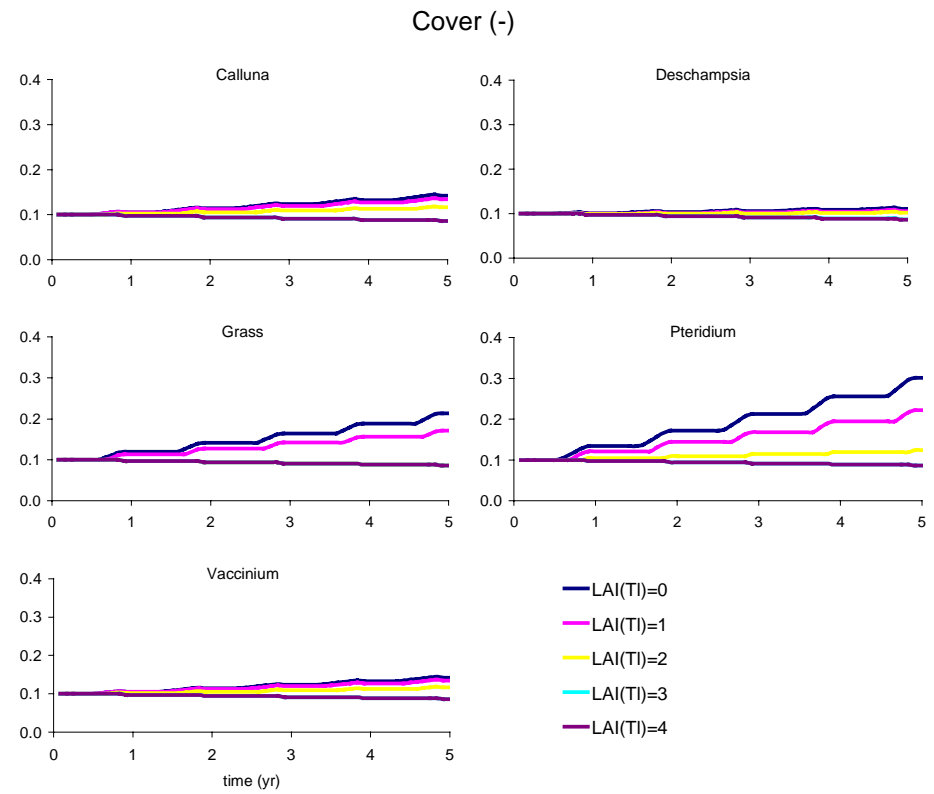


Figure MD-herbs-7. Effect of increasing LAI in the tree layer ( $LAI(TL)$ ) on cover of Calluna, Deschampsia, Grass, Pteridium and Vaccinium.

### 9.3.3 Effect of developing forest on herbs and grasses in understory

The main effect of a developing forest on the understory is that in time less and less light is available on the forest floor. This effect is evaluated here in a sensitivity analyses in which the LAI in the tree layer is increased from 0 (no tree layer) to 4 (closed forest).

A reduction in light availability in first reduces the net primary production of the species in the understory. Figure MD-herbs-4 shows that with increasing LAI in the tree layer, the productivity of the herbs declines exponentially.

This reduction in the production of plant dry matter affects the height growth, LAI and change in cover of the herb species. In FORSPACE, priority is given to increase in height, at the cost of not having an optimal foliage density and no lateral expansion (*Growth rate of foliage* in *Dynamics*- section). Figures MD-herbs-5-7 show that if the LAI in the tree layer exceeds  $2 \text{ m}^2 \text{ m}^{-2}$ , the lateral expansion is not possible anymore (new establishment does not play a role in this exercise) and that the maximal LAI and height of the species are not attained. Thus, with increasing forest density, a lower and sparsely foliated understory develops that slowly decreases in cover.

More specifically, if the LAI of tree layer equals  $3 \text{ m}^2 \text{ m}^{-2}$  then only *Deschampsia* can attain its maximum amount of foliage in the long-term, and the other species show a steady decline of LAI in time, both during the growing season and over the years. If LAI of the tree layer equals  $4 \text{ m}^2 \text{ m}^{-2}$  then only *Deschampsia* appears to maintain as a very sparse vegetation. At higher values of LAI in the tree layer, none of the herbs survive.

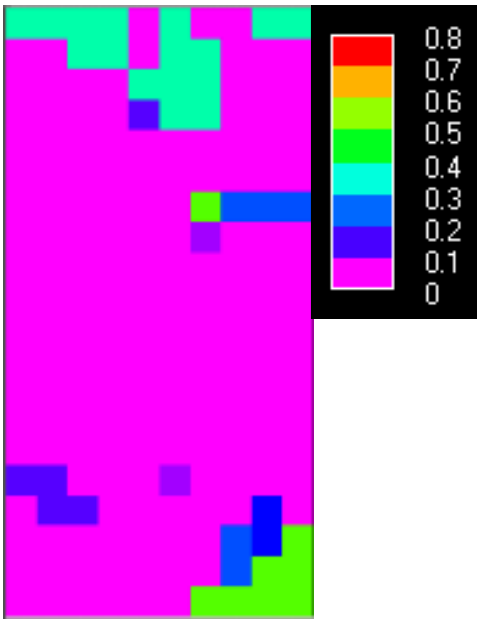
## 9.4 Spatial aspects

Dispersion of seeds from mother trees to its surroundings are a very important aspect of forest dynamics. The combination of locations that are suitable for germination of seeds and the proximity of a seed source is crucial for the understanding of forest dynamics of a given area. To show this feature of FORSPACE, a representation of a realistic area is required. For this exercise, a 200-ha large part of the Imbos of which the vegetation is known in detail, is used.

Figure MD-spatial-1 shows for this area for birch, beech, pine and oak the cover in the tree layer, as only adult trees are considered to produce seeds. Seeds are dispersed over the landscape depending on the number of seeds produced per individual tree, the number of adult trees and the dispersion range of the species. It can be seen in figure MD-spatial-1 that seeds are dispersed widely over the landscape but that the number of plots in which these seeds can germinate is much less, due to unfavourable conditions in the other plots in which the seeds are present. Another important point to note is that in FORSPACE germination of a species will not occur if seedlings of the same species are already present in the herblayer of the plot (see *Germination* in *Dynamics*-section)

## Betula

cover tree layer



number of seeds  
(max. scale: 100)

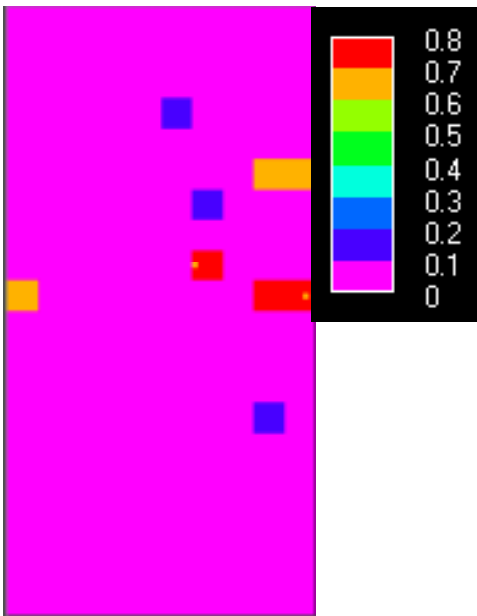


number of seedlings  
(max. scale: 100)

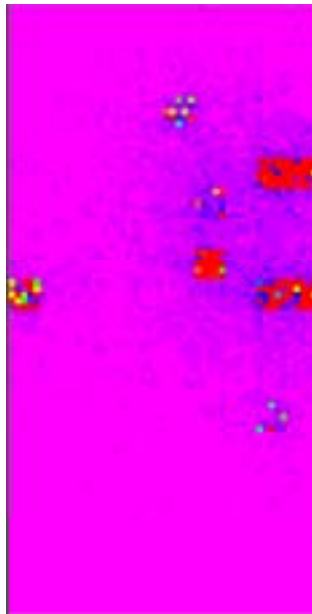


## Fagus

cover tree layer



number of seeds  
(max. scale: 50)

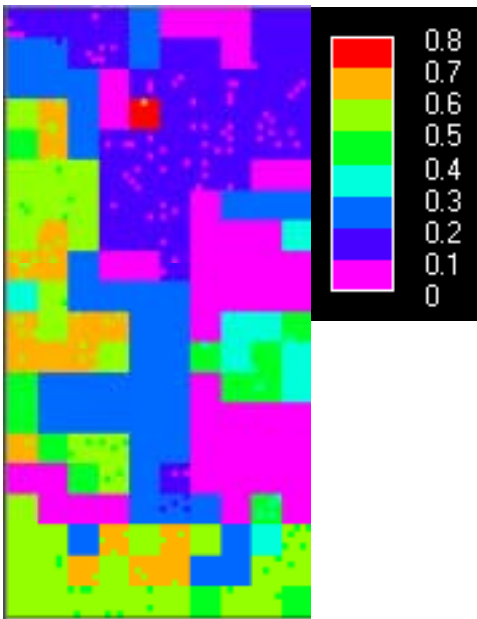


number of seedlings  
(max. scale: 50)

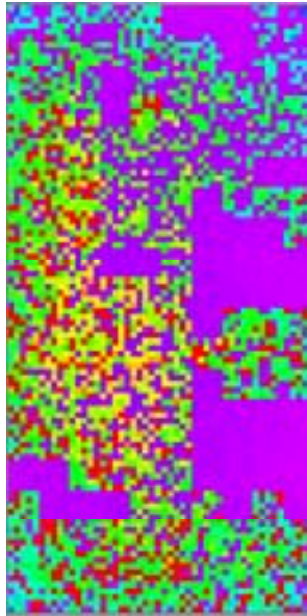


## Pinus

cover tree layer



number of seeds  
(max. scale: 100)

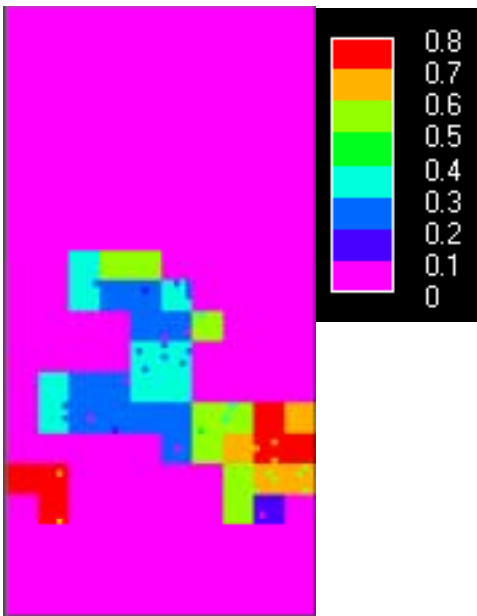


number of seedlings  
(max. scale: 100)

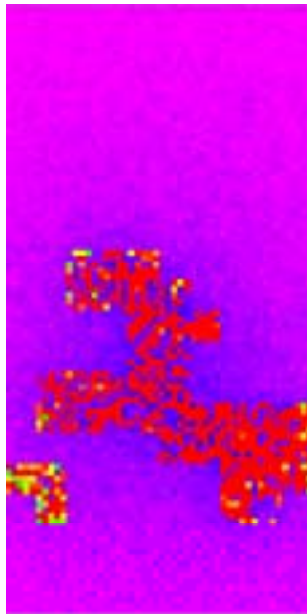


## Quercus

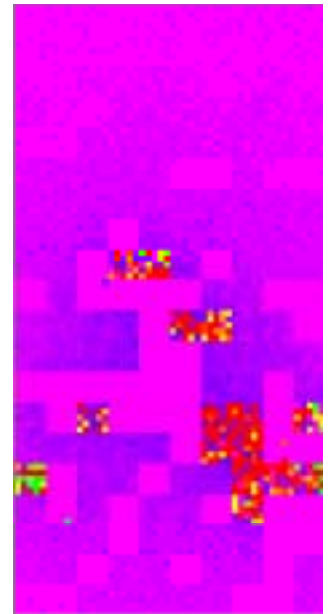
cover tree layer



number of seeds  
(max. scale: 100)



number of seedlings  
(max. scale: 100)



*Figure MD-spatial-1. Spatial aspects in FORSPACE: cover of trees in the tree layer, number of seeds and number of germinations per plot for birch, beech, pine and oak. The legend is truncated at a low maximum level to show the presence of very low numbers of seeds and seedlings. E.g many thousands of birch seeds can be present in a plot, but these all fall in the class > 100 seeds (indicated in red).*





## 10 Case study: the Imbos

To show the dynamics of FORSPACE for a realistic area, a number of scenarios are evaluated for the same area as presented in the previous paragraph. These scenarios include: forest development in the absence of grazing by large herbivores; forest development in presence of all herbivores (bovine, horse, red deer, roedeer, wild boar); forest development in presence of a single herbivore species; the impact of fire on forest development, both with and without the presence of herbivores.

These scenarios are evaluated for the herbivores with respect to the number of adult animals and the weight of the total population. For the plant species these scenarios are evaluated with respect to the number of occupied plots and the average cover of the occupied plots per species in the tree, shrub and herb layer, if relevant.

### 10.1 The Imbos

Figure CS-Imbos-1 shows the location of the case study as a section of the Imbos. The Imbos is part of the Veluwe. A mostly forested area of ca. 100.000 ha in the centre of The Netherlands. The Veluwe consists of a sandy soil with deep ground water tables and has a long history of heavy (over-)grazing on extensive heathlands. These heathlands are planted with Scots pine during the 19<sup>th</sup> century. The vegetation of the Imbos consists mainly of Scots pine with oak; heathlands in which Scots pine seedlings and saplings are established; and planted beeches along the lanes through the forest that are spreading its seeds and seedlings into the Scots pine forest.



## 10.2 Herbivores

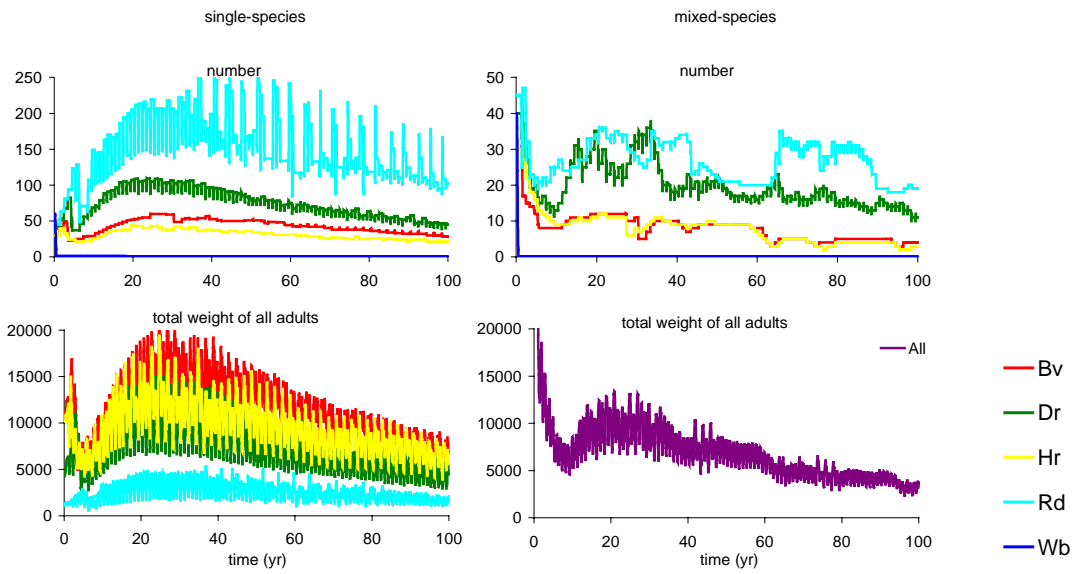
The study area appeared to be too small for continuous presence of wild boar. Wild boar feeds mainly on grass and acorns. The study area contains 2 ha of grassland only, and masting of oak is too infrequent to provide wild boar population a sustainably with food. Therefore wild boar will not be considered in the following analyses.

Figure CS-herbivores-1 presents the number of adults and the total weight of all adult herbivores present on the 200 ha section of the Imbos. This is done both when 1 species only is present in the area and when 4 species are present simultaneously. The single-species runs of FORSPACE show that for all herbivore species there is a steady decline in numbers over a period 100 years. This indicates for an area of this size that single-species grazing cannot stop the development of forest into closed forest with a sparse understory. The results show that with body size both the numbers decline, as well as the fluctuations in numbers. Roedeer can attain very high densities (on average 75 per 100 ha), but also strong fluctuations. Whereas bovine and horse attain much lower densities and also much less fluctuation in number. The total weight of all adults present in the area show that this is inversely related to body weight: the total bovine population can attain a much higher total weight than the roedeer population, whilst the horse and red deer populations take intermediate values.

The mixed-species runs of FORSPACE show the consequences of interactions between the different herbivore species when they compete for food. Compared to the single-species runs the densities of all species is much reduced (note different scaling of the Y-axis). On average the fraction of adult numbers in the mixed species scenario compared to the same species in the single species scenario is 19, 28, 26 and 20% for bovine, red deer, horse and roedeer, respectively. Furthermore, the fluctuations in the number of adults appears to be stronger also for the species with large body sizes. When comparing the total weight over all adults animals present in the area between the single-species and the mixed-species scenarios then the mixed species values take a relatively low position: less animal biomass is produced than the single-species bovine, horse and red deer populations, but more than the single species roedeer population.

The impact of fire on the dynamics of the herbivores (results not shown) is that for the given area size of 200 ha, bovine and horse in mixture with the other species cannot maintain a sustainable population even at a low fire frequency ( $P=0.0001$  probability per cel per year). This is because at low fire frequencies large areas are burned so that insufficient food is available in the area. Also at higher fire frequencies ( $P=0.001-0.01$ ) the area appears to be too small for a sustainable population of bovine and horse.

## herbivores on 200 ha of Imbos



*Figure CS-herbivores-1. Number of adults and total weight of all adult herbivores present on a 200 ha section of the Imbos, both as single species (1 species present in the area) and as mixed species (bovine, horse, red deer and roedeer simultaneously present in the area)*

### 10.3 Trees

To show the forest dynamics over the landscape both the number of plots that are occupied by a tree species were tracked and the average cover of all plots in which the tree species occurs. This will be shortly discussed for each of the layers in which trees may occur. The scenario's that are evaluated include the absence and presence of herbivores, either in mixture or as single species, and the absence or presence of fire with two different frequencies of occurrence.

Figure CS-tree-1 shows that rate of spread of beech and oak over the landscape is strongly reduced by the presence of herbivores. Apparently, many seedlings and saplings are eaten before they can reach the tree layer. The presence of herbivores does not affect the propagation of birch and pine over the landscape very much. For these species there is in general a steady decline in occupied plots due to competition with either beech or oak occurring in the same plot. Furthermore, there are only small differences between herbivore species in their effect on the propagation of a tree species. The same is true for differences between herbivore species in their effect on the average cover of occupied plots (Figure CS-tree-1). The absence or presence of herbivores does affect the average cover of plots occupied by beech and oak. Grazing increases the *average* cover of these tree species because due to a lower propagation over the landscape, much less plots contain new young beech and oak trees with a low coverage.

Figure CS-tree-2 shows that grazing has a strong impact on the propagation of tree species in the shrublayer. Grazing reduces the number of plots that are occupied by beech and oak, increases for birch and pine. There appears to be no significant effect of grazing on cover of occupied plots in the shrub layer, and also little differentiation between herbivore species.

Figure CS-tree-3 shows that the presence of herbivores has little or no impact on propagation of beech and oak, however grazing strongly increase the opportunities of germination and establishment of pine. Again there is little differentiation between herbivore species in their effect on the propagation of tree species over the landscape.

Figure CS-tree-4 shows the interacting effects of the presence of herbivores and the occurrence of fire on the number of occupied plots by a tree species in the treelayer. The effect of fire in the absence of grazing is a strong increase of the rate at which a tree species spreads over the landscape compared to the no-grazing/no-fire (Fig. CS-tree-1). The lower fire frequency used ( $P=0.001$ ) has a stronger effect than the higher fire frequency ( $P=0.01$ ) because in the former case larger areas are burnt. In the scenarios where there is both grazing and fire there is a strong effect on the forest development. This is especially the case for beech and oak, whereas this situation appears to be relatively beneficial for pine compared to the other species.

Figure CS-tree-5 shows the same scenarios for trees in the shrublayer. Comparing the no grazing/no fire scenario (CS-tree-2) with the no grazing/fire scenario (CS-tree-5)

then birch and to a lesser degree pine take advantage of the occurrence of fire. For beech and oak there is a strong interaction between grazing and the occurrence of fire, such that the number of plots with trees in the shrub layer is much reduced in the presence of herbivores.

Figure CS-tree-6 presents the interactions between grazing and fire of trees in the herb layer. For both beech and oak there appears to be little interaction, whereas for birch and to a lesser extent for pine the combination of grazing and fire is beneficial for the propagation of these species over the landscape rather than fire only. Comparing the no grazing/no fire scenario (CS-tree-3) with the no grazing/fire scenario (CS-tree-6), there appears to be little difference in the rate of spread of both birch and pine in the herb layer.

Summarising: the spread of both beech and oak over the landscape appears to be reduced by grazing, and this effect is stronger if an occasional forest fire occurs. These effects are due to the effect of herbivores on the shrub layer, rather on the trees of these species in the herb layer.

Also birch and pine take advantage of the occurrence of fire, but are much less affected by grazing, or grazing is beneficial for their spread because of its negative impact on beech and oak.

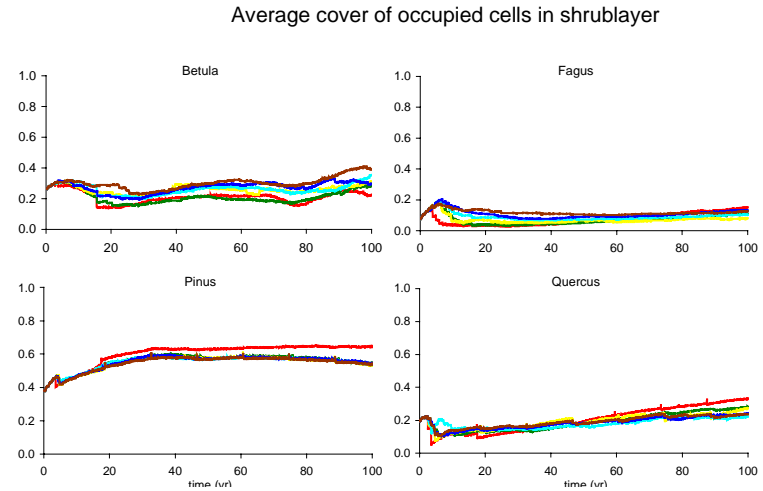
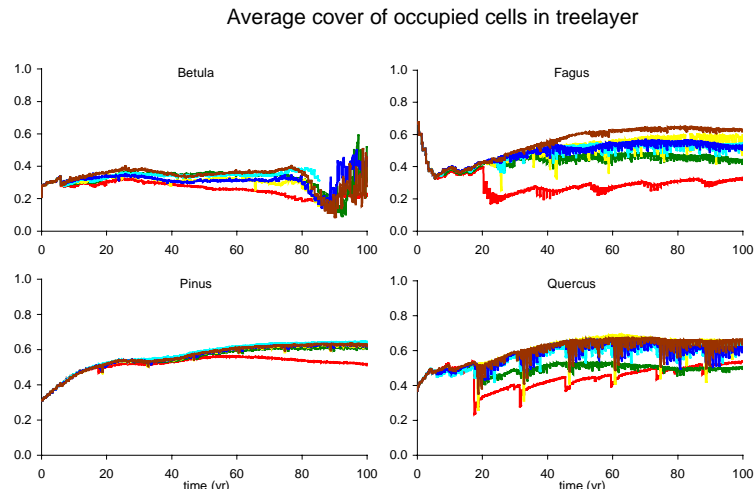
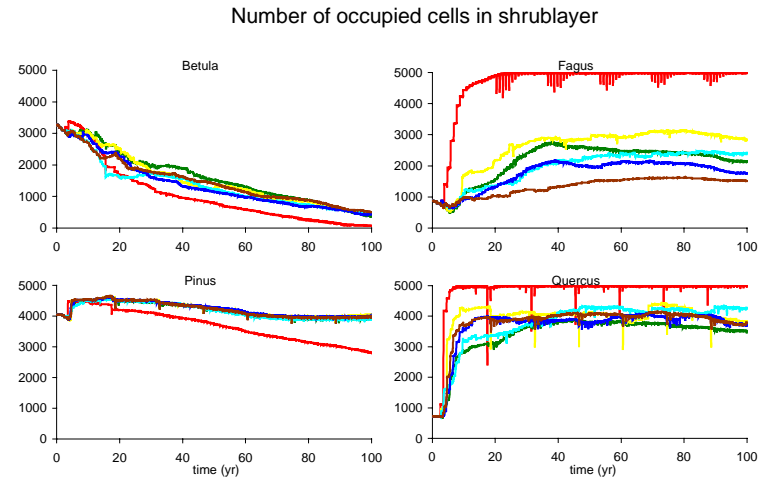
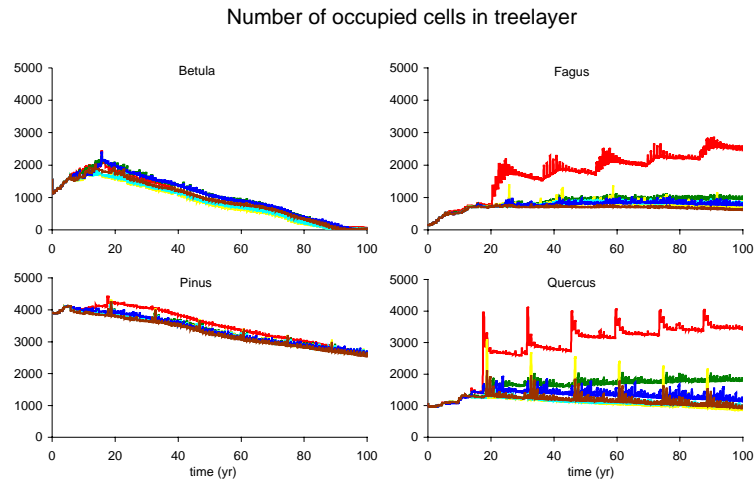


Figure CS-tree-1. Number of occupied plots and average cover of occupied plots on a 200 ha section of the Imbos per tree species in the tree layer under 6 grazing scenarios: no grazing; grazing by a single herbivore species and grazing by all herbivore species (see CS-tree-3 for legend)

Figure CS-tree-2. Number of occupied plots and average cover of occupied plots on a 200 ha section of the Imbos per tree species in the shrub layer under 6 grazing scenarios: no grazing; grazing by a single herbivore species and grazing by all herbivore species (see CS-tree-3 for legend)

Number of occupied cells in herblayer

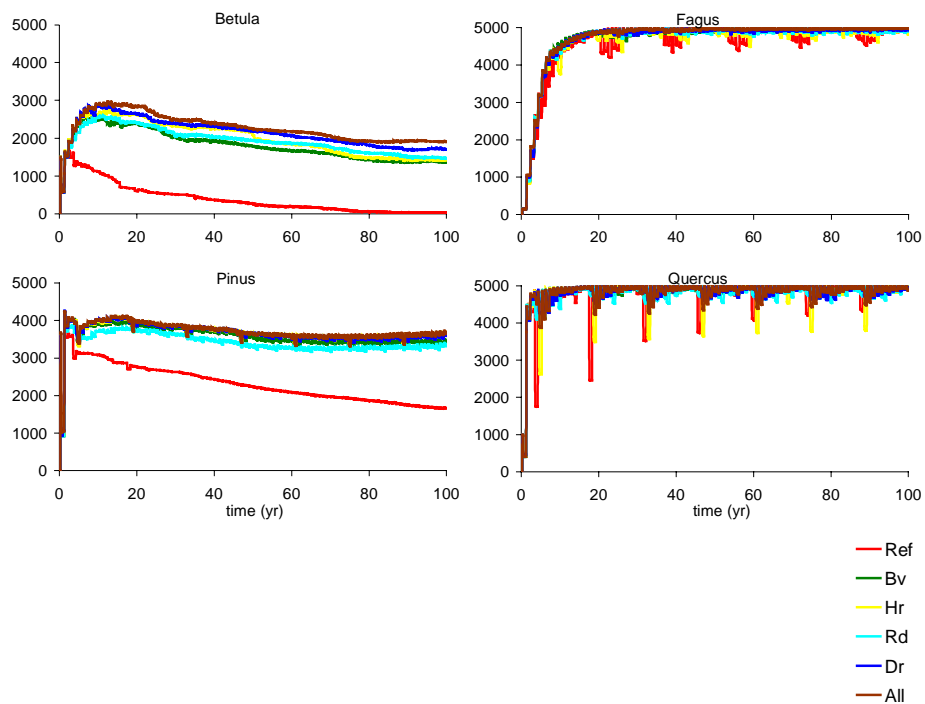


Figure CS-tree-3. Number of occupied plots on a 200 ha section of the Imbos per tree species in the herb layer under 6 grazing scenarios: no grazing, grazing by a single herbivore species and grazing by all herbivore species

Number of occupied cells in treelayer

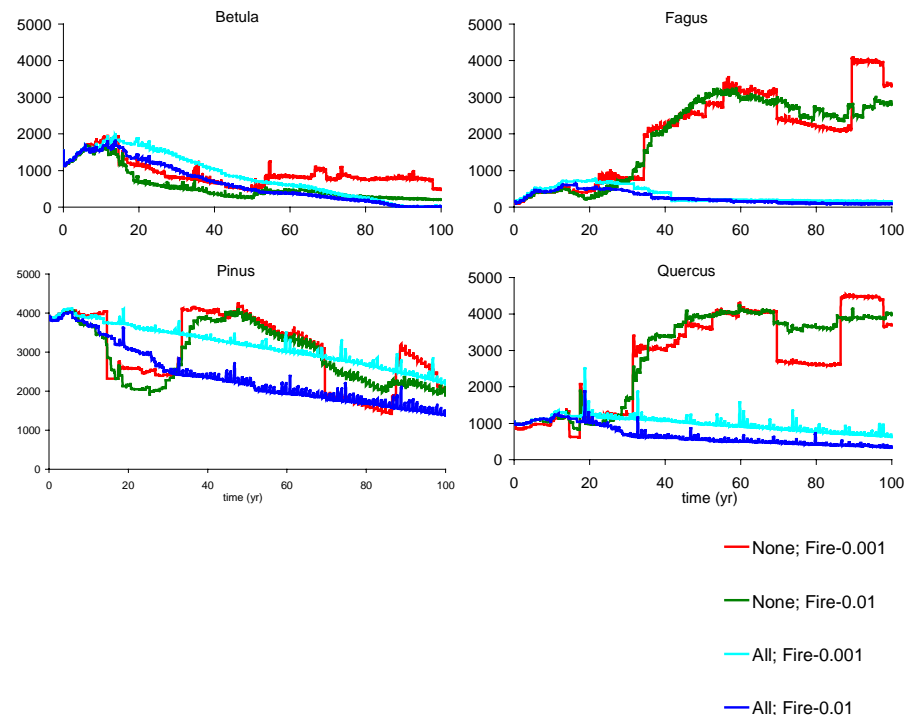
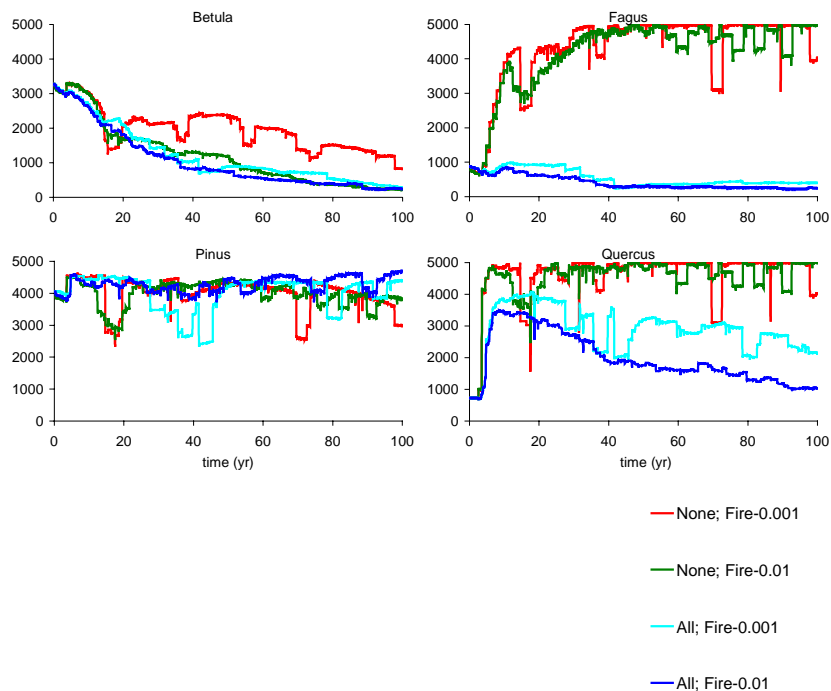


Figure CS-tree-4. Number of occupied plots and average cover of occupied plots on a 200 ha section of the Imbos per tree species in the tree layer under 4 scenarios: no grazing - fire frequency=0.001; no grazing - fire frequency=0.001; grazing by 4 herbivore species - fire frequency = 0.001; grazing by 4 herbivore species - fire=0.001.

Number of occupied cells in shrublayer



Number of occupied cells in herblayer

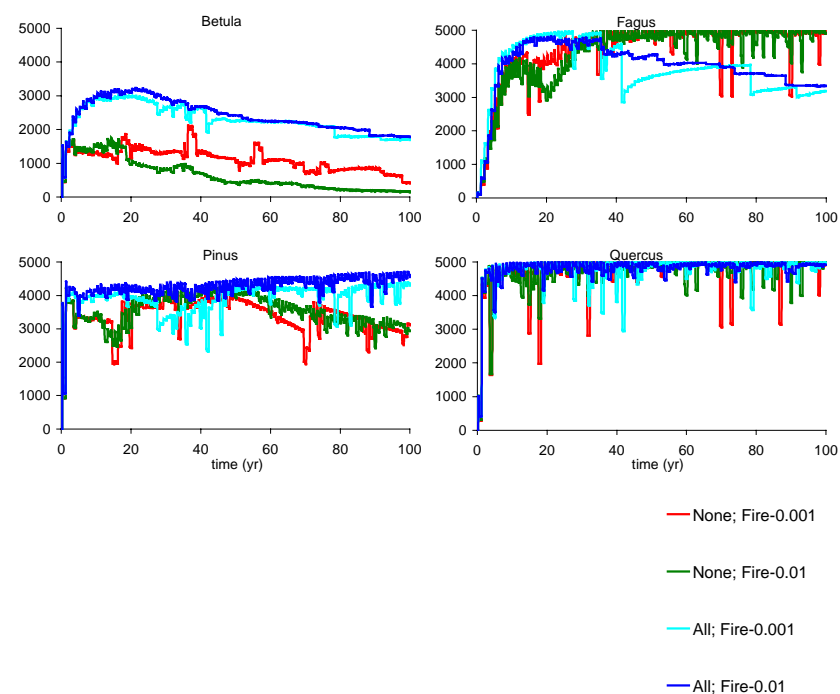


Figure CS-tree-5. Number of occupied plots and average cover of occupied plots on a 200 ha section of the Imbos per tree species in the shrub layer under 4 scenarios: no grazing - fire frequency=0.001; no grazing - fire frequency=0.001; grazing by 4 herbivore species - fire frequency = 0.001; grazing by 4 herbivore species - fire=0.001.

Figure CS-tree-6. Number of occupied plots and average cover of occupied plots on a 200 ha section of the Imbos per tree species in the herb layer under 4 scenarios: no grazing - fire frequency=0.001; no grazing - fire frequency=0.001; grazing by 4 herbivore species - fire frequency = 0.001; grazing by 4 herbivore species - fire=0.001.



## 10.4 Herbs

Figure CS-herb-1 shows that the presence of herbivores increases the propagation of *Calluna*, but reduces this for *Deschampsia*, Grass and *Vaccinium*. The long-term differences between the impacts of different herbivores is negligible except for *Deschampsia*. In that case roedeer has the least impact, whereas horse and bovine appear to reduce its propagation the most. The strong propagation potential of Grass and *Deschampsia* is consistently set back by grazing. Furthermore, the presence of herbivores has a strong advantageous effect on the average cover of Grass in the plots it already occupies. Grazing slightly reduces the cover of *Deschampsia*, but has no effect on either *Calluna* nor *Vaccinium*. For the latter two species the development of the forest has stronger impact on their cover than grazing has.

Figure CS-herb-2 shows the interacting effects of the presence of herbivores and the occurrence of fire on the number of occupied plots by a herbs and grasses. For *Deschampsia*, Grass and *Vaccinium* the rate of spread over the landscape is the fastest for the scenario with a low fire frequency and without herbivores. For *Calluna* the presence of herbivores in combination with fire is beneficial for its propagation, especially the higher fire frequency. Comparing the no-fire-scenarios (Figure CS-herb-1) with the fire-scenarios (Figure CS-herb-2), the results shows that fire is detrimental for the propagation of *Calluna*, *Deschampsia* and *Vaccinium*, but beneficial for Grass. Although *Calluna's* competitive ability increases in the grazing-no-fire-scenarios relative to the other herb species, the scenario with grazing only (CS-herb-1) is the most beneficial for *Calluna*. The presence of herbivores strongly reduces the potential propagation of Grass and *Deschampsia* by consistently removing seedlings from newly invaded plots.

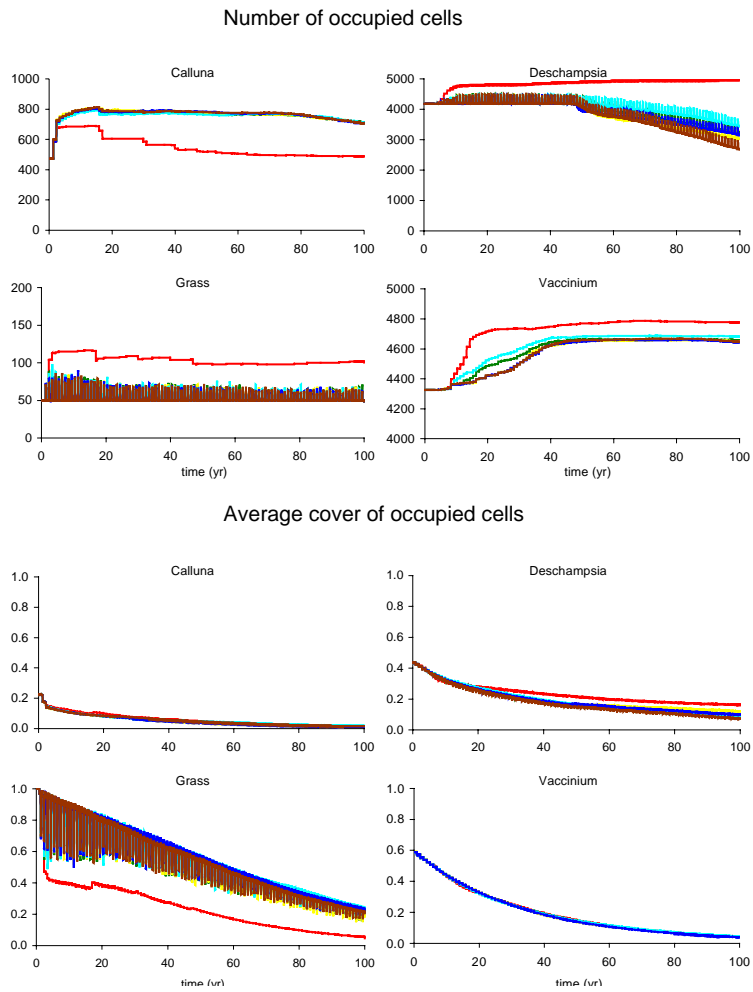


Figure CS-herb-1. Number of occupied plots and average cover of occupied plots on a 200 ha section of the Imbos per herb species under 6 grazing scenarios: no grazing; grazing by a single herbivore species and grazing by all herbivore species

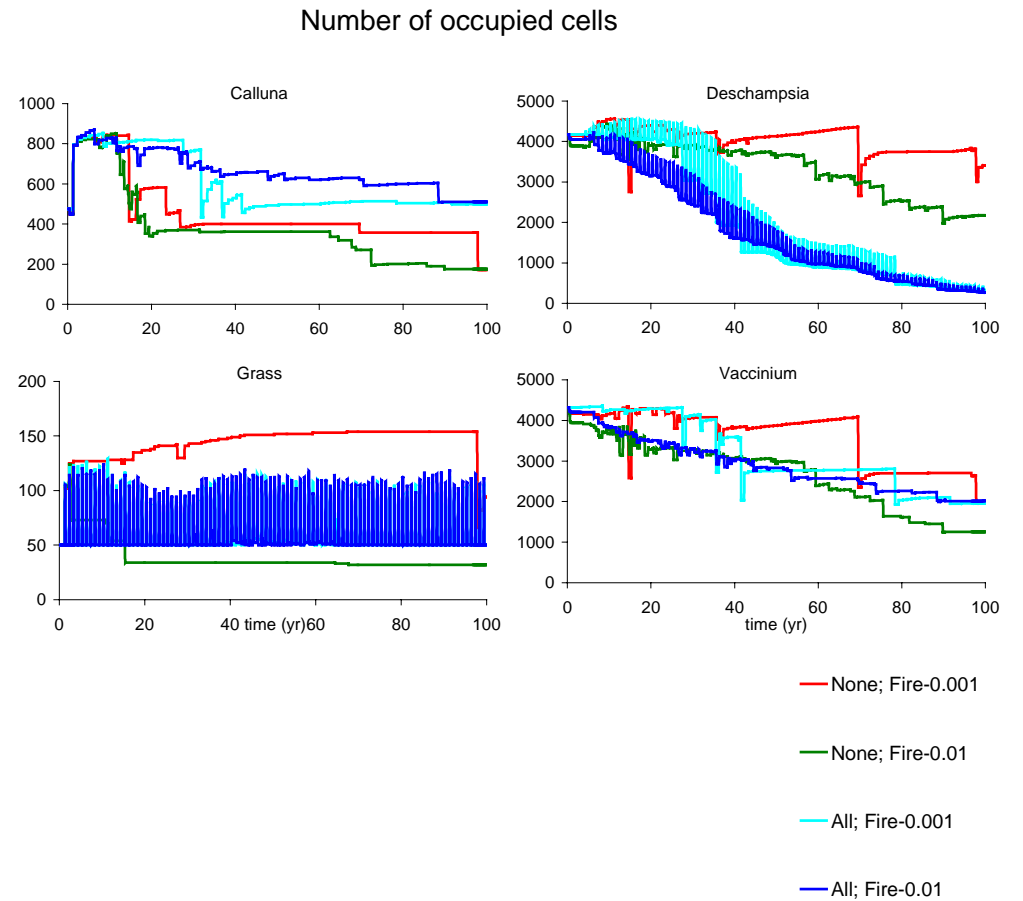


Figure CS-herb-2. Number of occupied plots and average cover of occupied plots on a 200 ha section of the Imbos per herb species under 4 scenarios: no grazing - fire frequency=0.001; no grazing - fire frequency=0.01; grazing by 4 herbivore species - fire frequency = 0.001; grazing by 4 herbivore species - fire=0.01.

## 11 Spatial analysis

*Rienk-Jan Bijlsma*

### 11.1 Introduction

#### 11.1.1 Scope

Spatially explicit simulation models become increasingly important at the regional and national scale. They provide insight into the consequences of processes, decisions and scenarios that affect landscapes to an extent that depends on features of the landscapes themselves.

At present, procedures for structuring and processing raster-based model output in an ecological context are far from standardized. This is because both spatial resolution and extent influence the analysis of spatial pattern. Although geographical information systems and other image-processing software provide many metrics that describe *e.g.* heterogeneity, diversity, granularity, connectivity and fragmentation, the interpretation of these measures on the basis of landscape features and from the perspective of one or more species is still in its infancy (see Spies & Turner, 1999) for a thought provoking review including references to the literature on landscape metrics).

This chapter offers a procedure for the analysis and ecological interpretation of time series of state variables resulting from models that describe the spatial dynamics of forest landscapes on the basis of the dynamics of establishment, growth and dispersal of structurally important tree, shrub and vascular plant species. Output from the ForSpace-model for several scenarios is used to illustrate the procedure.

#### 11.1.2 Basic principles

The following constraints underly the spatio-temporal analysis of model output:

- 1 Spatial resolution reflects the scale necessary for individual-based modelling of ecological processes at the landscape level. Therefore, landscapes of several (tens of) kilometers are represented by plots that are typically 20-100 m wide.
- 2 Temporal resolution reflects the time constant of successional forest dynamics. Typical time intervals measure 5-10 year. This resolution is much coarser than the time step used in the simulation model which is about a day, week or month.
- 3 The analysis must use commonly available software and be standardized to a large extent but at the same time be transparent and easily adaptable and extendable. This is accomplished by using Microsoft Access as database and Microsoft Visual Basic as programming language and user interface. Grids from ArcView Spatial Analyst can easily be exchanged as well.

### **11.1.3 User interface: SpatialAccess**

SpatialAccess allows for loading of model output, hierarchical classification, calculation of turnover rates and transition probabilities of cover types etc. The exchange of grids with PCRaster and ArcView Spatial Analyst is part of the interface as well.

SpatialAccess is written in Visual Basic 6 and uses DAO (Microsoft Data Access Objects) to manipulate (select, update, insert, delete) data in tables and queries present in a specified Access-database.

### **11.1.4 Standardized procedures: an overview**

The processing of model output proceeds by a number of procedures that will be described in separate sections. This paragraph provides an overall view of the analysis. The steps involved are (and see Fig SA-1):

- 1 An Access-database is created with standard tables and queries. This database will be used to load and process all scenarios for a common region. See section Description of the database.
- 2 SpatialAccess is used to enter general information and to load all model output (PCRaster grids) for each scenario separately. See section Description of standardized procedures § Loading model output.
- 3 SpatialAccess calculates values for total cover of tree, shrub and herb layer per plot and assesses overall percentage cover per species per layer for each time step. See section Description of standardized procedures § Summary statistics.
- 4 SpatialAccess classifies each plot within a system of predefined cover types. See section Description of standardized procedures § Classification.
- 5 For each time step SpatialAccess creates co-occurrence matrices for cover types. These matrices contain the probabilities that a plot with cover type *i* has a neighbour plot with cover type *j*. See section Description of standardized procedures § Co-occurrence probabilities.
- 6 For each time interval SpatialAccess calculates a transition matrix for cover types. These matrices contain probabilities that a plot with cover type *i* at time step *t* has changed to cover type *j* at time step *t*+1. See section Description of standardized procedures § Transition probabilities.
- 7 For the whole simulation run SpatialAccess calculates turnover rates for each cover type. Output are frequency distributions of age. See section Description of standardized procedures § Turnover rates.
- 8 Each (derived) spatial variable can be written in the form of a PCRaster-map or ArcView-grid using the Output-tab of SpatialAccess.

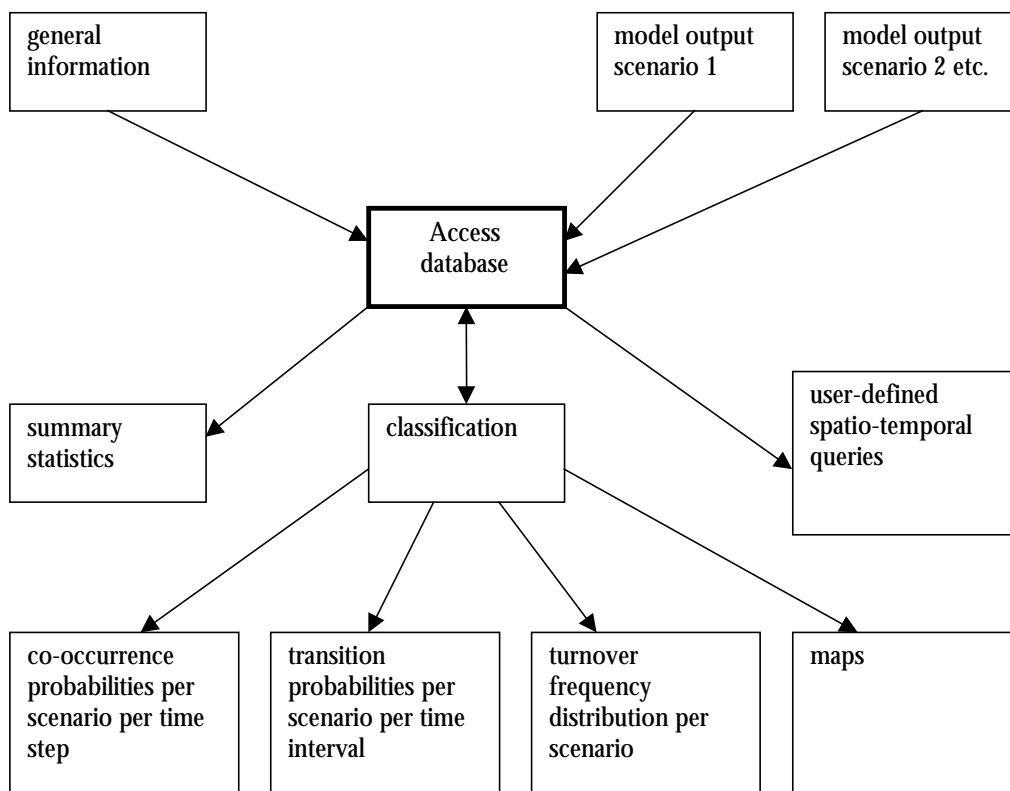


Figure SA-1. Standardized procedures for the loading and processing of grid-based model output using the SpatialAccess user interface.

### 11.1.5 User-defined procedures

The full functionality of Microsoft Access and Excel including VBA-modules can be used to analyse the database for both spatial, temporal and spatio-temporal features. This is especially important in a research environment. The performance of (derivatives of) state variables of single plots as well as their neighbours can easily be assessed thereby extending the opportunities for model debugging.

### 11.1.6 Case study and scenarios

An area of 1 x 2 km in De Imbos is used to illustrate the procedures. De Imbos is situated in the southern fringe of the Veluwe, a complex of push moraines and drift sand in the centre of the Netherlands. It is a former heathland area with some oak coppice, afforested with pine largely in the second half of the 19th century. De Imbos was used in previous simulation studies using grids with 1 ha plots. For the purpose of the present study, an 1 x 2 km subset was selected in order to evaluate model performance including gap dynamics: all plots have been divided into 20 x 20 m plots thereby retaining the initial values for all state variables.

Four model scenarios have been loaded, abbreviated by AA (all animals: cattle, red deer, roe deer and wild boar present as herbivores), NA (no animals), AF (all animals

and a fire regime), NF (no animals with a fire regime). These scenarios have been evaluated over a period of 100 year in 5-year intervals.

## 11.2 Description of the database

The Access-database is central to all analyses. The initial database consists of a number of tables and queries with well defined structures and relationships. For the present case study it is named **imbos.mdb**. In the course of the analysis more and more (user-defined) tables and queries will be added to the database. Table SA-1 describes the function of each (initial) table and query whereas Fig. SA-2 illustrates the relationships between tables after four scenarios have been loaded.

*Table SA-1. Description of the tables and queries available for standardized procedures.*

<i>table/query</i>	<i>function</i>
tblGeneral	static information; fields: unique plot number (idplot: primary key) and corresponding row (rw) and column number (cn) in the grid; former landuse (first cadastral map 1832); soil type (specified in tblSoil); type of grazing (specified in tblGrazing); missing value Yes/No
tblSoil	soil types with descriptions
tblGrazing	types of grazing and descriptions
tblDataTemplate	template for loading model output per scenario resulting in tblDataX, tblDataY etc. for scenario X, Y etc.; fields: month, idplot, cover type (CLS specified in tblCLS), percentage cover of herb layer (CH), shrub layer (CS), shrub layer made up of tree species (CSt), tree layer (CT), percentage cover of all species studied per layer (e.g. CHCal, CSSor, CHFag, CTFag for Calluna in herb layer, Sorbus in shrub layer and Fagus in herb en tree layer) and height of all species per layer
tblTotalPCT	overall percentage cover per cover type per scenario; fields: scenario (two-character string), month, cover type (specified in tblCLS) and percentage cover
tblCLS	cover types with descriptions
tblCLSCoOccurrence	co-occurrence probabilities for cover types per scenario per month; fields: scenario, month, iCLS (cover type), jCLS (neighbouring cover type), probability
tblCLSTransition	number of transitions between cover types per scenario for the interval (month, month+time interval); fields: scenario, month, CLS1, CLS2, number of transitions
tblCLSTurnover	ages per cover type found by screening all grid plots per scenario through time; fields: scenario, CLS, age
qryCLSCrossTab qryToCLSCrossTab	query (and auxiliary query) used to derive for each scenario the percentage cover per cover type per month
qryCLSTransition qryToCLSTransition	query (and auxiliary query) used to derive for each scenario transition probabilities for each combination of cover types per month
qryCLSTurnover qryToCLSTurnover1 qryToCLSTurnover2	query (and auxiliary queries) used to derive for each scenario the frequency distribution of ages per cover type

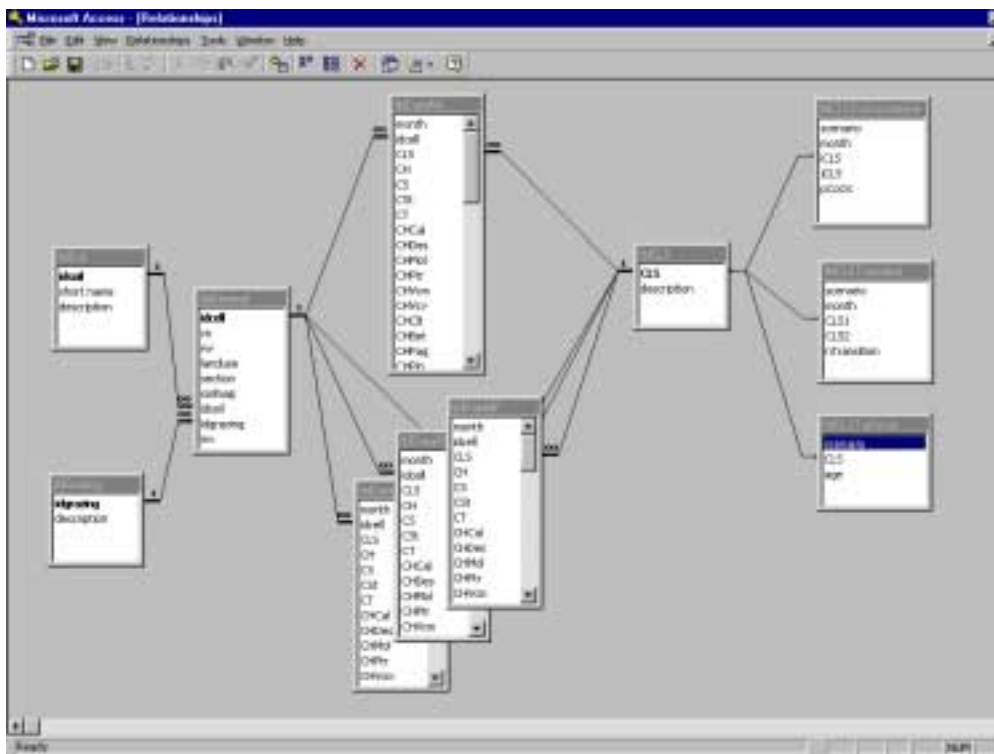


Figure SA-2. Relationships between the tables in the Imbos-database after loading four scenarios (AA, NA, AF and NF).

### 11.3.1 Loading model output

Before the model output is loaded, SpatialAccess requires the following information (asked for by the **tab General** and by separate windows): database name (select database window), name of the directory that contains the output files (select directory window), start month, end month and month interval, scenario (two-character string), clone maps for scalar and nominal input (PCRaster terminology) and (PCRaster) soil map if tblGeneral has to be filled first.

Model output generated by the PCRaster-model ForSpace consists of files (maps) for fraction cover or height (in decimal m) per species in a particular layer. This information is contained in the filename. *E.g* the map CBetH101.151 represents the cover values for *Betula* in the herb layer for month 1151. So at present, the **tab Input** is PCRaster-specific and used to indicate which tree (T), shrub (S) and herb (H) species must be loaded, for which variables, cover (C) and/or height (H), and how file names are structured with respect to variable, layer and species.

Each scenario is loaded in a separate table derived from tblDataTemplate. *E.g* scenario AA (all animals *i.e* herbivores) is stored into tblDataAA.

All (scalar) cover fractions and heights are multiplied by 100 thus representing (integer) percentages and centimeters, respectively, and stored as datatype Byte.

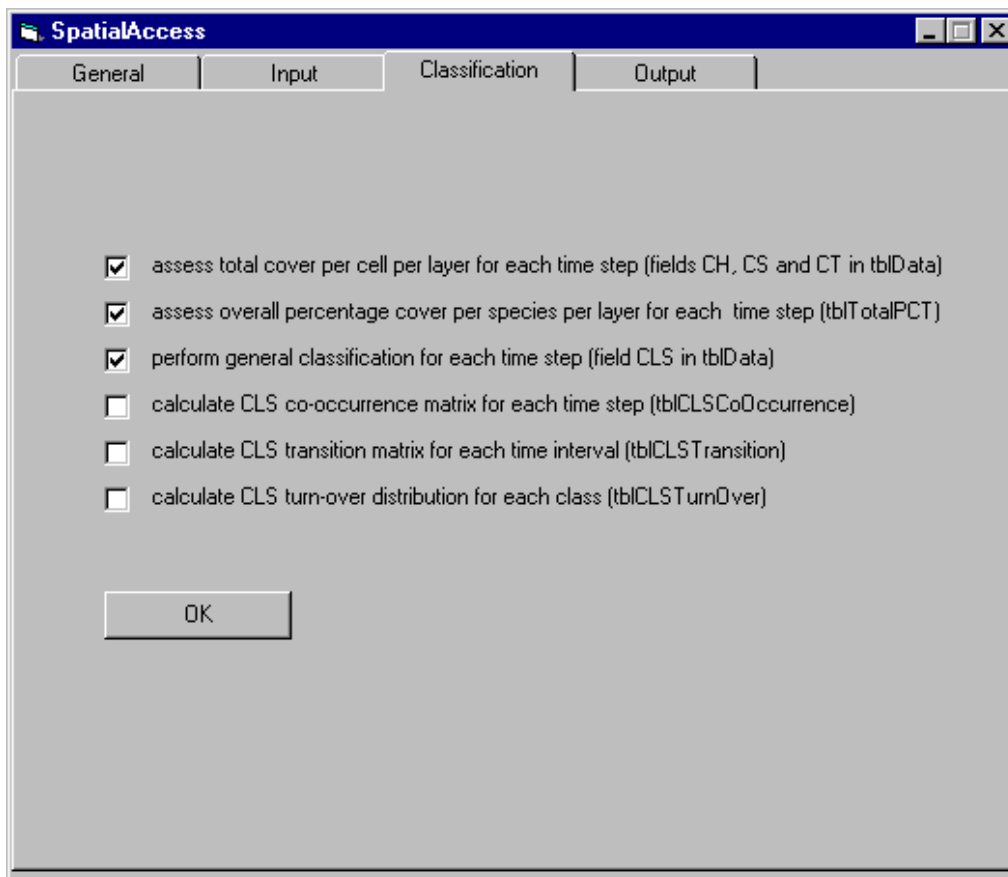


Figure SA-3. Check boxes on the tab Classification of SpatialAccess can be used to select standard procedures in the analysis of model output per scenario.

The **tab Classification** of SpatialAccess provide check boxes for the calculation of total cover values per layer per scenario and of overall percentage cover per layer and per species per layer for each time step. The latter values become available through table tblOverallPCT (Fig. SA-3). These data can be used to evaluate the behaviour of herb, shrub and tree layer or particular species for the whole study area and to compare different scenarios on the basis of these overall statistics in tabular format or as figures.

Figures SA-4 and SA-5 are examples. From these figures it becomes *eg* apparent that the scenarios AA (all animals) and NA (no animals) differ in affecting total herb layer (CH) as well as the dynamics of oak and beech in the tree layer.



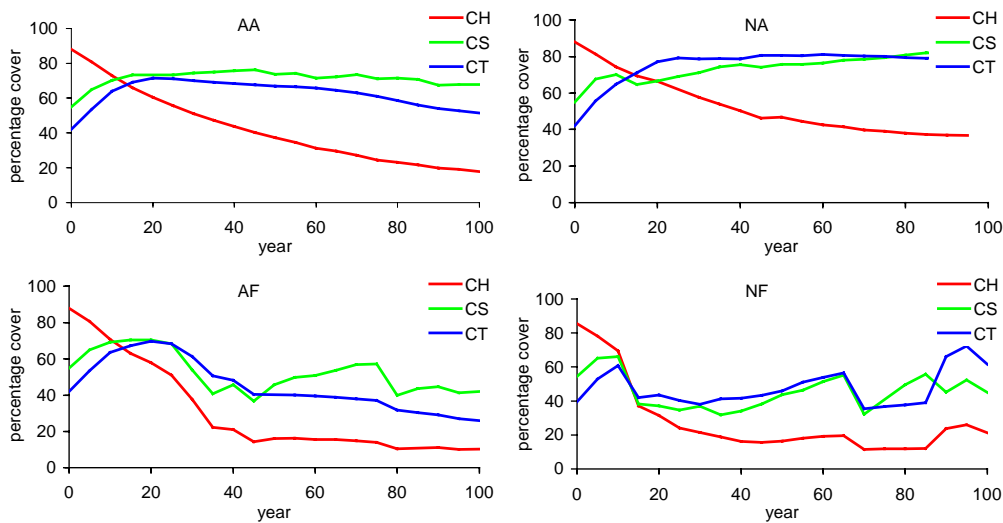


Figure SA-4. Dynamics of total cover of herb (CH), shrub (CS) and tree layer (CT) for the scenarios AA (all animals: cattle, red deer, roe deer and wild boar present as herbivores), NA (no animals), AF (all animals and a fire regime) and NF (no animals with a fire regime).

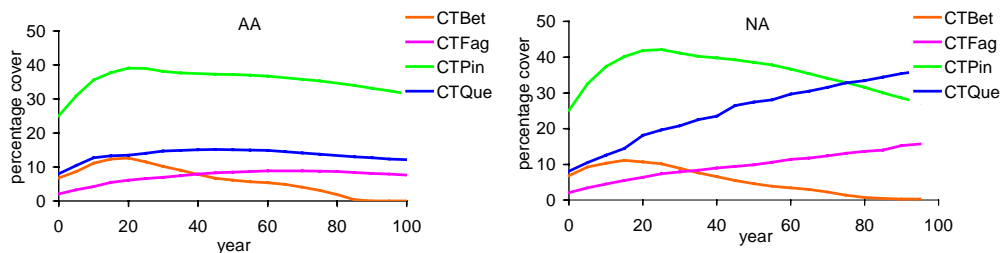


Figure SA-5. Dynamics of total cover of birch (CTBet), beech (CTFag), pine (CTPin) and oak (CTQue) in the tree layer for the scenarios AA and NA (see Fig SA-4 for scenario descriptions).

### 11.3.3 Classification

Some sort of classification per plot is needed to combine the large number of state variables into an ecological meaningful figure, such as cover type. Since, in the present case, these variables are generated by process-based models, their interpretation is straightforward: percentage cover per plot per species per layer (height values have not been loaded). For the Veluwe-area, *i.e.* for well-drained sandy soils, a hierarchical classification scheme has been developed based on total cover per layer and the dominance of woody species in tree and shrub layer (Table SA-2)

*Table SA-2. Classification scheme of cover types applied per plot. This scheme is valid for the Veluwe-area in the Netherlands only. Abbreviations: HL, SH and TL: herb, shrub and tree layer; CH, CS, CSt and CT: percentage cover of herb, shrub (total), shrub (made up of tree species) and tree layer; CLS: number of cover type (specified in tblCLS); Bet: Betula, birch; Fag: Fagus, beech; Pin: Pinus, pine; Que: Quercus, oak.*

cover type	subtype	CLS	cover% TL =CT	cover% SL =CS,CSt	%cover in TL	%cover in SL	additional constraints
bare soil		1	0	0			CH<10 soil =Zd/Zn
arable land		2	<20	CS<20			NOT 1 Cl>(SumHerbs)
heathland		3	<20	CS<60			NOT (1,2)
scrub		4	<20	CS≥60			
open forest	birch	5	≥20<60		Bet>(Pin,Que,Fag)		
	pine	6	≥20<60		Pin≥Bet Pin>(Que,Fag)		
	oak	7	≥20<60		Que≥(Bet,Pin) Que>Fag		
	beech	8	≥20<60		Fag≥(Bet,Pin,Que)		
forest	birch	9	≥60		Bet>(Pin,Que,Fag)		
	pine/pine	10	≥60	CSt≥20	Pin≥Bet Pin>(Que,Fag)	Pin>(Bet,Que,Fag)	
	pine/birch	11	≥60	CSt≥20	Pin≥Bet Pin>(Que,Fag)	Bet>(Que,Fag) Bet≥Pin	
	pine/oak	12	≥60	CSt≥20	Pin≥Bet Pin>(Que,Fag)	Que>Fag Que≥(Bet,Pin)	
	pine/beech	13	≥60	CSt≥20	Pin≥Bet Pin>(Que,Fag)	Fag≥(Bet,Pin,Que)	
	pine/hollow	14	≥60		Pin≥Bet Pin>(Que,Fag)		NOT (10-13)
	oak/oak	15	≥60	CSt≥20	Que≥(Bet,Pin) Que>Fag	Que>Fag Que≥(Bet,Pin)	
	oak/beech	16	≥60	CSt≥20	Que≥(Bet,Pin) Que>Fag	Fag≥(Bet,Pin,Que)	
	oak/hollow	17	≥60		Que≥(Bet,Pin) Que>Fag		NOT (15,16)
	beech/beech	18	≥60	CSt≥20	Fag≥(Bet,Pin,Que)	Fag≥(Bet,Pin,Que)	
beech/hollow	19	≥60		Fag≥(Bet,Pin,Que)		NOT 18	

This scheme largely reflects the successional stages corresponding to the potential natural vegetation of the Quercion-alliance as used by vegetation ecologists in

northwestern Europe. However, the scheme differs from this approach by explicitly including the vertical structure of the forest. This is because type and intensity of forest grazing determine both extent and species composition of the shrub layer and therefore future extent and species composition of the tree layer.

First, six general cover types are distinguished: arable land, bare soil (poor drift sand), heathland, scrub, open forest and forest. The latter distinction is based on the percentage cover of the tree layer: forest has a tree layer with at least 60% cover whereas the cover of the tree layer of open forest is between 20 and 60%. Second, both open forest and forest are subdivided into cover types. Open forest on the basis of the dominant tree species only, resulting in “open forest/birch”, “open forest/pine” etc. Forest is subdivided on the basis of characteristics (total cover and dominant species) of both shrub and tree layer. Not all combinations of dominant tree and shrub layer species have been included because, for the present resolution, many combinations are simply absent from the series of successional forest development, *eg* the rejuvenation of pine or birch under a canopy of beech. All forest types except birch forest have a subtype “hollow” that includes cases where the shrub layer (made up of tree species: CSt) covers less than 20% as well as shrub layers not dominated by tree species used to characterize subtypes. So in the (very unlikely) case of a beech forest with a planted shrub layer of oak with 80% cover, the cover type will be “forest/beech/hollow”.

Birch forest is an important separate type because presence of this rapidly dispersing pioneer species signals (past) disturbances ranging from single uprootings and larger canopy gaps to heathland abandoned by cattle or forest fires. The amount of birch forest as well as its pattern provide information on the presence and intensity of (past) disturbance regimes.

The **tab Classification** of SpatialAccess provides a check box (Fig. SA-3) to classify all plots present in the table tblDataX for scenario X by updating the field CLS. The description of the numbers assigned to cover types is specified in tblCLS.

### 11.3.4 Co-occurrence probabilities

A powerful way to analyse spatial relationships between cover types (or any other assigned nominal value) is by means of co-occurrence matrices calculated for adjacent plots over the whole grid. Almost all ‘texture measures’ used by image-processing software to quantify heterogeneity, diversity etc. are based on these matrices. An entry (i,j) of a co-occurrence matrix is filled by counting all occurrences for which a plot of type i has a neighbour of type j. In SpatialAccess this is implemented by looking only at neighbours to the right and below a plot and by lumping occurrences for pairs ij with j,i. An example is given in Figure SA-6.

pattern

1	1	3	3
1	1	2	3
1	1	1	3

neighbour pairs	occurrences	probabilities
1,1	8	0.47
1,2	2	0.12
1,3	2	0.12
2,3	2	0.12
3,3	3	0.17
	17	1.00

Figure SA-6. Example calculation of a co-occurrence matrix for a grid with three 'cover types'.

For this particular implementation the total number of neighbours equals the number of interior edges of the grid. The total interior edge length for a grid with R rows, C columns and plot size Z is  $[(R-1)C+(C-1)R]Z$ . The co-occurrence probabilities therefore specify the likelihood that a randomly picked edge belongs to neighbour pair (i,j). The higher the probabilities on the main diagonal of the matrix, the more coarse is the underlying pattern.

Since edges between cover types as defined in Table SA-2 have a definite physical and ecological meaning, the evolution of edge length through time provides valuable information as how edge habitat is affected by different scenarios. The **tab Classification** of SpatialAccess provides a check box (Fig. SA-3) to calculate co-occurrence probabilities for all neighbour pairs in the classified grid per scenario for each month. These probabilities (multiplied by 100) are stored in table tblCLSCoOccurrence. Figure SA-7 gives some examples resulting from queries on these table. The query used to make the figure for the dynamics of the percentage edge between cover types 'scrub' and 'open forest' is reads:

```
SELECT scenario,month,sum(pCoOc) as ScrubToOpenForest
FROM tblCLSCoOccurrence where iCLS between 5 and 8 and jCLS=4
group by scenario,month
```

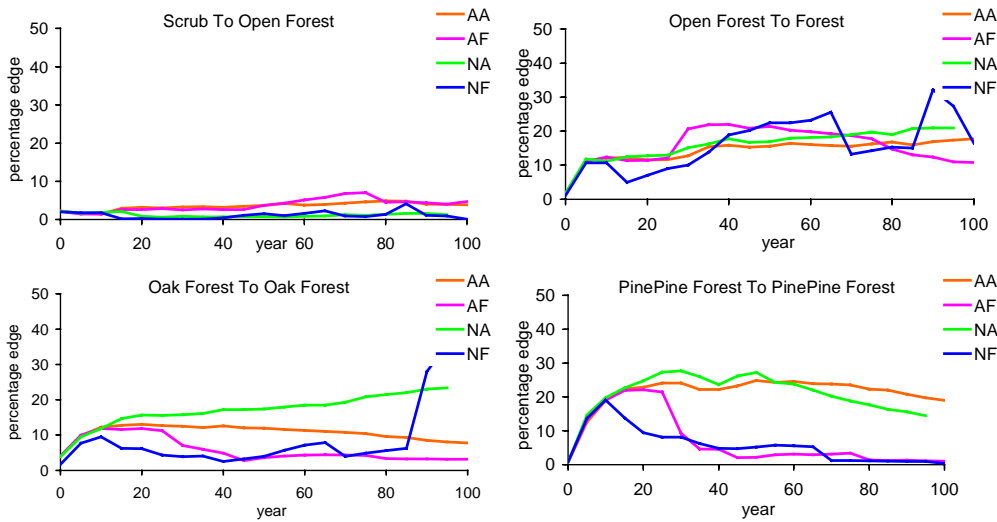


Figure SA-7. Percentage interior edge between combinations of cover types for four scenarios (see Fig SA-4 for scenario descriptions). Note the impact of fire regimes on the fragmentation of cover type 'forest/pine/pine' and the differential influence of grazing on edges of types 'scrub/open forest' and 'open forest/forest'.

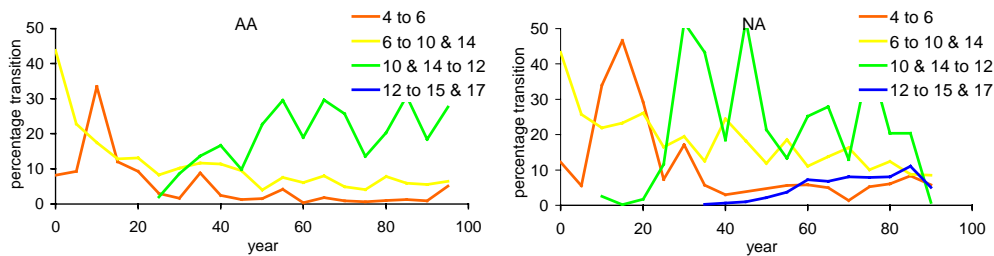


Figure SA-8. Percentage transition through time for the succession from scrub via (open) pine forest to oak forest. The numbers in the legend refer to cover types: 'scrub' 4, 'open forest/pine' 6, 'forest/pine/pine' 10, 'forest/pine/hollow' 14, 'forest/pine/oak' 12, 'forest/oak/oak' 15 and 'forest/oak/hollow' 17. Note that for the scenario with grazing (AA) about 70% of the forest initialized as 'forest/pine/oak' is transferred to 'forest/oak' between year 10-15. Grazing has a large influence on succession as shown e.g. by the frequent transitions from pure pine forest to pine forest with an understory of oak (10 to 12 & 14) in the absence of grazing (scenario NA).

### 11.3.5 Transition probabilities

The number of transitions from a specified cover type to another are available for all time intervals per scenario in tblCLSTransition. This table is filled by checking the appropriate box on the **tab Classification** (Fig. SA-3). Transitions probabilities (actually percentage transitions) are derived by the query qryCLSTransition. This query can be used to follow particular combinations of cover types through time. Figure SA-8 is an example where the succession from scrub via pine forest to oak forest is followed for the scenarios AA and NA. The query used to select the data '12

to 15 & 17' (i.e the transition from 'forest/pine/oak' to 'forest/oak/oak' or 'forest/oak/hollow') reads

```
SELECT scenario,month,sum(pTransition) as PineOakToOak
FROM qryCLSTransition where CLS1=12 and CLS2 in (15,17)
group by scenario,month
```

### 11.3.6 Turnover rates

The stability, turnover or residence time of cover types is important from an ecological point of view. Species that depend on (a combination of cover types) for establishment or the build-up of populations will strongly respond as soon as the turnover of (one of) these types changes. The **tab Classification** (Fig. SA-3) can be used to calculate (per scenario) frequency distributions of age for each cover type. The table tblCLSTurnover is used to store all ages encountered for each cover type per plot. The qryCLSTurnover gives the frequency distributions based on this table. It is very instructive to compare these distributions within and across scenarios. Figure SA-9 gives some frequency distributions for the scenarios AA and NA. The query qryCLSTurnover can also be used to calculate the mean age for each cover type. Of course these mean values are constrained by the length of the period of simulation. These values are given in Table SA-3.

*Table SA-3. Mean ages (residence times) for cover types for the scenarios AA (with grazing) and NA (without grazing). Note the significant influence grazing has on some types ('arable land', 'forest/pine/oak', 'heathland', 'scrub') but hardly any on others (e.g. most 'open/forest'-types).*

cover type	AA	NA	cover type	AA	NA
arable land	59	32	forest/pine/hollow	15	16
forest/beech/beech	44	38	forest/pine/oak	14	22
forest/beech/hollow	44	34	forest/pine/pine	50	46
forest/birch	27	24	heathland	24	12
forest/oak/beech	11	13	open forest/beech	16	13
forest/oak/hollow	39	25	open forest/birch	10	10
forest/oak/oak	47	33	open forest/oak	16	15
forest/pine/beech	9	12	open forest/pine	20	14
forest/pine/birch	19	14	scrub	18	10

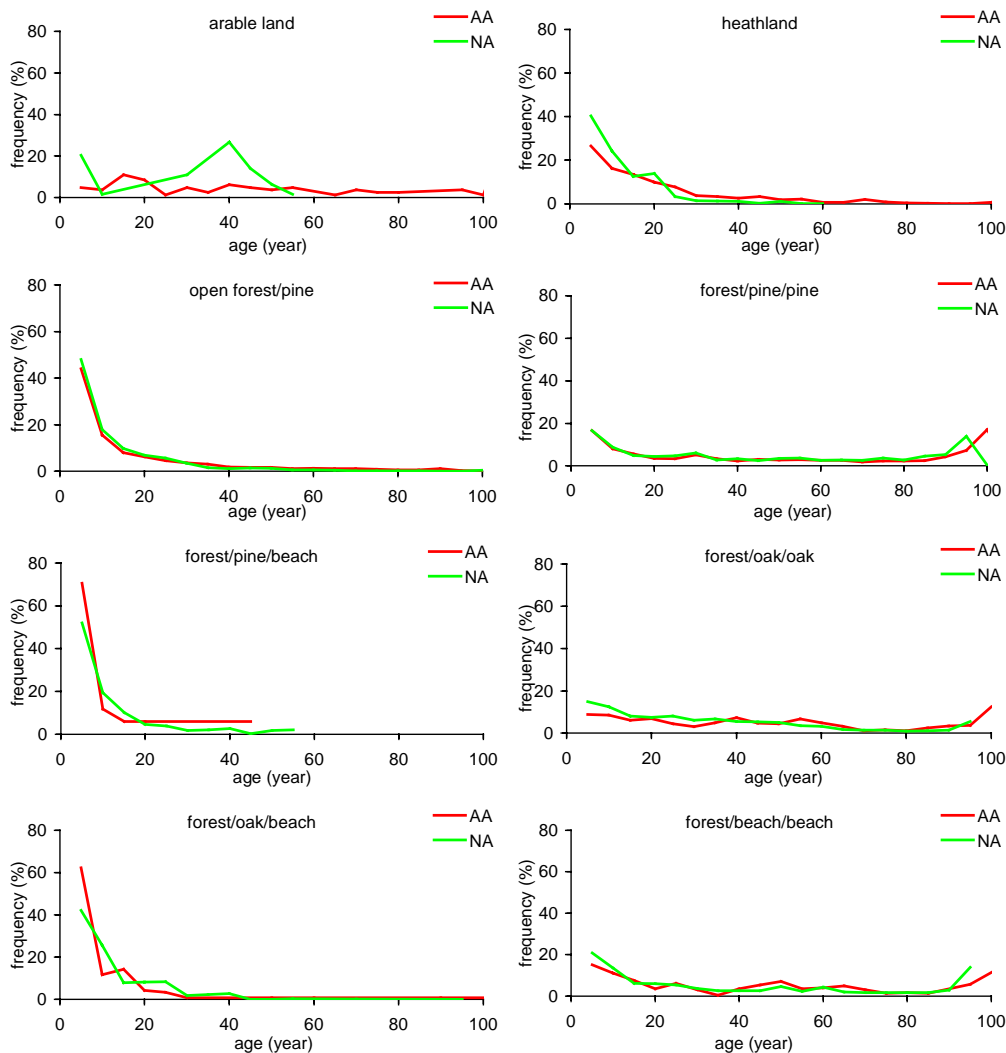


Figure SA-9. Frequency distributions of age for selected cover types compared across the scenarios AA (with grazing) and NA (without grazing).

## 11.4 Ecological questions translated into user-defined queries

In the previous section several standard procedures have been introduced that quite probably will prove to be useful in many spatio-temporal analyses of raster-based model output, especially so when applied to a set of model scenarios such as grazing and fire regimes. All tables and queries can be used to build more complex queries that will solve specific ecological questions such as:

- what is the turnover of the cover type of isolated plots, *e.g.* gaps in a forest, patches of birch?
- where are the most (in)stable plots located per cover type?
- what is the turnover of edge habitat?

- how many suitable habitat (expressed as a combination of cover types and/or edge habitat) is available through time within a certain radius of plots with specific characteristics, *e.g.* edge-habitat plot pairs?

From the perspective of species, spatio-temporal dynamics will affect opportunities for establishment, growth, survival and dispersal. A major challenge to both field ecologists and theoretical biologist is therefore to express ecological requirements of species and constraints on establishment, growth etc. into constraints on spatio-temporal features of (suitable) habitat at the landscape level. The procedures introduced in this chapter will be extended to meet this challenge.



## 12 Metapopulation dynamics

*Hans Baveco*

The spatial forest-succession model FORSPACE, developed within the project Landscapeforming processes predicts changing forest mosaics, as a result of both autonomous forest succession and disturbances due to fire, storm or herbivory.

A changing forest mosaic provides the background for many forest species. Some of these species will operate at such a spatial scale that we may assume their populations to function as a metapopulation. Suitable habitat patches may be inhabited by local populations, but frequently go extinct. Empty suitable patches may be colonized and become inhabited again. The balance between local extinctions and colonizations determines the incidence of such a metapopulation and its characteristics like metapopulation extinction risk.

To provide insight in the relation between metapopulation dynamics and the changing forest mosaic as produced by FORSPACE, we apply a simple spatially-explicit metapopulation model. It represents a species that will function as a metapopulation *on the spatial scale* of the current FORSPACE application. Only a subset of species inhabiting the forest will function as a metapopulation within the area, due to each species' typical spatial scale. Red wood ants (in fact several species) seem to meet this criterium, hence the name of the model (AntScape). However, no attempt is made (yet) to give a detailed and faithful representation of red wood ant life-history and population dynamics.

The functioning of metapopulations in static landscapes is quite well understood, especially from modelling studies. In contrast, little is known about metapopulations in dynamic landscapes, and even modelling studies are rare. In this report we first discuss the few insights currently available, in order to provide some sort of theoretical background. Next we analyse how a metapopulation might react to a changing landscape in terms of shifting habitat mosaics, defined by FORSPACE output maps under different scenarios.

### 12.1 Background

Few studies exist in which the relationship between landscape temporal and spatial structure, and population dynamics is investigated by means of spatially explicit models. Fahrig (1992) used a lattice-based patch-dynamics model, where habitat dynamics had a temporal scale as well as a spatial scale. The spatial scale related to the size of patches (groups of plots) that were "born" randomly; the temporal scale related to the patch "lifespan". She found that population size increased with increasing temporal scale and decreased with increasing spatial scale. However, the temporal scale appeared far more important.

Moloney and Levin (1996) investigated the effect of different disturbance regimes in a complex serpentine grassland simulation model (Wu and Levin, 1994). Their

conclusion is that the impact of disturbance depends upon a complex interaction between the life history characteristics of the species and the spatial and temporal structure of the disturbance regime. Therefore, predicting the impact will require an explicit understanding of at least some aspects of the spatial and temporal architecture of the disturbance regime.

Keymer *et al.* (2000) present a simple metapopulation model, and analyse the behavior of both the mean-field version (identical to the Levins 1969 model, but with landscape dynamics added) and the spatially explicit lattice-based version, an interacting particle system (ISP), see Durrett & Levin (1994).

In their analysis they clearly show in what respect the behavior of the dynamic landscape metapopulation differs from the behavior of the classical metapopulation in a static landscape. Relevant observations are given below, as well as a short presentation of the model.

### 12.1.1 A basic spatially implicit model

Landscape dynamics are incorporated by assuming for each habitat site a probability of turning into non-habitat of  $e$ , and for each non-habitat site a probability of turning into habitat of  $\lambda$ . Landscape dynamics (this is just a simple two-compartment model) will result in an equilibrium landscape with the fraction of habitat sites given by  $\bar{s}$ , being  $\bar{s} = \frac{\lambda}{\lambda + e}$ , and the expected habitat life span of  $\bar{\tau} = \frac{1}{e}$

In addition, there is the usual colonization rate,  $\beta$ , and an intrinsic extinction rate  $\delta$ . The combined metapopulation and landscape model is captured in the following mean-field equations:

$$\begin{aligned}\frac{dP_0}{dt} &= e(p_1 + p_2) - \lambda p_0 \\ \frac{dP_1}{dt} &= \lambda p_0 - \beta p_1 p_2 + \delta p_2 - e p_1 \\ \frac{dP_2}{dt} &= \beta p_1 p_2 - (\delta + e) p_2\end{aligned}\tag{197}$$

As in the classical Levins model, there is a stable equilibrium with

$$\begin{aligned}\hat{p}_0 &= \frac{e}{\lambda + e} \\ \hat{p}_1 &= \frac{\delta + e}{\beta} \\ \hat{p}_2 &= 1 - \frac{e}{\lambda + e} - \frac{\delta + e}{\beta}\end{aligned}\tag{198}$$

Taking the conditional incidence (dividing by the fraction of habitat sites),  $\hat{p} = \frac{\hat{p}_2}{\bar{s}}$ ,

and defining the effective colonization rate as  $\tilde{\beta} = \beta\bar{s}$ , and the effective extinction rate as  $\tilde{\delta} = \delta + e$ , results in a comparable expression for the equilibrium incidence as produced with the classical equation (Levins 1969):

$$\hat{p} = 1 - \frac{\tilde{\delta}}{\tilde{\beta}} \quad (199)$$

In words, the behavior of the dynamic landscape metapopulation is like that of the static landscape metapopulation, except that we have to correct the colonization rate for the fraction of habitat, and the extinction rate for the additional extinction due to landscape change.

To show the impact of a dynamic landscape, we put the original parameters back in the equation, yielding:

$$\hat{p} = 1 - \frac{1}{\beta\bar{s}} \left( \delta + \frac{1}{\bar{\tau}} \right) \quad (200)$$

In addition, other relevant quantities can be reformulated taking into account the dynamic landscape, *i.e.*  $R_0$  (the average number of propagules a local population produces during its life span, amounting to  $\frac{\beta}{\delta}$  in the classical equation).

$$R_0^* = \frac{\tilde{\beta}}{\tilde{\delta}} = \frac{\beta\bar{s}}{\delta + e} = \left( \frac{\beta}{\delta} \right) \bar{s} \left( \frac{\delta}{\delta + e} \right) = R_0 \left( \frac{\delta}{\delta + e} \right) \quad (201)$$

Note that the last term in the equation, is the ratio between intrinsic and effective population extinction rates! For metapopulation persistence,  $R_0$  needs to be larger than 1. From the previous equation, thresholds for the minimum fraction of habitat, and for the minimum expected habitat life span can be deduced:

$$s_{\min} = \frac{1}{\beta} \left( \delta + \frac{1}{\bar{\tau}} \right) \text{ and } \tau_{\min} = (\beta\bar{s} - \delta)^{-1} \quad (202)$$

The complete set of conditions for metapopulation persistence in dynamic landscapes thus becomes:  $R_0^* > 1$ ,  $\bar{s} > s_{\min}$ ,  $\bar{\tau} > \tau_{\min}$ .

The interacting particle system studied by Keymer *et al.* (2000) as the spatial explicit analogue of the mean-field model described above, is identical to the simplest version of the AntScape model, with local dispersal. The insights obtained by Keymer *et al.* (2000) thus directly apply to the AntScape model. They are summarized below.

The results of the IPS simulations depend on the expected fraction of habitat in equilibrium,  $\bar{s}$ . From percolation theory we know that there will exist a percolation threshold,  $p_c$  in the fraction of habitat in the landscape (Green 1994). Above this threshold (“super-critical”:  $\bar{s} > p_c$ ), almost all habitat sites are connected, with a few isolated sites. There is thus one large, spanning cluster. At the critical value (“critical”:  $\bar{s} = p_c$ ) there may be clusters of different sizes. Below the threshold

(“subcritical”:  $\bar{s} < p_c$ ) the habitat is fragmented into disconnected clusters embedded in a matrix of non-habitat.

As expected, Keymer *et al.* (2000) observe that for super-critical landscapes, the behavior is statistically similar to the behavior in homogeneous landscapes (all sites being habitat, as investigated by Durrett & Levin (1994)). In such a case, the IPS will converge to an equilibrium distribution.

Over the whole range, the IPS shows qualitatively the same behavior as the mean-field model; however the mean-field model overestimates the expected occupancy of the IPS, and the extinction thresholds, since it neglects the spatial structure. The discrepancy is small for large values of  $\bar{s}$  (super-critical landscapes); for sub-critical landscapes the discrepancy increase with decreasing values of  $\bar{\tau}$  (faster changing landscapes) and for species with decreasing  $R_0$  (less “infective” species).

### 12.1.2 Model AntScape

The AntScape model is tailored to use FORSPACE landscape input, simulating metapopulation dynamics with an identical grid as the underlying spatial setting. It is a simple, generic model, that may be extended to incorporate realistic detail, if required.

The scale of the local population conforms to the grid resolution: a grid-plot of 20 by 20 m (in the Imbos case-study) may be occupied by a single local population. The local population is defined as a red wood ant colony. The model is spatially discrete, (based on grid-plots) and also temporally discrete, calculating occupancy annually (timestep is one year). Using the variant where local population size (colony size) is not modelled as a continuous variable, but only presence/absence (or another finite set of states) is recorded, we have what is generally known as an interacting particle system (IPS), see Durrett & Levin (1994).

Colonies are assumed to have an intrinsic lifespan, reflected in an annual extinction probability. Red wood ants may have several dispersal strategies, of which two extremes are analysed in the model. In the first place, queens may disperse over considerable distances, accompanied by a (small) fraction of the original population. In the second place, existing colonies may give rise to new colonies in the near neighborhood, in which case a fraction of the donor colony moves to the colonized site. In the following we will use the terms *long-range dispersal* and *local* or *neighborhood dispersal* to refer to these colonization strategies, respectively.

With local, neighborhood dispersal, the AntScape model is identical to the ISP model described in Keymer *et al.* (2000), except that it is temporally discrete instead of continuous. However, this will have very little impact on the behavior; thus the results obtained by Keymer *et al.* (2000) will apply to the simplest AntScape model as well.

Parameters of the model thus include the number of dispersers annually produced per site (colony) and the annual extinction probability of an occupied site (colony). In case the habitat dynamics are produced by the model, we need to define the probability of a habitat site turning into non-habitat, and the probability of a non-habitat site to turn into habitat. Alternatively, timeseries of habitat maps are provided as input to the model, in which case the metapopulation dynamics will take place on

these predefined landscapes. The former approach makes it easier to make some general statement with respect to metapopulation persistence, as we can obtain and simulate dynamics on a landscape in equilibrium. The second approach enables us to deal with existing landscapes, that may be in some transient phase (not yet having reached any equilibrium).

## 12.2 Results

Time-series of FORSPACE output maps are analysed for the following scenarios:

- I. all herbivores present, no fire (“all”)
- II. all herbivores present, fire frequency 0.001 (“allF0.001”)
- III. no herbivores present, fire frequency 0.001 (“noF0.001”)
- IV. no herbivores present, no fire (“no-herbi”)

Maps represent a 50 x 100 lattice, with each plot measuring 20 x 20 m<sup>2</sup>, the total area thus amounting to 2 km<sup>2</sup> (200 ha).

We assume that the fraction incidence radiation reaching the herb-layer is indicative of the habitat-suitability, at least in the area studied. Figure MP.1 depicts the spatial distribution of this variable, for a selected number of years, for the four scenarios.

Several thresholds are tried to convert these continuous values into binary values (0 denoting non-habitat and 1 denoting habitat), *e.g.* 0.25, 0.50 and 0.75. The resulting binary maps for scenario III and for the same selection of years, are shown in Figure MP.2.

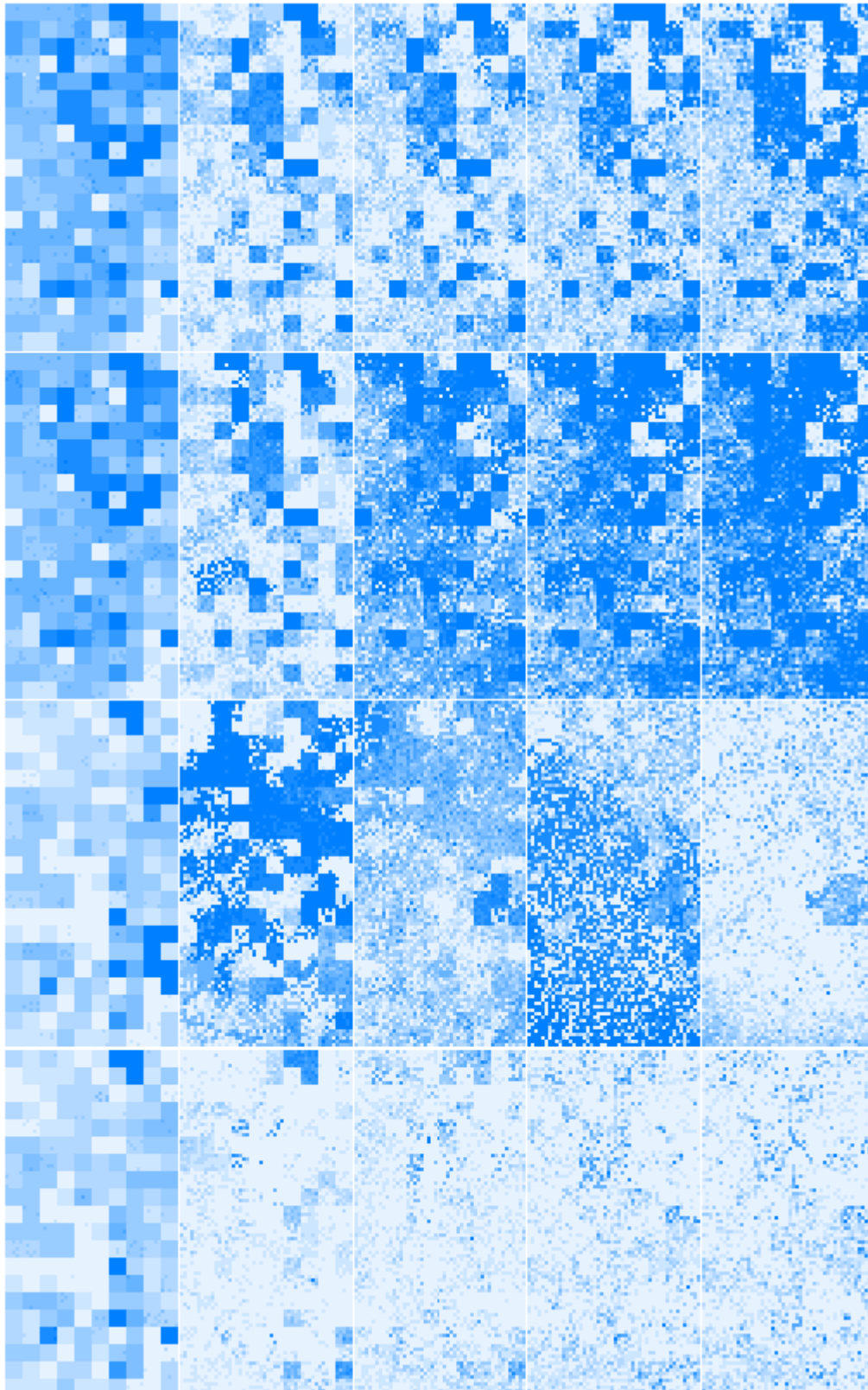
For the binary maps, simple statistics are calculated, including the number (fraction) of habitat sites in the lattice (coined *s*, in the terminology of Keymer *et al.* (2000)), see Figure MP.3. In addition, rates of landscape change are determined, by comparing the state of plots of the lattice, at consecutive times. The results are shown in Figure MP.4, showing the probability of a habitat-site to turn into non-habitat ( $\emptyset$ ), and the probability of a non-habitat-site to turn into habitat ( $\lambda$ ).

All scenarios show a development towards a more fine-grained landscape (Figure MP.1). The initial coarse-grained pattern dissolves gradually, but more slowly when herbivores are present (I and II).

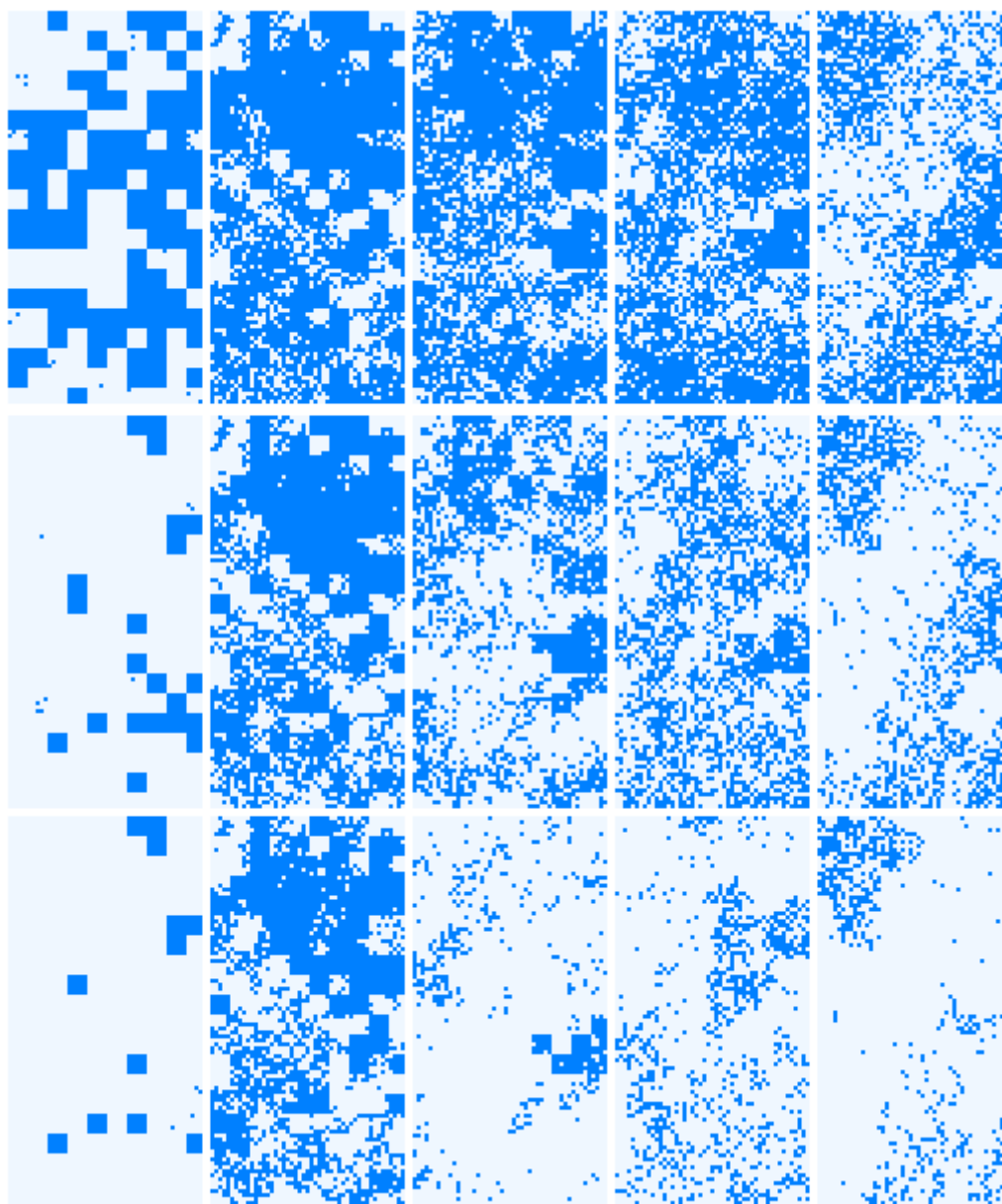
Looking at the amount of habitat (applying different thresholds) in Figure MP.3, without herbivores and fire (IV) a kind of equilibrium is quickly reached (a dense forest situation). On the other hand, when herbivores are present (I), the forest evolves slowly towards a more open forest. Within the scope of the simulations, no equilibrium composition is reached. When fires occur, even in a low frequency of 0.001, they have a high impact on the amount of habitat. Comparing scenario II with I, fire results in an occasional speed-up in the otherwise very gradual development towards an open forest landscape. When comparing scenario III with IV, we observe a cyclic pattern, where fires occasionally increase the openness of the forest, but their impact is counteracted by forest succession towards a dense forest cover.

The rates of change as depicted in Figure MP.4, provide information on the actual rates of landscape change. For scenario I both  $e$  and  $\lambda$  are low (*e.g.* for threshold = 0.50 well below the 0.1), thus explaining why an equilibrium forest composition is

not reaching within the simulation time. Also, the ratio of the two leads to the prediction that in equilibrium the fraction of habitat will be (slightly) larger than 0.5. For scenario IV (no herbivores, no fire) the reverse is true. While  $\lambda$  is low (considerable lower than 0.1),  $e$  is high (0.3 or higher). The overall rate of landscape change is thus much faster, leading quickly to an equilibrium landscape in which the fraction of habitat is low (the expected fraction  $\frac{\lambda}{\lambda + e}$  amounts to approximately  $0.02/(0.02 + 0.35) = 0.05$  for threshold = 0.5). Comparing scenario II (with fire) to I, fire clearly results in a higher  $\lambda$  over a short period (sudden creation of a lot of “openness”). Comparing scenario III with IV, we see that this short period of high  $\lambda$ , is followed by a considerably longer period of raised  $e$ , the rate of return to the dense forest equilibrium situation.



*Figure MP.1. Fraction of incidence radiation reaching herb-layer, at year 0, 25, 75, 95 (horizontally); 0->1 = light->dark. Top-down scenario I, II, III, IV.*



*Figure MP.2. Habitat maps for scenario III, no herbivores and fire-frequency 0.001 (dark = habitat; light = non-habitat) at year 0, 25, 75, 95 (horizontally). Top-down: thresholds of 0.25, 0.50 and 0.75.*



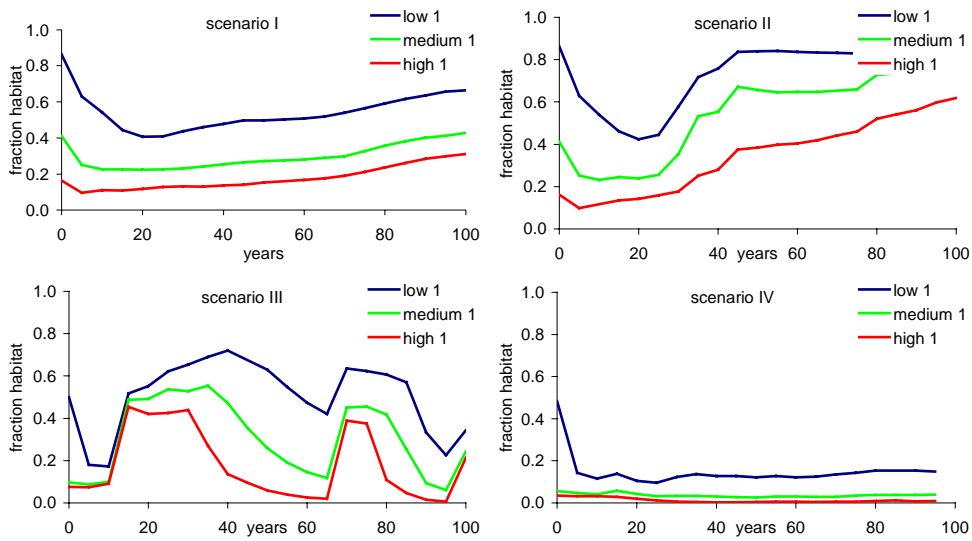


Figure MP.3 Fraction of habitat at 3 thresholds for scenario I (all herbivores, no fire), scenario II (all herbivores, fire frequency 0.001); scenario III (no herbivores, fire frequency 0.001) and scenario IV (no herbivores, no fire)

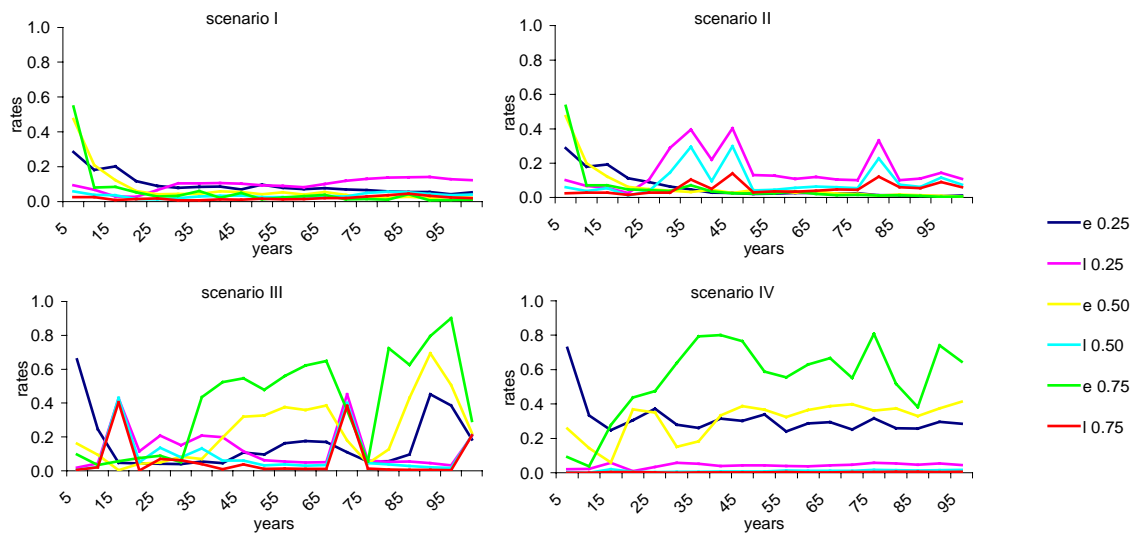


Figure MP.4 Rate of changes in habitat for the 4 scenario's at different probabilities of turning habitat into non-habitat,  $e$ ; and probabilities of turning non-habitat into habitat,  $\lambda$  (see eqn. 197, 198)

### 12.3 Discussion

In this section we provide a first attempt to link the dynamic habitat maps as produced by the four FORSPACE scenarios, to expected metapopulation behavior.

For the simplest version of AntScape, with local dispersal, the general results of Keymer *et al.* (2000) apply, and allow us to make some more qualitative predictions. Firstly, we make the assumption that we are looking at a landscape roughly in equilibrium – at least after an initial phase. Metapopulation fate then depends on the values of habitat life span and habitat incidence.

Habitat life span,  $\tau = \frac{1}{e}$ , is expected to be moderately high ( $20 * 5$  to  $30 * 5 = 100$  to 150 years for threshold 0.5) for scenario I (all herbivores), and low ( $3 * 5 = 15$  years for threshold 0.5) for scenario IV (no herbivores).

Habitat incidence,  $s$ , will be high for scenario I (at least in the projected equilibrium state), and low for scenario IV. The table below summarizes these qualitative results for all scenarios.

	I	II	III	IV
Habitat life span	long	long	Short (> IV)	short
Habitat incidence	high	high	Low (> IV)	low

Thus, scenarios I and II, both with herbivores present, lead to a combination of a slowly changing habitat landscape, with a high fraction of habitat. The fraction of habitat is likely to be above the percolation threshold. Starting from a single habitat site, species with local dispersal will thus spread through the whole landscape (though it may take some time for temporary corridors between habitat clusters to appear, due to the low habitat turnover rate). Fire is expected to cause occasional increases in the fraction of habitat, followed by a slow decrease back to equilibrium values. Thus, fire should lead to an on average higher habitat incidence, and faster spread of species through the landscape. Species with less “local” dispersal strategies, for instance with the ability to colonize sites outside the direct neighborhood, may prosper equally well in such landscapes (ignoring possible trade-offs between dispersal-capacity and other life-history parameters).

For scenarios III and IV, without herbivores, the fraction of habitat is generally (very) low, and likely to be far below the percolation threshold. Thus the actual spatial configuration, in terms of clusters of habitat sites, very much determines metapopulation incidence (and persistence). Starting from a single habitat site, a species with local dispersal will spread relatively fast through the landscape (due to the short habitat life span) but will attain only a low incidence. The habitat landscape may well be below the thresholds for the fraction of habitat or for the habitat life span, or the effective  $R_0$  (the average number of propagules a local population produces during its life span) may be well below 1. In such cases, the metapopulation is unlikely to persist. Species with less “local” dispersal strategies are expected to do much better in these landscapes, as they will colonize isolated habitat sites or isolated clusters of habitat sites. It is clear that scenario IV, no herbivores and no fire, offers

no perspectives for species that depend on the openness of the forest landscape. However, once fires occur, as in scenario III, the perspectives improve, as temporarily the landscape may offer a spanning cluster of habitat (above the percolation threshold), and the possibility of a rapid spread. The actual metapopulation dynamics in such case will probably be very much dependent on the spatial and temporal correlation of fire events.

## **12.4 Future work**

In future work, the qualitative predictions listed above should be tested by simulations with the spatially-explicit models such as AntScape. This applies above all to the scenarios leading to habitat landscapes below the percolation threshold, showing sets of isolated habitat clusters of different sizes. For these scenarios, special attention should be paid to 1) the difference in outcome when assuming different dispersal strategies, 2) the role of spatial and temporal correlation in disturbance events (fire).

To be able to make predictions on the fate of actual species (*eg* the several red wood ant species) in an actual landscape, the models should be extended with realistic detail. The simple presence/absence state variable for local populations should be replaced with colony-size, in order to take into account the time it takes for colonies to be established and grow. Dispersal rate should probably be related to colony-size, and the quality of the local environment should determine colony growth-rate.

The simplifying assumption that the fraction of incidence radiation on the herb-layer is the only factor determining habitat suitability, should clearly be replaced by more refined approaches to establish the quality of a site to a species. However, the actual metapopulation model is indifferent to the actual approach used to obtain underlying habitat maps.



## 13 General conclusions

Model FORSPACE is a spatial explicit and process-based model on forest dynamics at the landscape level, including processes for autonomous forest succession at the point level and landscape forming processes (lfp's), thus at the landscape level. The processes for autonomous forest dynamics include dispersal of seeds, germination, establishment, growth and competition, and mortality. The lfp's included in this study include grazing by large herbivores and fire. FORSPACE was also linked to tools to assess the dynamics of (bio-)diversity at the landscape level, both by spatial analysis and metapopulation dynamics.

In the previous chapters, the processes driving autonomous forest dynamics are described in detail; the methodology for the initialisation of a realistic area was presented; as well as the dynamics of the most important features of the model. This was done both for standardised conditions and for a realistic area, the latter was a section of 200 ha of the Imbos. Furthermore, the methods for spatial analysis and metapopulation analysis are presented, and applied to the same area.

During this study much emphasis was paid to attain a realistic representation of the landscape based on as little as possible information that should be gathered under field conditions because collecting detailed information in the field is very costly. However, preliminary runs showed that the initial number of trees per ha and the initial weights and sizes of the different plant organs strongly affect competition and mortality and thus the long-term outcome of the model.

The model dynamics under controlled conditions showed that based on the current initialisation and parametrisation, growth in monoculture and in mixture and forest dynamics are in most cases accurately predicted by the model for trees, shrubs and herb species, including grasses.

The case study for the Imbos demonstrated that there are important interactions between the autonomous development of a forest factors and landscape forming processes. The autonomous development of the forest is based on dispersion of seeds, establishment, growth, competition, mortality, which may be disturbed by grazing by larger herbivores and fire.

It can be concluded that the current version of FORSPACE is applicable to forest on sandy soils in the Netherlands.

### ***Future developments***

Additional processes that need to be included in the model include *eg* nitrogen dynamics in the vegetation and the soil. Nitrogen concentration in the different plant tissues is an important aspect determining the rate of decomposition of plant material and thereby soil formation and amount of litter. The soil characteristics and amount of litter determine the conditions under which seeds germinate and seedlings establish and survive. Nitrogen availability affects the competitive abilities of plant species thus ongoing nitrogen deposition affects the vegetation succession.

Other landscape forming processes that occasionally strongly affect the vegetation include storm and flooding. Furthermore, most forest landscapes in the Netherlands are managed in some way. Either to convert it from the current to a desired situation

or to harvest trees for economic reasons. Such management scenario's can be applied relatively easily for specific case studies. The same is true for the evaluation of spatial statistics summarising an entire landscape *e.g* with respect to recreational values or to diversity measures.

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