Acta Bot. Neerl. 45(4), December 1996, p. 543–556

REVIEW

Searching for patterns and processes: modelling of vegetation dynamics with Geographical Information Systems and Remote Sensing[‡]

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CONTENTS

Key-words: Calluna vulgaris, GIS, heathland, patterns and processes, Remote Sensing, spatial modelling.

INTRODUCTION

In vegetation there can be a significant difference between canopy densities of the location where adult plants grow and the location where seeds germinate and juvenile plants establish. The replacement of one species by another species is strongly determined by the spatial configuration of (seed carrying) plants and openness (gaps) in the vegetation, the ability to produce seed and the dispersal capacity of seed, and the competitive ability. Vegetation dynamics occur over a wide range of spatial and temporal scales. The understanding on individual species-to-stand scale is of significant benefit to developing an understanding of vegetation dynamics on larger scales. The possibility of using knowledge from species observations to infer vegetation functioning has been explored by vegetation scientists for a long time (Watt 1947). In vegetation, spatially localized and essentially random disturbances interrupt orderly processes that would otherwise drive the vegetation uniformly toward relatively monotonous end-states (Levin 1993). The result is that vegetation is patchy on virtually every level of space and time. The firmest basis for scaling vegetation dynamics involves the development of an understanding of the mechanism determining and governing patterns and processes.

Relating pattern to process is a fundamental challenge of vegetation science. Understanding spatial pattern formation has been one of the most active and productive

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[‡]This paper is based on a lecture presented at the 150th meeting of the Section for Vegetation Research of the Royal Botanical Society of The Netherlands held on 23 November 1995.

areas of vegetation research. For any set of patterns, there almost certainly will be a number of feasible mechanisms that could give rise to those patterns. Increased knowledge on the process mechanism of changes in species composition of vegetation increases the possibility for many applications in nature conservation and management practices. Although the importance of the mobile phase of plants has been recognized in relation to several environmental problems such as habitat destruction and habitat fragmentation, it is apparent how little is known on dispersal of seed and successive (re)colonization (Birks 1989; Greene & Johnson 1995).

Although analyses of patterns and processes of vegetation through simulation of ecological processes are common nowadays (e.g. Jörgensen 1988; Running *et al.* 1994), the investigation of patterns and processes in spatially explicit dynamic models is hardly common practice (Goodchild 1994). However, this type of model allows for investigating a number of spatial processes, which can, by definition, not be modelled by so-called one dimensional (1-D) dynamic models. However, the development of 1-D models and details of dispersal, establishment, growth and competition provide the basis for spatially explicit models of inter plant interaction. These models can be used to generate patterns that can be compared with actual patterns in nature. This paper describes the augmentation of an existing 1-D heathland competition model to a Geographical Information Systems (GIS ≈ spatially explicit) model. The authors show the advantages and consequences of including spatial information in comparison to the 1-D model. Special features of the GIS model allow for investigating patterns in the vegetation, which are impossible to investigate with 1-D models.

One of the major consequences of the use of GIS models, i.e. their strong demand for spatially explicit input data, can be mastered with the application of remotely sensed data. The relevance of the spatial extension of the model has been illustrated with a case study on patterns and processes of heathland vegetation in a field situation. The aim of this case study of the National Park 'De Hoge Veluwe' is to validate the GIS model and to show how an environmental factor, i.e. amount of atmospheric N deposition, might cause patterns in heathland vegetation (cf. Heil *et al.* 1991).

DEVELOPMENT OF THE GIS MODEL

Geographic Information Systems (GIS) are a set of computer-based tools that can be used to store, analyse and retrieve spatial information (Burrough 1986). GIS can be useful for storing the spatial distribution of the variables, and recently several examples of a fruitful linkage between GIS and dynamic modelling have been developed (Van Deursen & Kwadijk 1990, 1993; Heil & Van Deursen 1993; Van Deursen & Heil 1993). GIS can hold many data on the, albeit static, distribution of land attributes which form the control parameters, boundary conditions and input data for the model (Burrough 1986). This makes GIS an ideal platform for the development and application of spatial-distributed models. In general, GIS can be divided into two groups: vector GIS and raster GIS. Vector GIS stores the spatial information as a set of points, lines and polygons and maintains a special set of data tables for storing the topology of the data. Topology is explicitly maintained in vector GIS. Raster GIS create a grid of cells over the data and for each cell the system stores the most relevant data. Since a more or less predefined grid is used to store the spatial information, topology is an implicit part of the data structure and does not have to be maintained in separate tables. There are several advantages and disadvantages to both of the systems (see Burrough 1986). It is recognized, however, that while vector systems have a much larger spatial accuracy and can be very useful for maintaining spatial databases in the domain of clearly defined objects, raster systems have more analytical capabilities and are more suitable to be used with less well-defined objects and continuous fields. Because of these analytic capabilities, raster GIS is clearly prefered for ecological modelling. The GIS package used to develop the examples in this paper is PCRASTER (Van Deursen 1995; Van Deursen & Wesseling 1992), a simple raster GIS with special features allowing for dynamic modelling.

The 1-D model that was extended to a spatial distributed GIS model is a *Calluna vulgaris–Deschampsia flexuosa* competition model. It simulates the combined growth of *Calluna vulgaris* and *Deschampsia flexuosa* using several scenarios for atmospheric N-deposition and heather beetle outbreaks (Heil & Bobbink 1993a,b). The model involves the growth of *Calluna vulgaris* and *Deschampsia flexuosa* and their competitive relationship. Growth is expressed as the change in percentage canopy cover of the plant species. The algorithms for calculating canopy cover for the two species are according to Heil & Bobbink (1993a). The growth rate of both *Calluna vulgaris* and *Deschampsia flexuosa* increases as a result of increased nitrogen availability. The growth rate of *Deschampsia flexuosa* is significantly lower than that of *Calluna vulgaris* under relatively nutrient-poor conditions (<10 kg N ha^{-1} yr^{-1}). With relatively high levels of nutrient availability the growth rate of *Deschampsia flexuosa* increases with respect to the growth rate of *Calluna vulgaris* (cf. Heil & Bruggink 1987). The processes are described in detail by Heil & Bobbink (1993a,b). *Calluna vulgaris* can be affected by the heather beetle (*Lochmaea suturalis*, (L.) Thoms.), which is a monophagous beetle feeding on *Calluna vulgaris*. During a heather beetle outbreak *Calluna vulgaris* plants die off almost completely over large areas. When the heather canopy is abundant, the heather beetle affects *Calluna vulgaris* randomly (Berdowski & Zeilinga 1987). From experiments (Brunsting & Heil 1985) a relationship has been attained between the probability of occurrence of heather beetle outbreaks and nutrient availability. This empirical relationship is used in the model to introduce outbreaks as a function of nutrient availability in combination with percentage canopy cover of *Calluna vulgaris* (Heil & Bobbink 1993a,b; Bakema *et al.* 1992). As a result of a heather beetle outbreak, the model reduces the percentage cover of *Calluna vulgaris* to 1% of its original canopy cover. Consequently, the litter of the dead *Calluna vulgaris* is passed into the soil compartment. Nitrogen cycling occurs between the vegetation and the soil compartment. In the model there is a nitrogen pool in *Calluna vulgaris*, in *Deschampsia flexuosa* and in the soil. Nitrogen availability for the two plant species depends on amounts of atmospheric nitrogen deposition and on an amount of nitrogen mineralization from the soil compartment.

An important step when implementing a model such as 'Calluna' in the GIS environment is the definition of the compartments and fluxes, which are transformed in different type of maps, i.e. every compartment and flux has a spatially explicit position (Fig. 1). For creating a dynamic model, there are modules that can perform the following:

- modules that can be used for calculations for each of the grid cells in the digital maps;
- modules that can analyse the neighbourhood of certain cells, thus determining distances to other features or influences from nearby features in the digital maps;
- modules to display and summarize data stored in the digital maps and to print maps on paper;

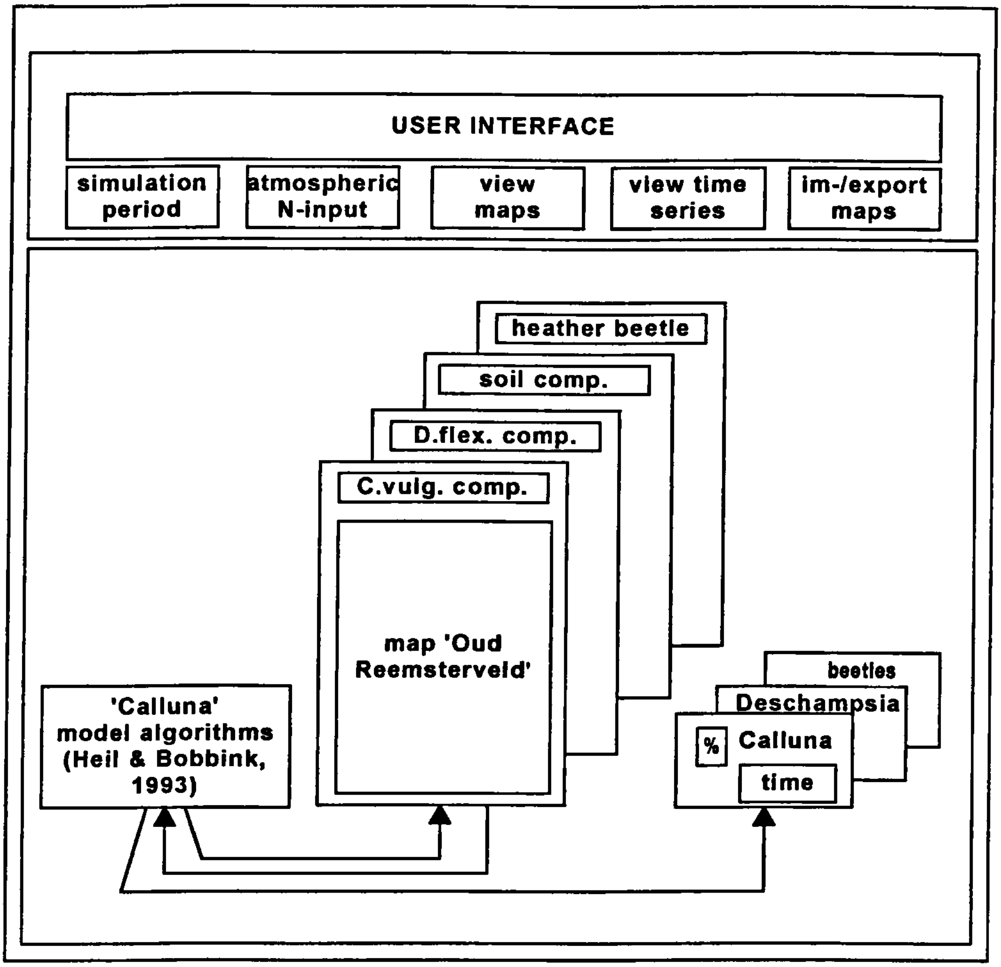

Fig. 1. Simplified diagram of the dynamic GIS model. The different options of the user interface, i.e. simulation period, scenario for atmospheric N-input, maps, time series and import/export of maps, can be used interactively during the simulation.

- modules to take care of the flow of commands for running a model based on the above-mentioned modules.

In addition to the 1-D 'Calluna' model two spatial processes are included in the GIS model, i.e. seed dispersal of *Calluna vulgaris* and *Deschampsia flexuosa*, and lateral spreading of heather beetles during pest years. Seed dispersal of *Calluna vulgaris* and *Deschampsia flexuosa* is implemented as a chance occurrence of seedlings controlled by the surrounding vegetation, i.e. gaps in the vegetation and the amount of vegetation to emerge seed producing plants within a species-specific predefined range, i.e. 0·5 m and 2·0 m for *Calluna vulgaris* and *Deschampsia flexuosa*, respectively (cf. Bruggink 1993). Beetle spreading is implemented as a lateral flux that describes the spatial distribution of the beetle population. This spreading is a stochastic function of existing beetle colonies and the amount of *Calluna vulgaris* available for feeding within a predefined range (cf. Brunsting 1982; Brunsting & Heil 1985).

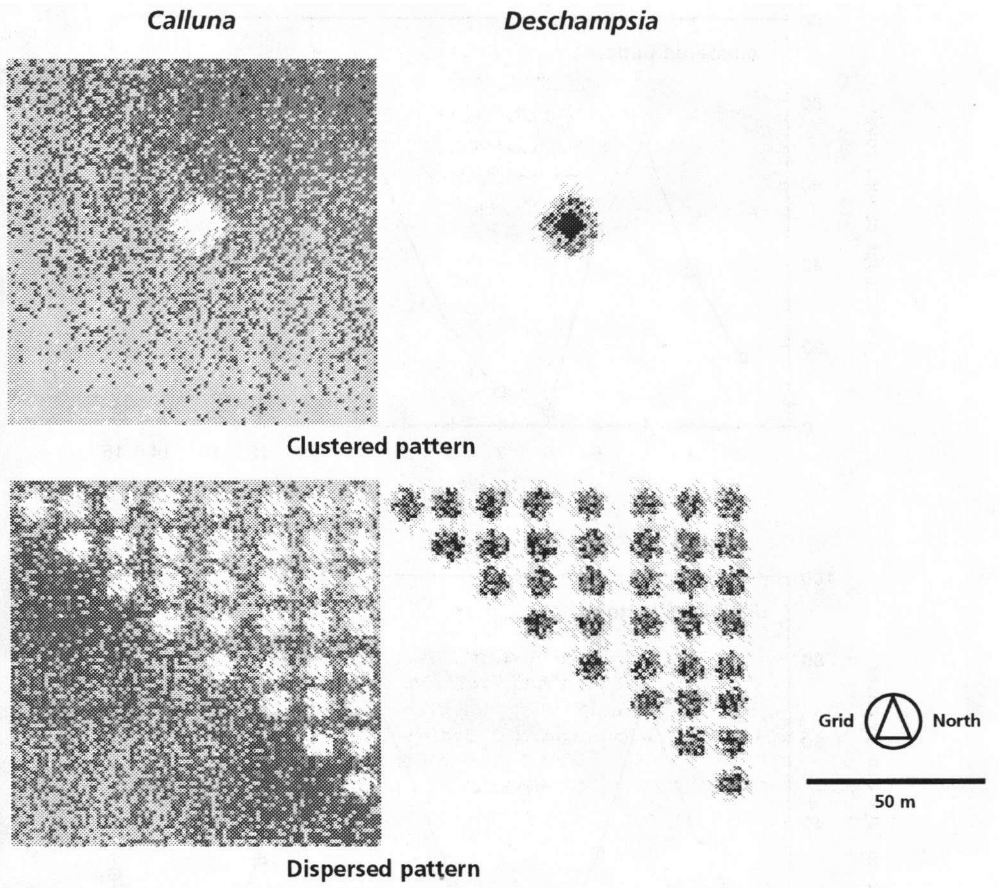

Fig. 2. Hypothetical pattern development in heathland vegetation as simulated with the dynamic GIS model under two initial situations (see also text).

To show the applicability of spatial modelling, this dynamic GIS model has been applied to two hypothetical situations, only differing in the spatial distribution of the initial situation. Both initial situations consist of an area of heathland existing of an average canopy cover of *Calluna vulgaris* of *c.* 10% and an average canopy cover of *Deschampsia flexuosa* of *c.* 0·5%. These percentages of canopy cover are based on field observations 2 years after sod cutting, a management regime that has been carried out with regular intervals in the ancient 'potstal' system (Gimingham & De Smidt 1983). In the first situation, *Deschampsia flexuosa* plants are clustered in the centre of the area, while in the second situation *Deschampsia flexuosa* plants are sparsely distributed ('dispersed') over the right diagonal corner of the area (Fig. 2). As shown by the results, applying exactly the same model to both situations yields totally different amounts of canopy cover after a simulation period of 15 years. As a result of the different initial patterns, the first simulation shows the area still dominated by *Calluna vulgaris*, while the second simulation shows a co-dominance of *Calluna vulgaris* and *Deschampsia flexuosa* in the right diagonal corner. This is also illustrated by the resulting time series from the GIS model showing the total coverage of *Calluna vulgaris* and *Deschampsia flexuosa* (Fig. 3). In the first simulation *Calluna vulgaris* and *Deschampsia flexuosa* have

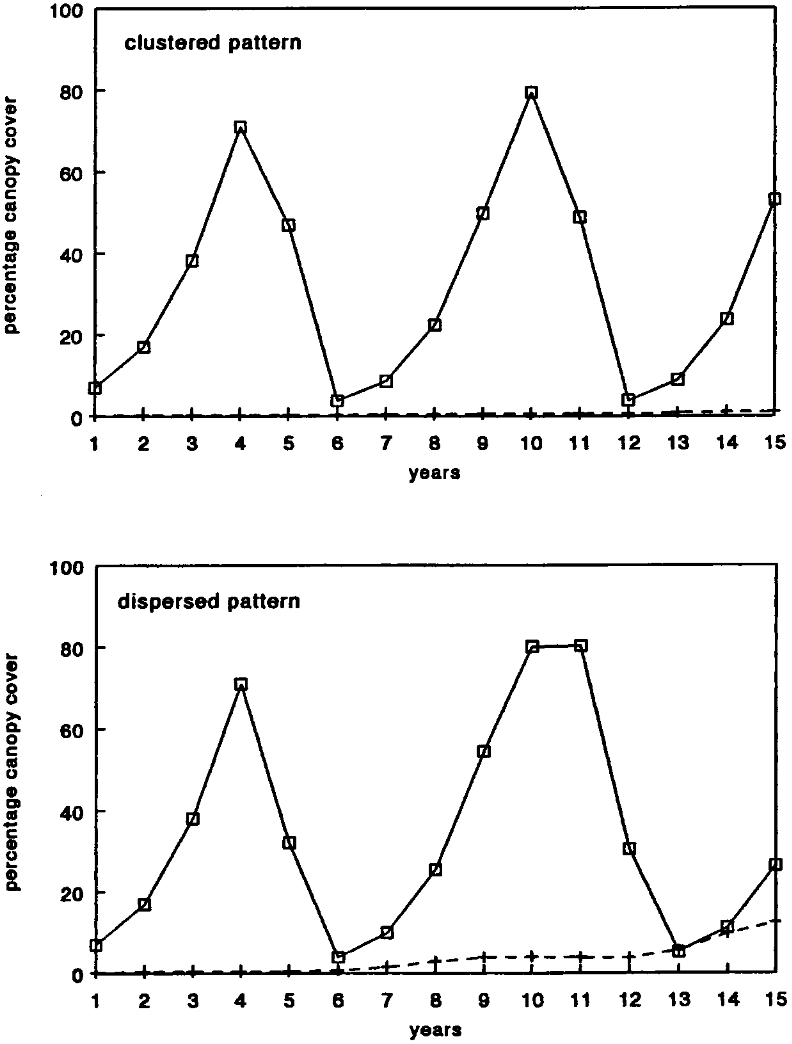

Fig. 3. Top: time series of the canopy cover of *Calluna vulgaris* (squares) and *Deschampsia flexuosa* (crosses) in the 'clustered' vegetation pattern. Bottom: time series of the canopy cover of *Calluna vulgaris* and *Deschampsia flexuosa* in the 'dispersed' vegetation pattern.

a total percentage cover of approximately 50% and 3%, respectively, at the end of the simulation period, while in the second simulation *Calluna vulgaris* and *Deschampsia flexuosa* have a total percentage cover of approximately 30% and 15%, respectively. It is obvious that, because the initial total amounts of canopy cover of both species in the two simulations were exactly the same, this result could not have been obtained with the original 1-D model. In order to prevent confusion, it should be stated here that the results with the 1-D model by Heil & Bobbink (1993a) have been obtained from 100 runs because of the stochastic behaviour of heather beetle outbreaks. In the original study by Heil & Bobbink (1993a,b), this was necessary to determine the critical load of atmospheric N-deposition for heathland vegetation. The application of the GIS model is more appropriate with respect to real field situations, as will be shown in the 'Oud Reemsterveld' case study (see further).

REMOTE SENSING DATA FOR SPATIAL MODELLING

One of the characteristics of spatial models is their strong demand for input data. As can be concluded from the above example, before one can apply the GIS model appropriate description of the initial situation of the vegetation pattern is required. Proper application of the GIS model requires a spatial-distributed description of the process parameters. Because the progress of different processes is dependent on spatial differences, data collection concentrates on the initial canopy cover of the two plant species. The same GIS model, as described above to show the importance of initial vegetation patterns in relation to spatial processes, has been applied to an area in the National Park 'De Hoge Veluwe', The Netherlands. The area used for the model is the 'Oud Reemsterveld' and its direct surroundings of *c.* 900 ha. The necessary input data to feed the model were obtained with Remote Sensing (RS) techniques. There are several ways to collect the necessary spatial data, i.e. in situ measurements (field work) and through remote sensing techniques such as aerial photography and satellite imagery. Which of the techniques is most appropriate depends, among others, on access and scale of the data needed.

In the case study we used a combination of aerial photographs and reported results of field work to establish the initial situation. The procedure to process the different data is shown in Fig. 4. To obtain the input data of the initial situation in 1980, aerial photographs were digitized and interpreted with the help of the published information (Heil 1984; Berdowski 1987; Berdowski & Zeilinga 1987; Aerts & Heil 1993). The initial situation consists of maps containing the spatial distribution of the canopy cover of the dominant plant species, i.e. of *Calluna vulgaris* and of *Deschampsia flexuosa* in 1980. In this case, *Calluna vulgaris* and *Deschampsia flexuosa* represent a favourable or a less favourable situation of the species composition of heathland, respectively. *Calluna vulgaris* and *Deschampsia flexuosa* can be considered as functional groups for different utilization types of heathland (cf. Heil & Aerts 1993). The spatial distribution of land use other than heathland in 1992, such as forest and arable field, but also recent management practices, have been used as a mask map in order to set constraints to the distribution of seed by either *Calluna vulgaris* or *Deschampsia flexuosa* in these areas. Moreover, from field observations the focal location of the heather beetle infestation in 1980 was also known (Brunsting 1982) and has been used to initialize a heather beetle pest. The GIS model has been applied to two different scenarios of atmospheric N-deposition, i.e. 10 kg N ha^{-1} yr^{-1} and 40 kg N ha^{-1} yr^{-1}.

To validate the model, the same type of information of the situation of the vegetation in 1992 has been derived from a Landsat Thematic Mapper (Landsat-TM) satellite image. Using standard image processing techniques (Wardley *et al.* 1987; Griffith *et al.* 1993; Lilesand & Kiefer 1994) a stratified classification was applied on bands 1, 2, 3 and 4 (three visible and one infrared band) to classify the vegetation and to derive the spatial distribution of the functional groups. The combination of bands 3 and 4 was used to derive the normalized difference vegetation index (NDVI), which is significantly related to the leaf area index (LAI) (Buiten & Clevers 1990; Reed *et al.* 1994). This combination was used to derive the spatial distribution of the individual canopy cover of both functional groups. Thus, before applying the model we have the initial situation in 1980

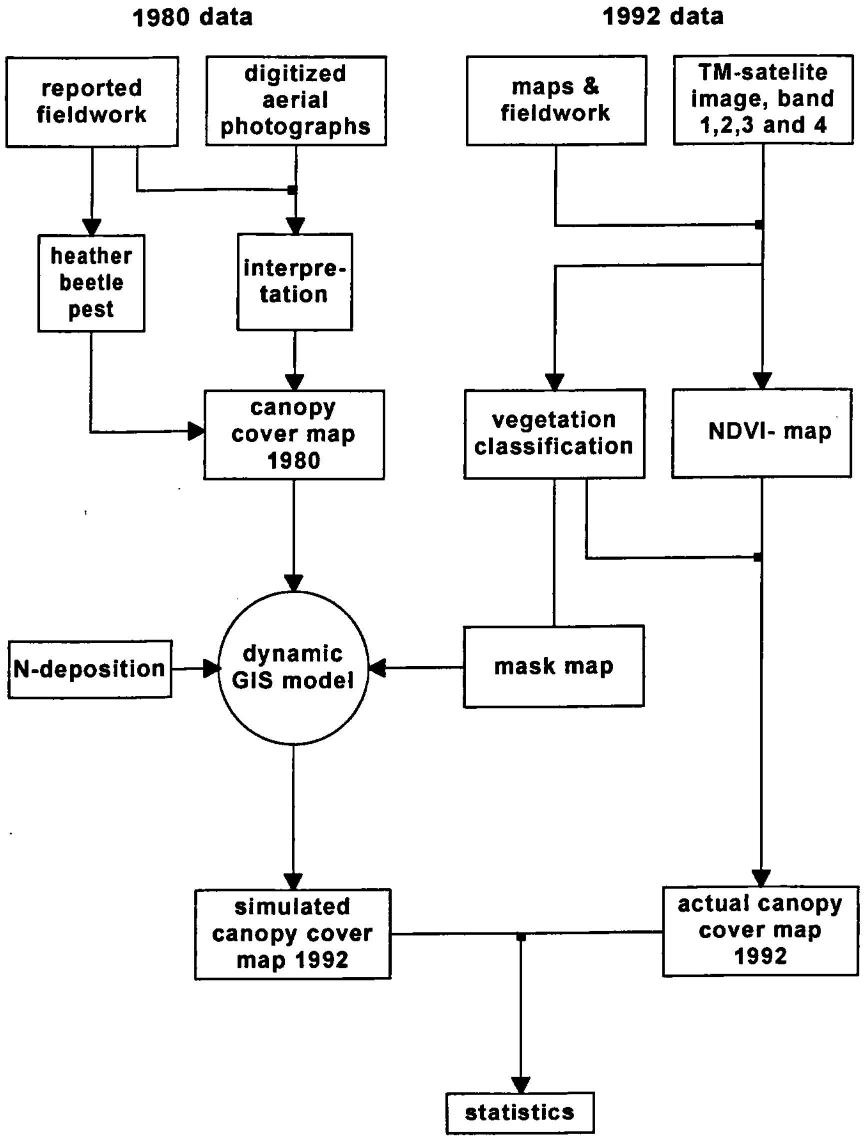

Fig. 4. Procedure to process the different data for spatially explicit (GIS) modelling of the 'Oud Reemsterveld' case study.

consisting of the canopy cover of both functional groups, and a validation situation in 1992 derived from RS also consisting of the spatial distribution of the canopy cover of both functional groups (Fig. 4). Before application to the model, both input and validation data were converted to the same resolution of 30 × 30 m.

RESULTS OF THE 'OUD REEMSTERVELD' CASE STUDY

Figures 5 and 6 show different maps of the canopy cover of *Calluna vulgaris* and *Deschampsia flexuosa*, respectively. The top left map shows the initial canopy cover of

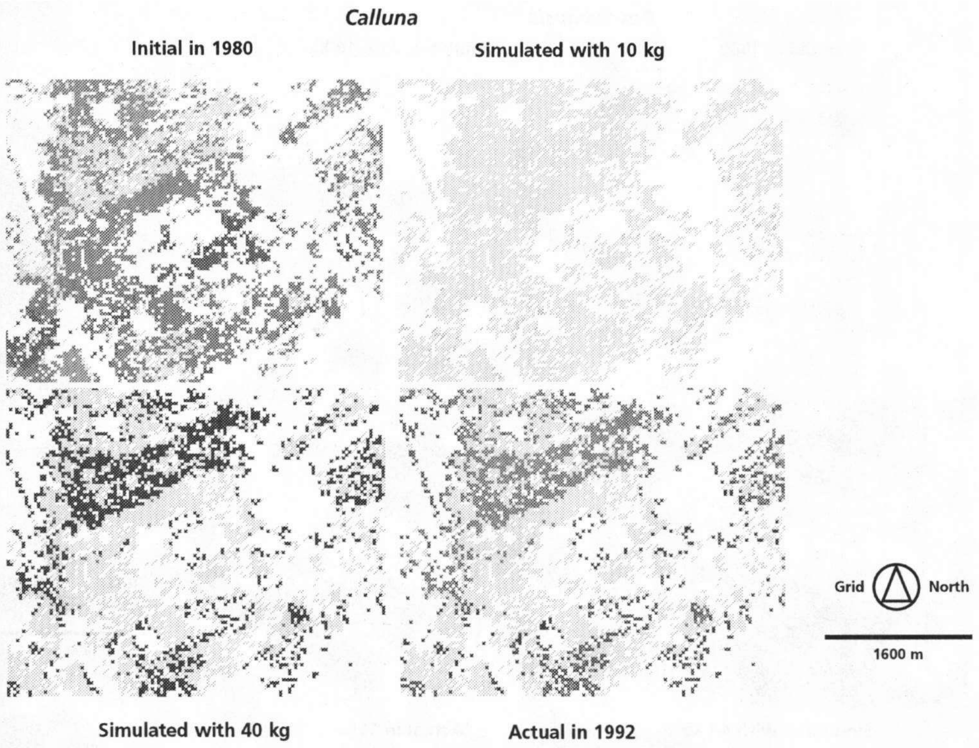

Fig. 5. Canopy cover of *Calluna vulgaris*: top left—initial situation in 1980; top right—simulated situation in 1992 under an atmospheric input of 10 kg N ha^{-1} yr^{-1}; bottom left—simulated situation in 1992 under an atmospheric input of 40 kg N $ha^{-1}yr^{-1}$; bottom right—actual situation in 1992. The different grey tones represent the different values of canopy cover (light grey=low canopy cover; dark grey/black=high canopy cover).

both functional groups in 1980. The top right map shows the results of the simulated canopy cover of both functional groups in 1992 under 10 kg N ha^{-1} yr^{-1}. The effect of this amount of atmospheric N deposition on the growth of both *Calluna vulgaris* and *Deschampsia flexuosa* results in a relatively low percentage of canopy cover of both species in 1992. In addition, the pattern of the canopy cover of both is fairly homogeneous. The bottom left map shows the results of the simulated canopy cover of both functional groups in 1992 under 40 kg N ha^{-1} yr^{-1}. As a result of the increased amount of N deposition, the pattern of the canopy cover under 40 kg N ha^{-1} yr^{-1} is significantly different from the pattern of the canopy cover under 10 kg N ha^{-1} yr^{-1}. The bottom right map shows the RS obtained map in 1992. In comparison with the RS obtained map it becomes clear that the pattern of the canopy cover of both functional groups is much better simulated under the 40 kg N ha^{-1} yr^{-1} assumption.

The correlation coefficients (R^2) between RS obtained canopy cover and simulated cover of *Deschampsia flexuosa* under the two N deposition assumptions are both highly significant (Table 1). However, there is a significant difference ($P<0{\cdot}01$) between the direction of the slope of the regression line under 10 kg N deposition and of the slope of the regression line under 40 kg N deposition. A perfect correlation between measured and simulated canopy cover should result in a slope value of one. It is obvious that the slope under 40 kg N deposition for both functional groups is much closer to one than

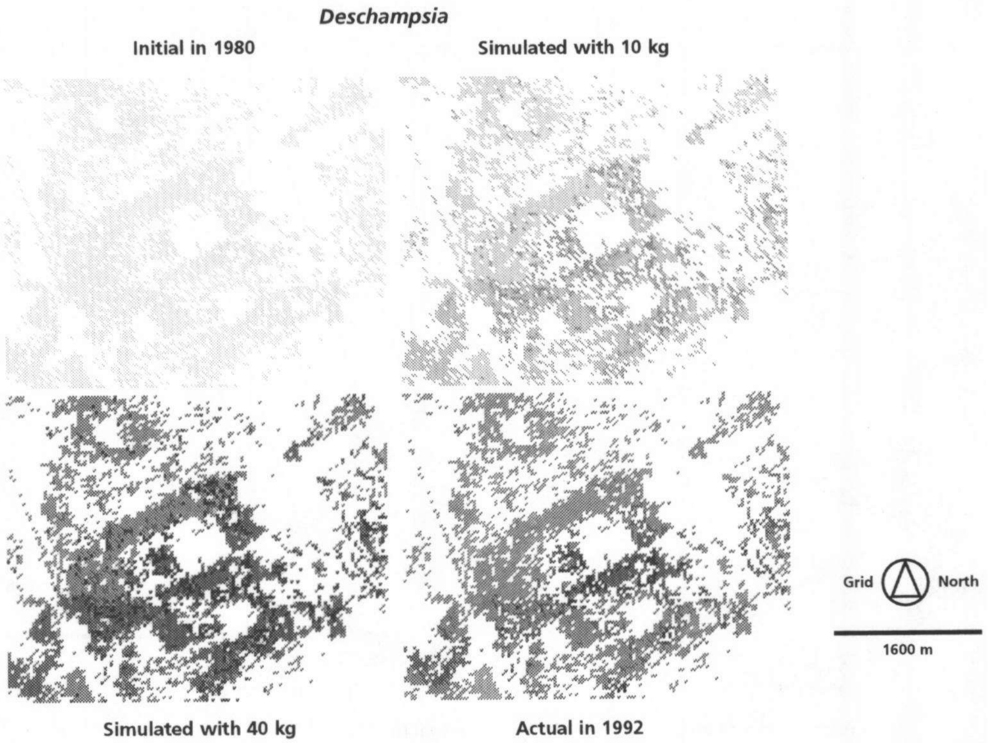

Fig. 6. Canopy cover of *Deschampsia flexuosa*: top left—initial situation in 1980; top right—simulated situation in 1992 under an atmospheric input of 10 kg N ha^{-1} yr^{-1}; bottom left—simulated situation in 1992 under an atmospheric input of 40 kg N ha^{-1} yr^{-1}; bottom right—actual situation in 1992. The different grey tones represent the different values of canopy cover (light grey=low canopy cover; dark grey/black=high canopy cover).

Table 1. Regression analysis of measured distribution and percentage canopy cover of *Calluna vulgaris* and *Deschampsia flexuosa* and simulated canopy cover of the same species under 10 kg N ha^{-1} yr^{-1} and under 40 kg N ha^{-1} yr^{-1}

10 kg N ha^{-1} yr^{-1}	: $Y_c=6{\cdot}495572+0{\cdot}340512\ X_c$	$R^2=0{\cdot}475^{**}$	$n=13056$
40 kg N ha^{-1} yr^{-1}	: $Y_c=0{\cdot}245963+1{\cdot}099221\ X_c$	$R^2=0{\cdot}993^{***}$	$n=13056$
10 kg N ha^{-1} yr^{-1}	: $Y_d=0{\cdot}053056+0{\cdot}672775\ X_d$	$R^2=0{\cdot}988^{***}$	$n=13056$
40 kg N ha^{-1} yr^{-1}	: $Y_d=2{\cdot}500629+1{\cdot}055333\ X_d$	$R^2=0{\cdot}923^{***}$	$n=13056$

Where Y_c=measured canopy cover of *Calluna vulgaris*; X_c=simulated canopy cover of *Calluna vulgaris*; Y_d=measured canopy cover of *Deschampsia flexuosa*; and X_d=simulated canopy cover of *Deschampsia flexuosa*. R^2=regression coefficient. Significance level $^{**}=P<0{\cdot}01$; $^{***}=P<0{\cdot}001$.

under 10 kg N deposition. This effect due to amounts of N deposition is even more pronounced on canopy cover of *Calluna vulgaris*. Here, the correlation coefficient (R^2) is even higher under 40 kg N deposition than under 10 kg N deposition, but also the slope of the former is much closer to one than of the latter.

If only a 1-D model version were available, the results of the model might lead to the wrong conclusion. The results of the corresponding time series of the total amount of canopy cover of *Calluna vulgaris* and *Deschampsia flexuosa* under the two different atmospheric N deposition assumptions, which can also be obtained from the GIS model, show that different amounts of N deposition have a different effect on the development of the canopy cover of both species during the simulation. However, the amounts of canopy cover of *Calluna vulgaris* in 1992, using either the 10 kg N ha^{-1} yr^{-1}or the 40 kg N ha^{-1} yr^{-1} deposition assumption, are both almost the same as the RS obtained canopy cover in 1992. That is to say, *Calluna vulgaris* has an average canopy cover of 15% (RS obtained) versus 12% (simulated), and 12% (RS obtained) versus 15% (simulated) under 10 kg N ha^{-1} yr^{-1} and 40 kg N ha^{-1} yr^{-1}, respectively. At the same time, *Deschampsia flexuosa* has an average canopy cover of 27% (RS obtained) versus 20% (simulated), and 25% (RS obtained) versus 30% (simulated) under 10 kg N ha^{-1} yr^{-1} and 40 kg N ha^{-1} yr^{-1}, respectively. From the results of the time series of the model ($\approx$a 1-D model), it could be concluded that both N deposition assumptions yield more or less a similar canopy cover of *Calluna vulgaris*, and to a lesser extent also of *Deschampsia flexuosa*, as the RS obtained canopy cover in 1992. However, from the results of the spatially distributed version of the GIS model, it is obvious that a deposition of 40 kg N ha^{-1} yr^{-1} is a much more realistic assumption.

DISCUSSION

The results of this paper demonstrate that spatial dynamics of vegetation (and animals) can also be simulated, that cannot be simulated properly with 1-D models. In particular, knowledge on the potential of the mobility of plants is still limited, which nowadays has become an important subject on themes such as habitat fragmentation and biodiversity in relation to environmental problems. In most West European countries, the decline of (semi-)natural vegetation has occurred as a result of changes in land use, but since the 1950s the remaining (semi-)natural vegetation is more and more threatened by environmental problems, such as air pollution and changes in water availability, etc. In these cases spatial-distributed models can be employed to simulate properly spatial processes.

However, the use of spatial-distributed models is not without serious disadvantages and it should be noted that most of these models rely on a number of assumptions that make their use at least uncertain (Klemes 1986; Beven 1989; Van Deursen 1995). Moreover, increased model complexity only yields improved simulation up to a certain level (Jörgensen 1988). The following problems may be associated with the use of these models:

- neither the definition nor the calibration of these models are well established;
- it is not clear if the point-based equations adequately describe three-dimensional, spatially heterogeneous and time varying processes in the real landscape;
- the model structure can influence parameter values significantly;
- the ability to validate the model is dependent on the errors in both input and output, and requires a different set of techniques and data than traditionally available.

These problems are not solved, and still require a great deal of research.

Both types of RS data, i.e. from aerial photography and from satellite imagery, have been used to estimate canopy cover and to collect spatially explicit data of both functional groups for initialization and validation of the GIS model. A problem with regression analysis of images is the inherently high degrees of freedom as a result of the large number of data in images. However, the pattern of the initialization map had a relatively low correlation with the pattern of the validation map, 60% and 45% for *Calluna vulgaris* and *Deschampsia flexuosa*, respectively. Although essential data for the GIS model, such as pattern and canopy cover, can be estimated with RS techniques, up to now this technique does not allow for the collection of soil parameters, e.g. for estimation of nitrogen availability, that would be valuable for further initialization of the GIS model. Areas, i.e. pixels, with the same canopy cover are now assigned with the same amount of nitrogen availability in the soil compartment. The application of the same amount of nitrogen availability under the same canopy cover leads to very useful results, as shown in the 'Oud Reemsterveld' case study, but the use of this type of information might lead to underestimates of the importance of the actual spatial distribution of soil nitrogen availability.

This paper has demonstrated that the combination of dynamic GIS models and RS information can be used to determine and to evaluate the consequences of patterns and processes in vegetation. It should be recognized that the dynamic GIS model developed here is not scale dependent. It could be applied on a relatively small scale of 1 × 1 m in the hypothetical study, as well as in the actual field study on a scale of 30 × 30 m. Major progress has been made with the construction of the dynamic GIS model about the (potential) effects of only two spatial processes on the patterns and processes of vegetation, because it contains the spatial distribution of opening up of the canopy (by a heather beetle pest in this case) and of seed dispersion from different functional groups which are considered to be important in the process of replacement in vegetation. With this dynamic GIS model the vegetation as a whole can be studied and interconnections or feedbacks between spatially and horizontally explicit processes can become visible.

SUMMARY

For some time vegetation scientists have used simulation models to describe ecological relations and processes. These models are mostly used to gain insight into the functioning of plant species, such as growth performance and competitive ability under different conditions. However, most plant species have a mobile stage during their life cycle, when seeds or vegetative components are dispersed. Including this spatial behaviour of plant species in simulation models requires the characterization of the spatial relationships between population dynamics of plant species and the spatial distribution of the species. Until recently, the dynamic models used to describe vegetation dynamics were so-called one-dimensional models. In this paper the advantages of the application of a GIS model for spatially explicit modelling of vegetation dynamics have been described. Application of spatial models requires a spatial-distributed description of plant species (or species groups) in the vegetation. Additionally, several remote sensing techniques in combination with field data were used to demonstrate how spatially distributed information of vegetation can be applied to simulate dynamics of patterns and processes in vegetation.

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