CHAPTER 10

Ecological modeling of short-term plant community dynamics under grazing with and without disturbance

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1. Introduction

1.1 Models of plant community- and ecosystemdynamics

A simulation model is a simplified presentation of a system in the real world around us, where this system is a perceived -limited- part of reality. The user determines the system with respect to his own purposes and to the natural structure of the real system (Penning de Vries, 1984). The identification of the system involves (i) the scale, including patch size (spatial size), the time steps plus duration and organization level, (ii) the variables to be explained (e.g. vegetation dynamics, animal behaviour, meat production, forage availability), (iii) the 'independent' variables and parameters, the use of which is determined by organization level and a prior insight of the user. It is important that the model should be 'open', i.e.

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there is opportunity to include variables which later appear to be important.

The decision as to which type of model is to be built depends mainly on the aims of the project. In the context of vegetation and landscape research these aims can either be to predict the changes to be expected or to understand the mechanisms causing these changes (= explanation). In the first case it is a primary requirement that the model and the simulation programme are widely applicable. In the second case, i.e. causalanalytical models, this generalization follows from the spatial and temporal dimensions of the real system that was initially chosen to collect data from. This model starts with a theoretical consideration of the internal structure of the system. In such models a sequence of steps, i.e. building the model, writing the programme, executing the simulation, validating the parameters, analyzing the sensitivity of the model, may be repeated, leading to a different, improved structure than the one-the process started with. A model can either be stochastic or deterministic or a combination of both. A general rule is: a deterministic model is contructed first and stochastic parts are added only if it proves essential.

The use of discrete time steps instead of differential equations has it advantages when describing a complex ecological system: 1. Ecosystems are rarely in a state of static equilibrium and, even under constant environmental conditions, are continuously changing (Grubb, 1979). Such dynamic change is better described with a discrete model. 2. Natural discontinuities in time exist (diurnal, yearly). The parameters in the system, having 'time' in their dimensionality, can be measured or estimated in a direct way with a constant time step from experiments and field observations. Climatological and other information, which is supplied in yearly or daily observations, can be applied directly. 3. A simulation can have three approaches: 'event', 'activity' or 'process' (Graybeal & Pooch, 1980). An event occurs at a point in time, an activity occurs over a period of time, a process is a continuing change. The scale on which one looks at the system should be chosen in such a way that changes can be described in terms of 'events' and 'activities', rather than 'processes'.

The discrete model obviously has also its disadvantages. The most important of these is the fact that the outcome of continuous processes is systematically underestimated (De Wit & Goudriaan, 1978). If parameters are used (by means of adjusting and 'tuning') to fit the simulated results with observations, these estimated parameters will have systematic errors. This should be taken into account with parameter-evaluation.

1.2 The use of an explanatory model

The necessity for one or other type of model is largely determined by the number of variables concerned and the complexity of their interrelations. Purely descriptive models, such as those underlying multivariate techniques (e.g. transition matrices) have the limitation of not allowing for mutual interrelations between independent variables. Another disadvantage of this type of model is that mutual effects of abiotic and biotic factors cannot be described or will not be revealed. In most cases the results of such analyses can only be formulated in terms of hypotheses. Frequently these hypotheses only have a local validity even after having been tested by means of an experimental approach.

Do explanatory models really give an 'explanation' or do they remain at the level of 'theory' or 'hypothesis'? Taking into account that a fieldphenomenon is practically never reproducable, and that any explanation of such a phenomenon is therefore different to an explanation of a physical event, simulation can best be considered as a link in a closed chain of observation, theory, hypothesis, experiment and simulation. The most important function of the explanatory model seems to be to bring information (characteristics of variables, interrelations, existing submodels) together into a manageable form.

In general, the separation of studies of biocoenoses into descriptive or causal-analytical is subjective and artificial and therefore irrelevant. However, studies such as the present one, which is aimed at understanding patterns and dynamics on a certain level of organization from properties on the next lower level, can perhaps be classed as 'causal-analytical'.

A serious problem in simulating plant community dynamics is the great number of parameters involved in such a simulation. It has been said that: 'with five parameters I can draw you an elephant, with two more I can let it dance the mazurka'. The number of parameters needed to make the results fit observations must therefore be kept as low as possible, and the parameters should only be varied within the limits of observation and of scientific probability. It is essential that all parameters are measurable, and are expressed in imaginable dimensions.

The question of whether sufficient environmental and population/life-history data have been collected to explain the dynamics of a system can only be answered by means of a set of mathematical equations. These equations have to present ecological reality as well as possible, given the necessary simplifications. The set of equations must be structured usually in a systems-flow-diagram. This constitutes the model. This model must be translated into a computer language and can than be used for a simulation. The initial state of a simulation is of primary importance, it has to consist of real (observed) values. If the results of the simulation are consistent with observed dynamics, then it may represent reality.

1.3 The modeling of disturbance

Disturbance can be simulated by constructing a mathematical model of a system, and then subjecting the model to events, that can be regarded as a disturbance, with respect to that system, taking into account the relevant scale (spatial, temporal, integration level). The word 'disturbance' should only be used with reference to a given system (or family of systems) and a given scale. For example, grazing is certainly a disturbance for an individual leaf, or in most cases an inidividual plant. It is also a disturbance for a grassland community just taken into grazing, but not for a community after a couple of years of grazing.

The problems and possibilities of modeling disturbance can best be illustrated by a simple and well-known example (Fig. 1). A model can be constructed to describe the effects of disturbance on organisms in a petri dish, based upon the assumptions: (i) reproduction is positively proportional to the population size and (ii) there is a maximum population size, determined by available resources and space. If we further assume that (iii) death does not play a significant role in the chosen time span, and (iv) any increase in the speed of growth, due to an increasing population size, and decrease, caused by approaching the carrying capacity, are equally important, then the logistic equation can be used. If growth is temporarily disturbed by adding a toxin to the petri dish on the fourth day of the experiment, the growth formula can then be modified using a simple, descriptive equation to quantify the results. This class of models to describe the results of disturbance, will be called 'type A'. If, however, the



Fig. 1. (Logistic) growth curves of hypothetical populations. Undisturbed growth rate (AX) = 0.25; carrying capacity (KX) = 1000. Equation: $DX/DT = AX \star X \star (1 - X/KX)$. Disturbance 'A' reduces the growth rate to minimally 0.025 during T(20-40). Than: AX = ABS(T-30) \star 0.025. Disturbance 'B' is an invasion of a second organism at time = 20. Equations:

 $DX/DT = 0.25 \star X \star (1 - X/1000) \star (1 - 2.00 \star Y/1000)$ and $DY/DT = 0.50 \star Y \star (1 - Y/1000) \star (1 - 0.50 \star X/1000)$. For further explanation see text.

culture is infected with a bacteria, which eleminates the organism in a few days, a serious modification of the mathematical model is needed. Since two populations are mutually affecting each other, an extension of the scale of the model is necessary to encompass a higher level of organization. This class of modeling of disturbance will be called 'type B'. Examples of the B-type modeling of disturbance are those of Doyle (1981), simulating the effects of hurricanes on the structure of tropical rain forest, West et al. (1980), simulating the influence of air pollution on temperate forest and Miller et al. (1984) simulating disturbance in a tundra ecosystem with the model 'AR-TUS'.

The validity of a model of a system has its limits, which should be defined so that they equal the limits in general of the environmental (vector-) space to which the system is adapted. Disturbance occurs when these boundaries are exceeded, i.e. conditions transcend the limits of adaptation (or flexibility) of the system. Hence the modeling of disturbance needs a model on a more extended scale (spatial and/or temporal and/or level of organization) than the undisturbed system itself.

The following definition of disturbance might be useful in this context: 'any event exceeding the environmental conditions to which the system is is adapted'. Disturbance is not identical to unpredictable variation of a normally variable factor to which variation a system is adapted. Every factor in a system has its own 'predictable unpredictability'. Terms like 'adaptation to disturbance' or 'continuous disturbance' are not useful. Each system has its own autogenic dynamics: short-term and long-term, random, cyclic and/or directed (succession). After a system has been disturbed, it no longer exists in its previous form as it has been replaced by a different system with its own dynamics but, after a certain period of time, convergent succession may cause the disturbed and the undisturbed systems to become identical. The classification 'disturbance-dependent system' can only be applied to the instable, temporarily existing situation, following a disturbance.

1.4 The aims of modeling short-term plant community dynamics

The understanding and causal explanation of an ecosystem or plant community requires knowledge of 'the species life-history and physiological characteristics which determine, to a large extent, potential population responses to the changing competitive environment' (Peet & Christensen, 1980). Ellenberg (1954) argued that: '...questions came up with respect to the causes of these strict relations (between the mosaic of plant communities and environmental conditions). These questions can be answered by three supplementary means: (i) quantitative comparison of numerous communities and their habitats. (ii) quantitative analysis of relevant environmental variables and of characteristics and performance of plants in their own habitats, (iii) experimental studies under more or less simplified conditions'. The second and third of these can be achieved more succesfully with the help of an explanatory model.

An explanatory model of plant community dynamics must contain characteristics of the species present, including their repsonses to the relevant environmental factors. Interference between species populations has to be included in such a model, which has to separate competition for dif-



Fig. 2. Generalized design of an explanatory model of plant community dynamics. Disturbance is defined as an event exceeding the limits of validity of the model.

ferent resources (Fig. 2). One can regard the system as 'a mozaic of phytocoenoses' consisting of subsystems namely the vegetation patches, or homogeneous or heterogeneous pieces of vegetation, depending on how the investigator wishes to define them. Each of these subsystems has its own flexibility with respect to changes in environmental conditions. Any change wich exceeds these limits is a disturbance of the subsystem. The limits of validity of the ideal model should equal the limits of adaptation (flexibility) of the system as a whole. In this case the disturbance may cause the replacement of one subsystem by another, which is already part of the main system, i.e. within the limits of validity of the model, hence being of 'type A'. If an environmental factor exceeds these limits, death of individuals and/or extinction of populations starts to play a role, open space may be generated, and invasion of new genotypes or species may occur (Gremmen et al., 1984). To quantify these changes a 'type B' model is needed. Many species can be potential invaders, depending on the composition of the seedbanks, their presence in adjacent areas, the time of the year, the weather, etc. Since potential invaders can be of various life forms and strategies, it is a very complex task to model these changes.

Disturbance of a plant community, or any other system, can be described in two dimensions, namely intensity and duration or frequency. The time dimension of disturbance has not been covered in this study. Although, in most cases, disturbance will cause destruction of living phytomass or accumulated detritus (Grime, 1979; Reiners, 1983), it is better that this effect is not included in a definition.

In spite of the problems of simulating disturbance, such an excercise is useful, since it may give the user an idea of the trends and general patterns, that are likely to occur. It is also an excellent method to test the basic model and to find its weak spots and errors. This kind of simulation will only be predictive in the very short term. Inductive models, based on numerous observations, will be more effective for long-term prediction.

2. Description of the model 'EGRAS'

2.1. General

The model 'EGRAS' ('Ecological Grassland Simulator') is concerned with a section of the former Lauwers Sea, which was a part of the Wadden Sea (in the north of the Netherlands), which was embanked in 1969. The actual area involved ('Schildhoek en Pampusplaat') is approximately 200 ha and was designated a feeding area for wintering and transmigrating wild fowl in 1979. However, this aim was endangered with the increasing amount of litter and standing dead material and increasing dominance of Agrostis stolonifera, especially in the dryer parts of the area. Therefore, since 1982, the area has been grazed by young cattle at a stocking rate of about 1 animal per hectare. The cows enter the area annually in early June and leave it in October. A large exclosure has been established for the purpose of scientific research. Data concerning vegetational changes, herbage accumulation and herbage removal by cattle and water fowl and the changing (desalinating) abiotic environment have been published (Joenje, 1978, 1979, 1982). Other information concerning growth characteristics and mutual competitive ability of some plant species, was collected in the cause of this study.

The aim of this project was to develop a model



Fig. 3. State variables and driving factors influencing the growth of a species in a site.

and a simulation computer programme, explaining short-term fluctuations and changes of vegetation composition from physiological characteristics of plant species and populations. The decision as to which abiotic factors were to be considered was initially left open. The initial version of the programme only contained total nitrogen, chloride and cattle grazing. This proved to be insufficient. The abiotic part of the model was therefore extended to include soil moisture, weather characteristics and the partitioning of nitrogen into soil available N, soil non-available N and biomass N (Fig. 3).

The earlier model 'ARTUS' (Miller et al., 1984) dealt with one day steps on one square meter sites and described the growth, above and below ground, of ten plant species, six of which were mosses. It differed in spatial scale and specification from the present study. Instead of describing a complete nutrient budget and explaining the phytomass production and allocation using independent driving factors, this study attempts to discover which abiotic factors, and which inter-population interference parameters, are minimally required to understand observed spatial and temporal variation in quantitative species composition. This is a synecological problem rather than merely an investigation of an ecosystem. A number of solutions and assump-



Fig. 4. Flow diagram of a single step (1 day) of the simulation programme 'EGRAS'. 'Condition I' represents the state of the system at the end of the previous day (day 1), 'conditions II' represents the state at the end of day 2. For further explanation see text.

tions from 'ARTUS' have been used in 'EGRAS'.

The area was subdivided into a grid of hexagonal plots, each sized 400 m². These sites were each classified, with the help of a vegetation map of the area (Reitsma, 1981). All operations were carried out on a summarizing 'map', containing 25 different quadrats (total size 1 ha.) representing the present vegetation typology. The programme used one day time-steps. The duration of a complete simulation was one grazing season. A simulation of the changes in the late autumn, winter and early spring (with water fowl grazing) has not yet been accomplished. Under a set of assumptions, the most important of which was that all relevant changes in vegetation composition took place between May and October, it was possible to simulate the dynamics in subsequent years. The initial state in all simulations was the actual (described) state in May 1982, at the start of the new management, which caused a disturbance, according to the definition.

The model uses five plant species namely Agrostis stolonifera, Aster tripolium, Phragmites australis, Puccinellia maritima and Salix repens, which constitute at least 50% of the vegetation coverage in about 80% of the area.

An outline of the model is presented in Fig. 4.

The three main processes, represented by thick arrows in the figure, are mainly independent. All three use the state at the beginning of the step (day) and are used in the sequence: 1. grazing, 2. growth & death, 3. abiotic interference. Since there are a few operational links between the lines, the programme is not completely indifferent to this sequence. However, a change of sequence of operational steps never resulted in a difference of more than 0.44% over an entire growing season. Listings of the most important equations and most parameters are given in the appendix. The simulation programme was written in PASCAL. This programme was not meant to be applicable for other areas than the one just described.

The simulated system in this study is a 'landscape' rather than an 'ecosystem', since it deals with an ecological mosaic of ecosystems which is always highly heterogeneous (Godron & Forman, 1983).

2.2 Growth & death

The growth equations (appendix) use discrete versions of the logistic equation, based on relative growth rate of plant species per unit area (RGRMAX) and with the maximum possible phytomass per species per unit area occupied (SCMAX). The maximum growth rate is diminished by several effects. In the equations these effects are represented by factors which can have values between zero (growth stops) and one (no effect) (Fresco, 1982). The environmental factors considered to influence growth are:

- 1. C: competition with the other species populations for resources other than nitrogen
- 2. ND: nitrogen as a deficient factor
- 3. NT: nitrogen as a toxic factor (factors ND and NT represent a complete response curve with respect to nitrogen)
- 4. ST: sodium chloride as a toxic factor
- 4. G: grazing intensity
- 5. T: temperature
- 6. L: light
- 7. W: soil water.

Most of the parameters (see appendix) have been obtained either experimentally or from literature.

The total of environmental influences which restrict the relative growth is a factor $C \times ND$ $\times NT \times ST \times G \times T \times L \times W =$ TGLF ('Total of Growth Limiting Factors'). The total biomass of a species in a site is divided into living (SCLI) ('Standing Crop - Living') and dead (SCDE) standing phytomass. The below ground biomass had to be neglected because of inadequate information. The equations, describing growth of a species, the transitions from living to dead standing material and from standing dead crop to litter are:

$$RGR(t) = RGRMAX \times TGLF(t)$$
 (1a)

 $DSCLI(t) = RGR(t) \times (1 - SCLI(t)/SCMAX) \times SCLI(t)$ (1b)

$$\begin{aligned} & \text{SCLI}(t) = \text{SCLI}(t) - \text{DEATH} \times \\ & \text{SCLI}(t-1) \end{aligned} \tag{1c}$$

$$SCDE(t) = SCDE(t-1) - DECOD \times SCDE(t-1) + DEATH \times SCLI(t-1)$$
(1d)

DECOD (g/g/day) represents the coefficient of transformation from standing dead material to litter, which values were obtained from personal

observations in the area mentioned and from literature. DEATH and DECOD are calculated within each one-day-run. DEATH (g/g/day) is directly proportional to the total growth limitation by causes other than by approaching the carrying capacity (factor TGLF). If this growth limitation exceeds a value that is given per species (GDLI, 'Growth and Death Limitation'), the relative amount of dying remains at a constant value (MINDE).

Each species occupies a certain amount of area, e.g. AREA(j) for species j and the growth state parameters concern this covered area. For the area of a species in a site to expand, there has to be open, uncovered, surface (OPAREA), i.e. a species has to establish in the bare soil. This can be done either by germination or by vegetative propagation. Germination per unit open area is a function of: (i) chloride conditions in the upper soil layer, (ii) the air temperature, (iii) the amount of living seeds present. Variable (iii) was large for the five species considered, though variable both in space and time, therefore seed was not assumed to be a limiting factor. The vegetation propagation is a linear function of: (i) available open area (OPAREA), (ii) the speed of growth, though Jaquard & Heim (1983) found a asymptotic non-linear relationship between sprout and tiller production in Dactylis glomerata, (iii) the length of the boundary between open area and vegetation, both in the site and in adjacent sites, (iv) chloride in the upper soil layer, (v) potential horizontal extension of other species.

2.3 Grazing

The grazing has been simulated as the grazing of one single 'supercow'. For the test-map of $25 \times 400 \text{ m}^2 = 1$ ha, this 'supercow' was equal to one single cow (except for the disturbance 'overgrazing', see later). The total amount of biomass consumed by a cow increases from 5.2 kg dry matter per day in early June to 10.8 kg in med-August, than remains constant for the rest of the grazing season. The relative preference of the cows for the various species was expressed in parameters PRSP(j), obtained by means of observations in the area. The total amount of phytomass grazed in a site is divided over the species proportionally with

$$((SCLI(i,j) + SCDE(i,j)) \times PRSP(j)$$
(2)

The minimum amount of above-ground phytomass remaining after grazing was estimated for each species from the results of field measurements (RESIDU(j)). The relative grazing preference values for a given site i are calculated next (every day):

$$RPSI(i) = PRLO(i) \times PRFO(i) \times PRAD(i)$$
(3)

where PRLO is the 'locality preference', determined by factors such as the regular routes of the cattle to sleeping sites, the presence of fences, etc. PRFO is the 'forage preference' (Goodall, 1969), which is proportional to the logarithm of the standing crop and to the preference for the species. PRAD is determined by the preferencevalues of adjacent sites.

After the calculation of PRSI-values, each of the sites is classified into one out of five equidistant preference-classes. The grazing starts in a randomly chosen site of the highest class. This site is grazed, until its classification drops down one class. Next the grazing continues in the nearest site (if necessary chosen at random) of the highest class.

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2.4 Abiotic factors

Since no evidence is available that nutrients other than nitrogen are limiting or controling factors in the system, the nutrient-conditions are represented by nitrogen only. The amount of total nitrogen remains constant in each site (400 m^2). The total amount of nitrogen (NITOT) is divided into: (i) a fraction in the live standing crop of each of the species j (NISCLI(j)), (ii) a fraction in the dead standing crop (NISCDE(j)), (iii) the fraction in the litter and in other forms not directly available to the plants (NINAV) and (iv) the fraction which becomes available during the time-step (NIAV).

Amounts of nitrogen are expressed in the

model relative to standard units (u.N. = units nitrogen). This dimension has been adopted because of a transmission of the results of experiments. The plant responses to nitrogen in these experiments were considerably more exact and reproducible than a chemical re-analysis of the amount of nitrogen. Therefore nitrogen values derived from simulation are not easy to compare with those from chemical soil analysis. There is a significant non-linear, but monotonous relationship between values derived from the model 'EGRAS' and those measured in the field.

The amount of nitrogen in the newly-grown biomass depends on parameters of the species and the amount of available N:

$$NIFPL(i,j) = P1(j) + P2(j) \times$$
$$ln(NIAV(i))$$
(4)

where NIFPL(i,j) is the relative amount of nitrogen in the new biomass of species j in site i and Pl(j) and P2(j) are constants, obtained from simulation, using the results of growth experiments with varying nitrogen concentrations.

The models applied here for the simulation of decomposition and availability of nitrogen are those of Olson (1963), Davidson et al. (1978), Runge (1983) and Kemmers & Jansen (1985). Olson's decay coefficient is a function of temperature and soil moisture:

$$NIIN(t) = NIIN(t-1) + f(sum(NISCDE), DECOD - DECOL \times NIIN(t-1)$$
(5a)

$$NINAV(t) = NINAV(t-1) + DECOL \times NIIN(t-1) - DEMIN \times NINAV(t-1)$$
(5b)

$$NIAV = NIAV(t-1) + DEMIN \times$$
$$NINAV(t-1) - f(growth)$$
(5c)

where NIIN is the detritus input (expressed in u.N.) and DECOL is the decay coefficient (a function of temperature and soil moisture) and DEMIN is the demineralisation constant. Each site was treated as a closed system with respect to soil fertility.

The biomass which is removed by the cattle (in-

cluding the trampled biomass and the consumeloss) immediately loses its nitrogen to NINAV. The model would be improved using time delays for the decay of urine, faeces and lost litter, but so far no adequate information is available.

The salinity of the majority of the area has been declining slowly since the embankment was finished in 1969, but there is still considerable temporal and spatial variation which controls vegetation composition. So far no suitable model, describing the relationships between salt, moisture, soil texture and topography has been found in literature. A simple empirical model has been developed. Because of the yearly fluctuation of the salt values desalinisation has not been taken into account in the five-year runs of the simulation. The model assumes a negative linear relationship between soil moisture condition and the salt concentration, if there is no water above the soil surface. The maximum salt concentration under extremely dry conditions (SAMAX) has been shown to be a function of the percentage of the soil surface which is not covered with vegetation. However, there is some circular reasoning in this part of the model. Therefore it is better regarded descriptive, rather than explanatory.

Weather conditions have been taken from monthly reports of the Royal Netherlands Meterological Institute (K.M.N.I.) at Leeuwarden Air Force base (ca. 40 km from the area). The average temperature and the total amount of radiation were used for the simulation of the plant growth, whereas precipitation and evaporation were used for the estimation of soil moisture conditions.

2.5 Simulation of a sequence of seasons

During the winter season (mid-October until May), the area is at first intensively grazed by transmigrating water fowl (Joenje, 1985). Later (December to February) there is more extensive grazing by overwintering wigeons. In the spring grazing by migrating geese and ducks can again be observed. Data concerning winter-grazing have recently been collected, they have not been incorporated into the model.

Most of the parameters in the model reach their validity-limits at minimum average diurnal temperatures, such as those in the middle of October. An extension of the model to that of a whole year is being worked on, but has not yet been accomplished.

Sequences of not more than five years were simulated; in each case the simulation started in early June 1982. The weather conditions of 1982 were repeated five times, so as to facilitate interpretation; the spring and summer of 1982 were average, except for a rather dry early summer. If we assume that all changes in relative vegetation composition occur during the summer season, that the biomass removed by winter grazing and death during winter is replaced by spring regrowth, and that the percentage standing dead material remains at the value it had after the first (1982) grazing season, simulation of the period October till May can be replaced by a data operation and a restart (Fig. 5).

Although the programme simulated vegetation dynamics in all 25 sites at each simulation run, for simplicity only six sites have been chosen for a final interpretation (Table 1).

Table 1. The six 400 m ² sites (out of 25), selected for presentation and interpretation. The species name	es in italics are those of species
with an initial (1982) standing crop of more than 100 g/m ² .	

Site nr.	Rel. salt cond.	Rel. moist. cond.	Soil texture	Vegetation type
[1.2]	fresh	dry	clay	A.stolonifera/P.australis/S.repens
[1.3]	fresh	dry	sand	P.australis/S.repens
[2.2]	s/f	d/w	s/cl	A.stolinifera/A.tripolium/P.australis/P.maritima
[3.3]	s/f	wet	clay	A.stolonifera/S.repens/A.tripolium/P.maritima
[5.3]	salt	wet	clay	A.stolonifera/A.tripolium/P.maritima
[5.4]	salt	wet	clay	P.maritima/A.stolonifera/A.tripolium



Fig. 5. A scheme of the simulation of a sequence of years. The events in the winter period are not simulated, but approached as one single event by means of an estimation procedure (see text). The programme has been run without grazing, with grazing and with overgrazing in the second year. Where a shortage of forage occurs, the cattle are removed and no grazing occurs for the remainder of the season.

2.6 Disturbance

Three types of disturbance were simulated: (i) an extremely dry season, simulated by lowering the soil water level by 30 cm over the entire area in the second year of the simulation and returning it to normal in the third year, (ii) raising the soil water level by 30 cm in the second year and returning it to normal in the third year, (iii) quadrupling the stocking rate in the second year and returning it to normal in the third year.

Under high grazing pressure a food shortage could occur in the simulation. If the amount of consumable forage was less than 20% of that needed by the cattle (5.2 - 10.8 kg of dry matter per cow per day) during ten sequential days, the simulated cattle was removed from the area, which than remained ungrazed during the rest of the season.

3. Results

Simulated values for living phytomass did not depart significantly from the observed values over the growing season (Table 2, Fig. 6). Simulation tended to underestimate *P.maritima* and *A.stolonifera B* (with abundant flowering and little tillering), but overestimates *A.stolonifera A* (with abundant tillering and not much flowering) in general. The results of the simulation of living and total phytomass are, when compared with observed values, satisfactory, but can be improved. However, the computer programme failed to simulate changes in the percentage standing dead phytomass correctly, especially in the ungrazed simulation of 1982 (Fig. 7). The cause of this seasonal pattern is still unknown, therefore cannot be simulated. The simulated patterns in the following year, 1983, are according to expectation; a decrease of the percentage standing dead matter until July/August and an increase in the late summer and autumn. The peculiar pattern of A. *stolinifera* B in 1983 underlines the necessity to investigate the relationship between weather conditions and the dying of the phytomass.



Fig. 6. A comparison of simulated values of living aboveground phytomass with observed values in the growing season of 1982. Meaning of the columns in each histogram from left to right: 1. A.stolonifera B (with rapid tillering and no or hardly any flowering); 2. A.stolonifera A (with relatively little tillering and abundant flowering); 3. P.maritima; 4. A.tripolium. The bold-line histograms represent the simulated values, the thin-line histograms observed values.



Fig. 7. Standing dead matter as a percentage of total (living + dead) phyto-mass. Observed values in 1982 (A) and 1983 (B), compared with simulated values (C). Squares: A.stolonifera*A; triangles: A.stolonifera*B; open circles; P.maritima; closed circles: P.australis.

Simulations of 'wet' and 'dry' years indicated that: 1. Bare ground (up to 91% in the second year) was recolonised slowly, taking at least three years; 2. *A.stolonifera* was least influenced by ei-

Table 2. The depature (% difference) of the simulated living phytomass from observed values of four species in five months during the 1982 growing season. The A.stolonifera A form with rapid vegetative propagation and hardly any flowering; A.stolonifera B has abundant flowering and relatively little vegetative tillering. The analysis of variance shows a significant difference between the species, but no difference between months. The data are the same as those used in Fig. 6.

	Jun	e July	Aug.	Sept.	Oct.	Total
A.stolonifera*	A +3	0 -52	+36	+43	+47	+104
A.stolonifera*	B - 2	0 -22	- 6	- 6	- 3	- 57
P.maritima	1	0 -36	-29	-29	-29	-123
A.tripolium	+1	7 +13	-29	0	0	+ 0
Total	+2	7 –97	-28	+ 8	+15	- 75
Item	D.F.	M.Sq.	F			
Species	3	2339.17	4.85	5*		
Month	4	490.24	1.018	3 n.s.		
Residual	12	481.78				



Fig. 8. An example of a graphical presentation of the results of a five years simulation (site [1.3]). The winter period between two subsequent years causes a discontinuity! From top to bottom: not grazed, 'normally' grazed and overgrazed. Legenda: bold lines: *S. repens*; thin lines: *P. australis*; 'long' interrupted lines: *P. maritima*; 'short' interrupted lines: *A. stolonifera*; dotted lines: *A. tripolium*.

ther 'dry' and 'wet' years, although its standing crop was lower after the disturbance, it recovered quickly; 3. *P.australis* was most affected by the 'dry' second years, when it failed to re-establish, but was benefited by the 'wet' years. 4. *S.repens* was hardly affected by the 'dry' disturbance, but was greatly benefited by the 'wet' second year; 5. *P.maritima* was not affected by 'wet' years but was benefited from the 'dry' disturbance, especially in the sites where the species was absent: there it established; 6. *A.tripolium* invaded, resp. increased after either 'dry' and 'wet' disturbance; all events causing an increase of bare ground were obviously beneficial for the establishment and competitive situation of *A.tripolium*.

For the graphical presentation of a five-year simulation (not grazed, grazed and overgrazed) of a site see Fig. 8. The results of these more-year



Fig. 9. The state of twelve biotic and abiotic variables on day nr. 210 (August 28.) of the fifth simulated year. All variables were independently divided into 5 equidistant classes, represented by the five different dot sizes. The colums represent the simulated regimes 'not grazed' grazed and 'overgrazed', the rows stand for the six sites (Table 2). The intervals of the outcomes of each variable, used for the classification are: *A.s. tolonifera* 0–149 g/m²; *A.tripolium* 0–21 g/m²; *P.australis* 0–244 g/m²; *P.maritima* 0–28 g/m²; *S.repens* 0–449 g/m²; nr. of species per site 2–4; eveness (rel. Shannon measure) .118–.998; standing crop 17–698 g/m²; standing dead 0–379 g/m²; %% open area 23–93%; mineral nitrogen 59–1000 u.N.; salt (rank numbers) 1–18.

simulations (1982-1987) could, of course, not be compared with actual values. However, many trends, such as the disappearance of willow under grazing, the establisment of Sea Aster in disturbed places and the advantage of the halophytic species under grazing, are consistent with observations. The simulated effects of the grazing and overgrazing on twelve biotic and abiotic variables are presented graphically in Fig. 9. The effects of grazing on the phytomass of the species was further subjected to multivariate ordination, using 'Detrended Correspondance Analysis' (Gauch, 1982). For that purpose simulated values on day nr. 210 of the fifth year were used. The results (Fig. 10) show that grazing changes vegetation containing a great deal of S. repens and P. australis into vegetation characterized by A. tripolium and A. stolonifera. Vegetation originally dominated by A. stolonifera, A. tripolium and P. australis was not greatly affected by grazing. The overgrazing in the second year causes a species replacement towards A. tripolium and P. maritima in all cases.

Finally, the dynamics of the plant species pop-



Fig. 10. The results of a DECORANA-ordination with the untransformed phytomass-data of the 210-th day of the fifth year. The data of the five species in the six sites under the regimes 'not grazed' ('NG'), 'grazed' ('OG') and 'overgrazed' ('O') were used.

ulations under the three simulated treatments ('not grazed', 'grazed' and 'overgrazed') were compared (Table 3). This comparison makes clear that the halophytes *P. maritima* and *A. tripolium* benefit from overgrazing when compared with 'normal' grazing. For *P. maritima* an extremely high grazing density even seems to be more beneficial than a normal density, at least in relatively dry habitats. *A.tripolium* remained stable in the salt sites, whereas it increased strongly in phytomass in the fresh and dry sites. An exception is the intermediate site 2.2, where it was replaced by *P.maritima*.

4. Discussion

The questions to be answered with the help of the results of this simulation model are: 1. Simulation models are simplifications of actual processes; to what extent do they improve our knowledge of mutual interference of biotic and abiotic factors and predict changes in species composition? 2. Is THIS model a sufficient description of THIS system \cdot in other wordt: do we or don't we need other variables and/or other relationships to understand the dynamics of this grassland-system? 3. Does the extension of the model – perhaps into circumstances which will never be observed – supply us with information with respect to the

Grazing															
site	-	+	4×	-	+	4×	-	+	4×		+	$4 \times$		+	4×
1.2	+2	+2	+2	0	0	+ 3	0	0	+3	+1	t −2	-2	+2	-3	-3
1.3	+3	+3	+3	0	0	+ 3	0	+3	+3	+2	+1	$^{-2}$	+2	3	-3
2.2	+2	+2	+2	+2	0	+ 2	+2	-2	-2	+2	-1	-2	0	0	0
3.3	+2	+2	+2	+1	0	0	+1	0	0	+1	-3	-3	0	0	0
5.3	-1	+1	-1	+2	+2	+ 2	+2	0	0	0	0	0	0	0	0
5.4	-1	-3	-1	+2	+2	+ 2	+1	0	0	0	0	0	0	0	0
sum	+7	+7	+7	+7	+4	+12	+6	+1	+4	+6	-5	-9	+4	<u></u> —6	6
	A.stc	olonifera	7	P.ma	ritima		A.trip	olium		P.au	stralis		S.repe	ens	

Table 3. Dynamics of the species populations in each site for each of the grazing simulations over five years. Explanation of the figures: +3 = establishment, +2 = increase of phytomass of at least 100%, +1 = increase of <100% but >=20%, 0 = stable (change of phytomass <20%) or absent, -1 = decrease <100% but >=20%, -2 = decrease >3=100%, -3 = disappearance.

general rules concerning disturbance and, if so, what degree of generalization do these results justify?

4.1 Evaluation of the simulation approach

The problem 'finding a combination of species properties such that the actual vegetation dynamics can be explained adequately', can be approached in a more simple way. Assuming that three environmental gradients affect species composition: nutrient poor (sand) vs. rich (clay), fresh vs. salt and not grazed vs. grazed, the species parameters can be looked for which can be expected to describe the species' ability to maintain or to establish in a given habitat. These parameters could be: 1. concerning the nutrient poor environment, the minimum amount of nitrogen required for growth (MINN); 2. concerning the rich environment, the speed of growth (RGRMAX); 3. concerning the fresh environment, unknown; 4. concerning the salt environment, the maximum tolerated amount of salt in the soil (LETC); 5. concerning the not-grazed situation, unknown; 6. concerning grazing, the vulnerability of the species with respect to grazing (LETG). Values for all these parameters were determined experimentally.

Since the relative weight of each of those parameters was not known, they were replaced by their rank numbers (Table 4). Average rank numbers for each of the habitat types give an indication of the rank order of abundance of the species in a habitat type. When compared with either observed and simulated values, these predictions turned out to be a rather close approach. The parameters RGRMAX, MINN, LETC and LETG therefore provide a good description of the behaviour of these five species in the area studied.

Table 4. Prediction of the species composition, based on rank numbers of the most important simulation parameters. The Fig. I, II and III indicate relative abundance, derived from average rank numbers. For further explanation see text.

	poor	ric	:h	fresh	salt	nc	ıt-g.	grazed
A.stolonifera	2.5	5		3	3	2.:	5	4.5
P.maritima	2.5	4		3	4.5	2.:	5	4.5
A.tripolium	2.5	3		3	4.5	2.:	5	2
P.australis	2.5	2		3	1.5	5*		3
S. repens	5	1		3	1.5	2.:	5	0**
grazing	+	+	+	+	-		-	_
nutrient	R	Р	R	Р	R	R	Р	Р
salt	F	F	S	S	S	F	S	F
A.stolonifera	ш	ш	III	Π	Π	III		
P.maritima	II	Ш	III	III	III	Ι	III	
A.tripolium			II	I	Ι		III	
P.australis						п	Π	III
S.repens							II	III
compare with	3.3	1.2	5.3	5.3	5.3	3.3	5.3	1.2
site(s)		1.3	5.4	5.4	5.4		5.4	1.3

The simulation does, however, provide more information than such an analysis and the simple relationships given above. Effects, such as disturbance and the influence of varying weather conditions can only be investigated with the help of a simulation programme, where the relationships between the variables are expressed as mathematical equations. Changes in the model can be evaluated whether or not they provide an improvement by means of comparison with actual values. However, this type of simulation approach is yet only possible for simple species-poor communities.

4.2 The sufficiency of the model

The model described here has developed by gradual extension. It is still being extended, for example the species *Calamagrostis epigeios* and *Alopecurus geniculatus* have recently been included. The edaphic factors were selected gradually. Climatic variables have been introduced after simulations showed them to be necessary.

The addition of externally developed sub-models and the development of sub-models as separate projects constitutes a danger in that they can introduce a large number of variables and parameters. The programme would then acquire a pretention which it cannot prove. In this context: the nomenclature and the origin of the parameters concerning the nitrogen-cycle could suggest that this model simulates a nitrogen cycle, but this is not so: in fact this has been emphasised by the use of an exclusive relative dimension (u.N). The aim of the procedures used in this model is to describe the relevant variations in soil fertility, taking into account factors such as changes of the nitrogen contents of newly formed phytomass, and competition for nutrient as a resource. Having studied the results of greenhouse experiments and field observations, we concluded that those phenomena were indispensable for the understanding of vegetation dynamics.

Sensitivity analysis of the parameters used showed the simulation model to be not too sensitive with respect to variation in any parameter. An independent variation of each of the parameters, with plus and minus ten percent, resulted in a maximum deviation of two percent. Initial values do have a clear effect. In the simulations demonstrated observed field values were used as starting values. The influence of (properties of) plant species that were not included in the model could not be determined.

Considering that the within-season dynamics did not depart systematically from the values that were measured in 1982 and 1983 (Table 2, Fig. 6), the conclusion can be drawn that the variables chosen and the values given to them, closely approach reality in this arithmetical arrangement.

If the model is used for further prediction, the system must be observed for a longer period of time, and more experimental disturbance must be imposed: more theory-building may also be needed. Even then it is not sure that simulation will be more successful than an inductive prediction. In order to formulate hypotheses, and to design experimentation, simulation is a time-saving alternative to experiments, and as such an attractive approach.

4.3 The use of simulating disturbance

In the introduction of this paper we tried to explain that building an explanatory model of disturbance in plant communities is a task which cannot, in general, be fulfilled. Through the occurrence of unexpected events the reliability of a prediction with such a model would be low. To obtain insight in the course of processes to be expected after disturbance, the plant species, involved in the simulation should represent sufficient variation of life and growth forms. With respect to strategies the dispersion mechanisms are of particular importance.

The effect of every major disturbance is that it causes an increase in bare ground. In the area studied this means that through stronger evaporation at the soil surface this is to cause an increase of the concentration of sodium-chloride in the upper soil layer, though this may be reversed by 'wet' disturbance. The saltier environment is beneficious to halophytic plant species as has been observed in salt marsh systems (Hansen, 1982), although Bakker (1985) found that grazing benefitted halophytic plant species, where no increase of the salt concentration in the top soil could be measured.

Simulation cannot replace numerical analysis (direct or indirect) of the biocoenoses in question. Explanatory simulation and description by means of numerical techniques rather supplement each other in the process of getting to understand vegetation dynamics (Weinstein & Shugart, 1983).

The results of this simulation confirm theories about the recovery of biocoenoses after disturbance with some time delay (Reiners, 1983). The speed with which this recovery takes place in the simulation may not entirely reproduce reality.

Application of the model to disturbances has led to a better insight in its limitations, so that a number of improvements could be carried out. We conclude that causal/logical models of systems-dynamics are adequate tools, helping us to improve our understanding of processes leading to structural changes in vegetation. The main value of a model is probably the experience gained during its construction. A model which is not yet finished, or perhaps never will be finished, might therefore be among the most valuable.

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Appendix. Information concerning the most important functions and parameters in 'EGRAS'.

Parameters expla	anation	Value				
		Agr.	Aster	Phrgm.	Pucc.	Salix
RGRMAX	max. rel. growth g/g/day	.31	.20	.13	.21	.08
SCMAX	max. carr. cap. g/m ²	884	884	2000	884	2000
INTIJ	coeff. of comp. 0–1	all values 0,	except Phrgm.	and Salix, exclu	iding (1) all sp	ecies.
MINN	min. req. N-tot for growth dimensionality of N: text	300	300	300	300	150
LETN	lethal N-tot in soil	all values V	ERY large.			
LETC	lethal NaCl in top soil	97.5	162.5	19.8°	162.5	13.5
GROPT	optimal grazing press. 0–1	all values 0				
GRLE	lethal grazing press. 0–1	1.00	1.00	.27	1.00	.05
TEMIN	min. air temp. for growth C.	2	2	2	2	2
TEOPT	opt. air temp. for growth C.	20	20	20	20	20
TEMAX	max. air temp. for growth C.	30	30	30	30	30
LIMIN	min. light for growth J/cm ²	100	100	100	100	100
LIMAX	max. light for growth J/cm ²	2500	2500	2500	2500	2500
WAMIN	min. water level cm	-20	-20	-50	-20	-50
WAMAX	max. water level cm	+ 30	+10	+30	+10	?

1. Procedures concerning growth and death

 $\begin{array}{l} PLGR(i) = RGRMAX \times \\ (1-SCLI/SCMAX) \times C \times ND \times NT \\ \times ST \times G \times T \times L \times W \end{array}$

All factors except RGRMAX: 0 < = factor < = 1;

For explanation of the factors: see text.

2. Procedures concerning grazing

The total consumable biomass in the area = SCTOT.

The ungrazed residual (varying per species) = SCRES.

The speed of consumption increases linearly with (SCTOT-SCRES), if (SCTOT-SCRES) is less than a constant SCSAT (Noy-Meir 1978).

The angle of increase depends of the time of the year.

If (SCTOT-SCRES) > = SCSAT then

GRSP (speed of grazing in g/day) equals GRSPMAX (a constant).

For calculation of the preference-class: see text.

The amount of living and dead biomass, removed from the site by trampling:

For each species:

SCLITR = $(ARTR \times SCLI)/AREA$, where ARTR = AREA × C3 × 32/400 and

 $SCDETR = (ARTR \times SCDE)/AREA.$

The coefficient C3 is a function of soil moisture and the growth form of the species. The figure '32' is a consequence of an assumption that each cow-step affects 1 dm^2 of the surface.

The loss of biomass by grazing (not-consumed, not-trampled) has been estimated at 1%.

All the nitrogen in the removed biomass returns to the system.

Parameter explanation		Value							
		Agr.	Aster	Phrgm.	Pucc.	Salix			
SCRES	residual s.cr. after grazing g dr.m./m ²	25	50	200	25	°250			
PRSP C3	relative graz. pref. a constant, depend. of	.17	.26	.28	.26	.03			
	growth form (s. above)	.015	.050	.024	.015	.050			

ą

3. Procedures concerning abiotic factors

Parameter explanation		Value				
		Agr.	Aster	Phrgm.	Pucc.	Salix
P1	min. N-intake u.N./g	.0254	.0339	.0014	.0536	.0141
P2	N-intake u.N./g per ln u.N. available N	.0028	.0028	.0099	.0085	.0000

Salt as a function of vegetation coverage:

 $SAMAX = -0.021 \times SUMAREA + 2.329$; SAMAX is an absolute value (kg NaCl).