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ON THE APPLICATION OF CHAOS THEORY TO ANALYSE FLUCTUATIONS IN WET MEADOWS: PRELIMINARY RESULTS

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ABSTRACT - The very complex behaviour of non-linear systems can make any predictability in the longer term extremely difficult if not impossible. Chaotic dynamics is likely to be the rule rather than the exception in natural ecosystems. In this context, new possibilities are offered by tools of chaos theory with the application of simple but non-linear mathematical models that might be able to describe a major part of the dynamics of the level of aggregation we are observing. The authors present preliminary results based on the application of an interacting particle system (IPS) model to analyse long-term investigations of vegetation dynamics in permanent plots.

KEY WORDS - Fluctuations, chaos theory, cellular automation, interacting particle system.

INTRODUCTION

"Changes are unforeseeable and (so far known) chaotic, i.e. in no way directed" (Klötzli, 1995). A conclusion that is often derived from long-term (> 10 years) investigations on vegetation dynamics in permanent plots (for lit. see e.g. Bakker *et al.*, 1996). Community dynamics is considered as neither haphazard nor completely directed (Anand & Orlóci, 1997). The very complex behaviour of non-linear systems can make any predictability in the longer term extremely difficult if not impossible. Ecologists often face restrictions of the classical viewpoints and methodology. Previously, irregular fluctuations in real data were interpreted as a consequence of random environmental fluctuations or sampling errors (May & Oster, 1976). But that such fluctuations may arise in deterministic models in which all parameters are known exactly has been quite remarkable (Begon *et al.*, 1996). Thus, the classical theories became restricted to be realistic only in special cases (Anand & Orlóci, 1997). Considering ecological systems and therefore addressing hypotheses closer to the true complexity of nature, these special cases are very rarely realized. Chaotic dynamics is likely to be the rule rather than the exception in natural ecosystems (Hastings *et al.*, 1993).

In the early seventies, even simple models on population dynamics were seen to display chaotic fluctuations (May, 1974; 1976; May & Oster, 1976). Since then, the science of non-linear dynamical systems (i.e. chaos theory) has generated much interest and is growing at an ever accelerating speed (Czárán, 1998), providing a promising framework in which to pose questions about vegetation dynamics and allowing for much more flexibility in modelling (Anand, 1997). One main approach in the search for chaos in real populations is the development of techniques for distinguishing chaos from random noise in the analysis of time series. Whereas in a system that is merely 'noisy' the forecasting accuracy is roughly independent of the prediction interval, in chaotic systems however, the accuracy of forecasts falls off with prediction time (Begon *et al.*, 1996). Two main types of mathematical models are offered, namely differential models and interacting particle systems (IPS) (Czárán, 1998). In this investigation the analysis is based on the second methodology.

MATERIAL AND METHODS

OBSERVATIONS IN FIELD ECOLOGY

In the "Lüneburger Heide" (northern Germany) permanent plots were established in the mid-seventies in different wetland communities and surveyed annually (Klötzli, 1994). From the analysis of the time series (one example is given in fig. 1)

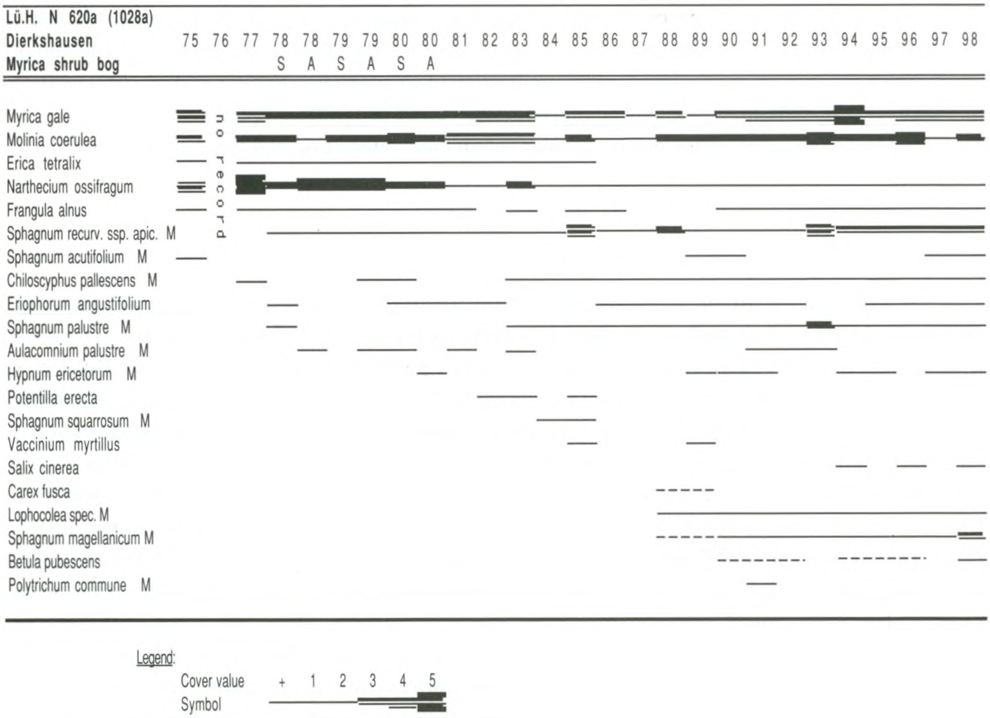


Fig. 1 - Example for field data (Gagelbusch)

five different types of species development resulted (fig. 2), describing the mode how species can behave in the long run (cf. Klötzli, 1995). According to our findings, species can show constant numbers with only small fluctuations. They can fluctuate considerably in numbers but appear permanently in the plot, important changes sometimes occur extraordinary rapidly, e.g. from one year to the next. Species can grow in numbers or appear from a former unknown cryptic state. Or, they can decay or disappear, often due to unforeseeable dieback. Sometimes, a pathogenic influence seems to cause or accelerate decay. Finally, species can display intermittent behaviour by irregularly appearing on a plot.

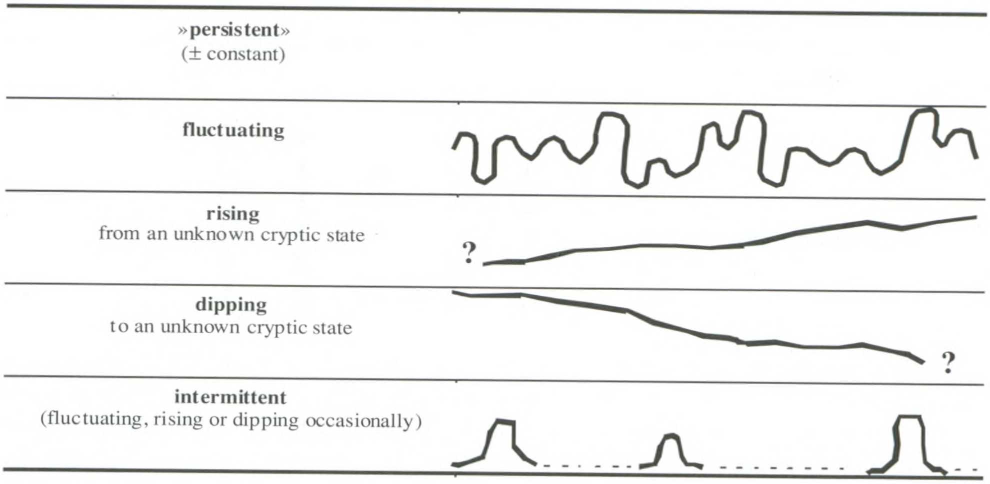


Fig. 2 - Fluctuation types

With respect to the five types of development Klötzli (1995) concluded that there is only limited predictability regarding the development as well as fluctuations of species, the rapidity of change and the way species behave. The application of tools from chaos theory on this rather complex system should give more confidence in the interpretation of observed fluctuations in nature.

SIMULATION MODEL

The data in field ecology are generated from complex natural ecosystems. Known and unknown environmental factors are present and an innumerable quantity of species influence the system. With the concentration on a particular group of living beings (e.g. 5 plants) and the record of data representing just a limited number of the present environmental factors, the system has been drastically simplified. Nevertheless, our observations revealed a degree of complexity clearly not reproducible with linearized theories. Chaos theory offers new possibilities with the application of simple but non-linear mathematical models that might be able to describe a major part of the dynamics of the level of aggregation we are observing (Gassmann *et al.*, in prep.).

The principle of the IPS is based on non-linear relations (rules) and feedback effects. In a first approach a two-dimensional IPS has been used to describe the time evolution of plant species on a test area given by 20x20 pixels. The model-system contains 5 different species and every pixel represents the stand for exactly one actor (a representative of one of the five species) at a time. The structure consists of only one layer. In the following interaction matrix the interrelationships between these actors are defined.

Interaction matrix :

Actor	1	2	3	4	5
1	**3**	**-3**	**0**	**1**	**-3**
2	**-2**	**5**	**0**	**2**	**-2**
3	**0**	**-1**	**3**	**1**	**-2**
4	**0**	**0**	**0**	**-5**	**0**
5	**-1**	**0**	**0**	**0**	**3**

By convenience, the values attributed to the different elements of the matrix are integers between –5 and +5. The values are derived from the experience of field ecologists being familiar with the investigation area and the observed behaviour of the considered species. The diagonal elements of the matrix describe the intraspecific preference, all the others describe the degree of interspecific preferences. A persistence factor for each particular plant is described by the so-called site advantage, representing balancing the advantage of already occupying one pixel for the following time step.

Site advantage:

Actor	1	2	3	4	5
	4	**1**	**3**	**2**	**1**

The next group of sensitivity vectors describe the effects of external factors as e.g. environmental parameters. In the first step, two such parameters were included.

Sensitivity vectors:

Actor	1	2	3	4	5	
	-1	**1**	**1**	**1**	**0**	e.g. light
	0	**0**	**0**	**0**	**1**	e.g. humidity

No trend of the environmental parameters was taken into account. The fluctuations of the external factors were simulated on the basis of Gaussian distributions.

At the beginning, a random distribution of the actors is chosen with every pixel attributed to one of the different species. The evolution dynamics defining the modification of a given pattern within one year is described by interactions involving:

- the eight nearest neighbours of each cell,
- the considered cell itself,
- the site advantage and
- the sensitivity to the external parameters.

According to this approach, the pixel itself and its eight nearest neighbours "vote" for the species that will be on the pixel the following year. The result of this "vote" is further modified by the site advantage and sensitivity effects. To suppress boundary effects, periodic boundary conditions were chosen, i.e. the calculated rectangle is considered as one period of a repeating infinite pattern. The time is calculated in iteration steps of one year. A more detailed description of the model used in this study will be published elsewhere by Gassmann *et al.* (in prep.), further information on the use of IPS (also called "cellular automata") in biological studies are given e.g. in Silvertown *et al.* (1992) or Belde & Richter (1997).

RESULTS

Although quite a simple model with relatively few parameters was chosen, all the five types of development "constant, fluctuating, growing, decaying and intermittent" could be simulated (fig. 3).

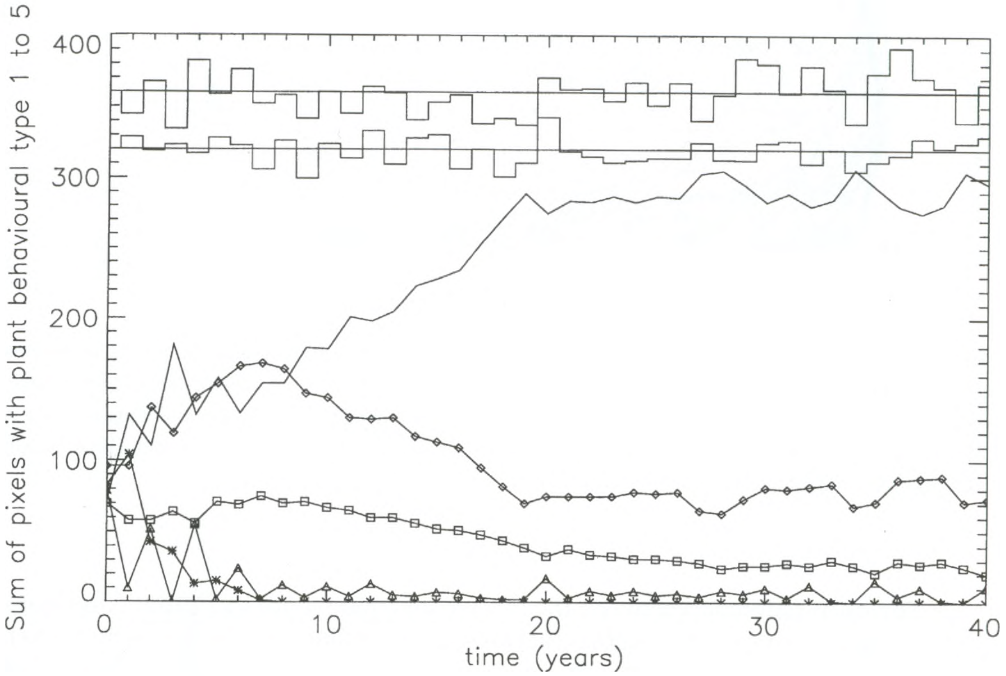


Fig. 3 - Typical example for the development of the five plant behavioural types over 40 years. The number of pixels occupied is given for type 1 (line), type 2 (line with squares), type 3 (line with diamonds), type 4 (line with triangles) and type 5 (line with asterisks). The two environmental factors are displayed in arbitrary units at the top of the figure. Note the occurrence of the five different types of development termed constant (type 1,3 after year 20), fluctuating (type 3 years 0-20), growing (type 1 years 0-20), decaying (types 2,5) and intermittent (type 4).

Therefore, simulated runs of the model match the observed behaviour in natural ecosystems. Executing different runs with the same intra- and interspecific interrelationships showed a strong dependency for the development from the initial conditions and external variables (fig. 4).

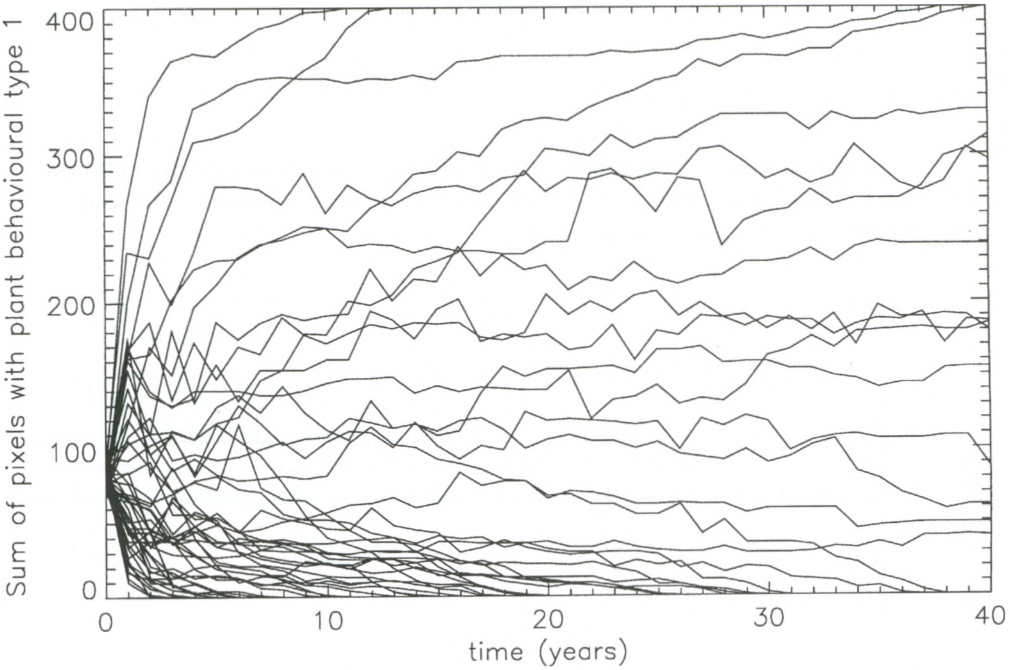
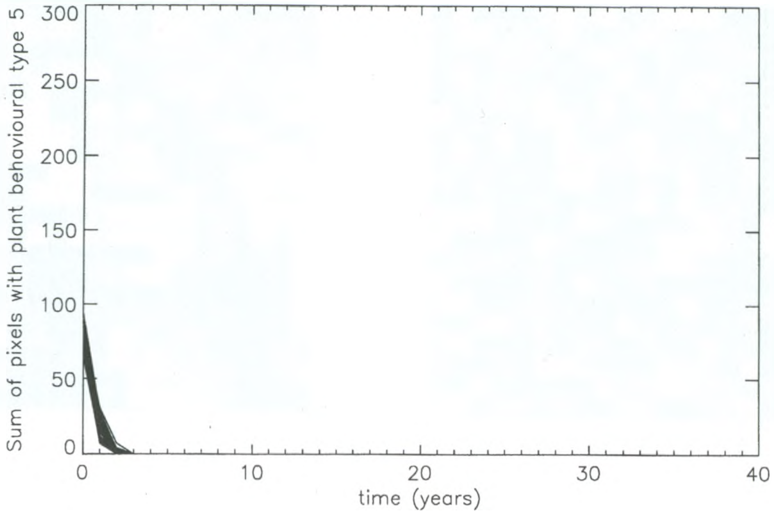


Fig. 4 - 50 histories for development of plant behavioural type 1 with different random initial distributions of plant types and different random environmental factors, but with unchanged interaction matrix, sensitivity vectors and site advantage vector. Note the very different type of development plant type 1 is able to show. If it finally will occupy the whole area or if it will die out depends on the initial distribution and the environmental history.

The only difference between the 50 runs in figure 4 are the initial conditions and the fluctuations of the external factors (but with constant standard deviations), both derived from a random number generator. The result shows a broad range of possibilities of developments. Even the slight change of one pixel in the initial conditions could already initiate a completely different pattern in the further development. This sensitivity often called as "butterfly effect" limits the predictability for the future development of complex systems (Lorenz, 1963). In different runs the same actor may display different fluctuation types depending on the initial conditions and the development of the external factors. So, a variety of alternative developments is presented, implying further uncertainties for predictability in the long-term.

Constant external factors can lead to an earlier "extinction" of particular actors (fig. 5a), reducing the diversity of the system and ending in an impoverished pattern of only one (monoculture) or two remaining actors. For particular behaviour types, the pattern of the external factors is crucial for their existence. Fluctuating external factors may offer opportunities for the appearance of particular species (compare fig. 5b).



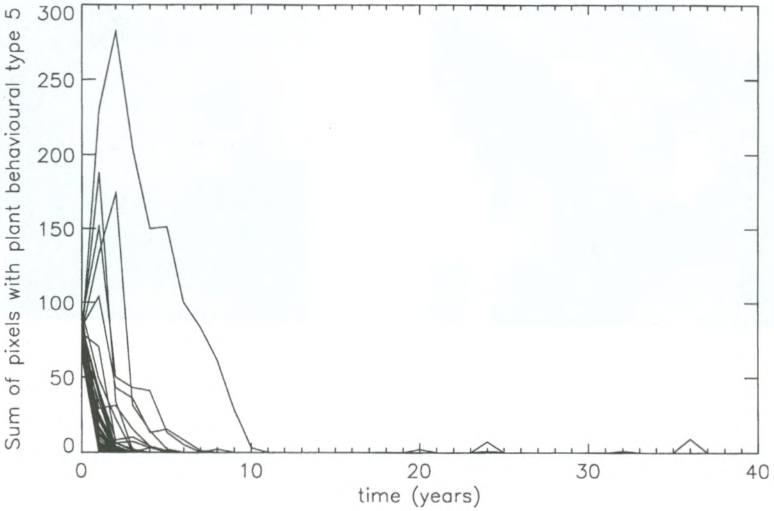


Fig. 5 a-b - 50 histories for plant behavioural type 5 with different random initial distributions without environmental fluctuations (a, top) and with fluctuations present (b, bottom). Fluctuations clearly increase average lifetime of plant type 5 and allow intermittent recurrence (see years 20, 24, 32, 36).

Finally, a formation of patches could be observed in every run (see fig. 6), whatever initial conditions were chosen.

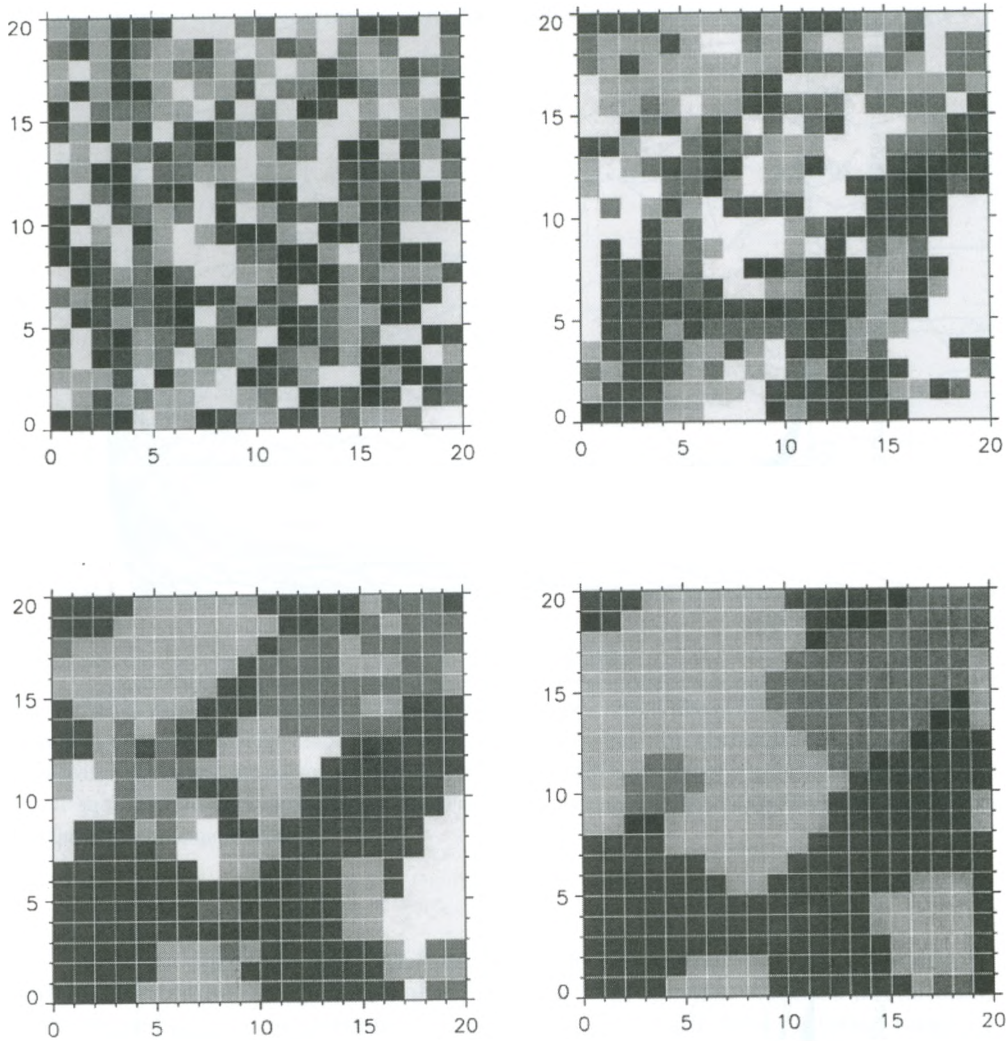


Fig. 6 - Distributions of plant behavioural types for the development shown in fig. 3 after random initialisation (year 0, top left) and for years 1 (top right), 3 (bottom left) and 8 (bottom right). Plant behavioural types 1 to 5 are represented as dark grey, grey, light grey, black and white respectively. Type 5 (white) dies out within 8 years and type 4 (black) , though not present in year 3, emerges at the boundaries between types 1 and 2 in year 8 (intermittency). The emergence of patterns is clearly reflected by the decreasing complexity of the pictures.

CONCLUSIONS

The schematic characterisation of a plant community by an interaction matrix and a few sensitivity vectors seems possible. Although by far not every detail of a natural ecosystem can be illustrated with the model, at least some insight in the complex relationships and behaviour of interacting elements of the system can be given. The use of IPS-models seems to be an adequate approach. Silvertown *et al.* (1992) applied IPS to simulate standard competition experiments and the results are considered to be as relevant to real communities as is the experiment, which generated its parameters. The authors of the present study take another step forward, by applying the methodology of IPS on long-term series of field studies. Parallelities between the results of the model and the interpretation from observations in the field are feasible. The model permits to replicate the five fluctuation types, the dependence from the initial conditions as well as from fluctuating external factors and the formation of patches, all patterns of behaviour that are well known from living systems (e.g. Begon *et al.*, 1986; Remmert, 1992). Thus, important traits of the dynamics are reproducible and in the short-term expected to be predictable, but unpredictable in the long-term (compare also Anand, 1997).

The results presented in this paper underline the importance of the details in the initial conditions. Minor changes may result in substantial long range effects. Similar instabilities must be expected to arise from small changes of the external factors. Relevance for field ecologists is given by the fact that such models may provide informations for short-term development of a complex system. However, absolute limits are set for the predictability of natural systems in the long run (compare also Oreskes *et al.*, 1994). Most natural systems and the interrelationships therein are too complex to be easily comprehensible (Hastings *et al.*, 1993). Therefore, dealing with complex ecosystems always ever implies an arrangement with uncertainties. Nevertheless, numerical models can provide insights for a better understanding of the dynamical and structural instabilities of ecological systems and yield more confidence in the interpretation of observed fluctuations in nature.

REFERENCES

ANAND M., 1997 – *The fundamental nature of vegetation dynamics – a chaotic synthesis*. Coenosis **12**(2-3): 55–62.

ANAND M. and ORLÓCI L., 1997 – *Chaotic dynamics in a multispecies community*. Env. & Ecol. Stat. **4**(4): 337–344.

BAKKER J.P., WILLEMS J.H. and ZOBEL M. (eds.), 1996 – *Long-term vegetation dynamics*. J. Veg. Sci. **7**: 145–228.

BEGON M., HARPER J.L. and TOWNSEND C.R., 1986 – Ecology. Individuals, Populations and Communities. Blackwell Oxford.

BEGON M., MORTIMER M. and THOMPSON D.J., 1996 – *Population ecology. An unified study of animals and plants*. 3rd Edition. Blackwell Oxford.

BELOE M., RICHTER O., 1997 - Zellulärer Automat zur Simulation der Sukzession auf Niedesmoorstandorten bei underschiedlichen Managementmassnahmen. Verh. Ges. Ökol. **27**: 189-198.

CZÁRÁN T., 1998 – Spatiotemporal models of population and community dynamics. Chapman & Hall, London.

GASSMANN F., KLÖTZLI F. and WALTHER G.-R., in prep. – *Simulation of observed behaviour types of plants and plant communities.*

HASTINGS A., HOM C.L., ELLNER S., TURCHIN P. and GODFRAY H.C.J., 1993 – *Chaos in ecology: Is mother nature a strange attractor?* Ann. Rev. Ecol. Syst. **24**: 1–33.

KLÖTZLI F., 1994 – *Grundsätze ökologischen Handelns.* DVGW Schriftenreihe Wasser **78**: 9-24.

KLÖTZLI F., 1995 – *Projected and chaotic changes in forest and grassland plant communities. Preliminary notes and theses.* Ann. Bot. (Roma) **53**: 225-231.

LORENZ E.N., 1963 – *Deterministic non-periodic flow.* J. Atm. Sc. **20**: 130–141.

MAY R.M., 1974 – *Biological populations with non-overlapping generations: stable points, stable cycles and chaos.* Science **186**: 645–647.

MAY R.M., 1976 – *Simple mathematical models with very complicated dynamics.* Nature **261**: 459–467.

MAY R.M. and OSTER G.F., 1976 – *Bifurcations and dynamic complexity in simple ecological models.* Am. Nat. **110**: 573–599.

ORESKES N., SHRADER-FRECHETT K. and BELITZ K., 1994 – *Verification, validation and confirmation of numerical models in the Earth sciences.* Sci. **263**: 641-646.

REMMERT H., 1992 – Ökologie. Springer Berlin.

SILVERTOWN J., HOLTIER S., JOHNSON J. and DALE P., 1992 – *Cellular automaton models of interspecific competition for space – the effect of pattern on process.* J. Ecol. **80**: 527-534.