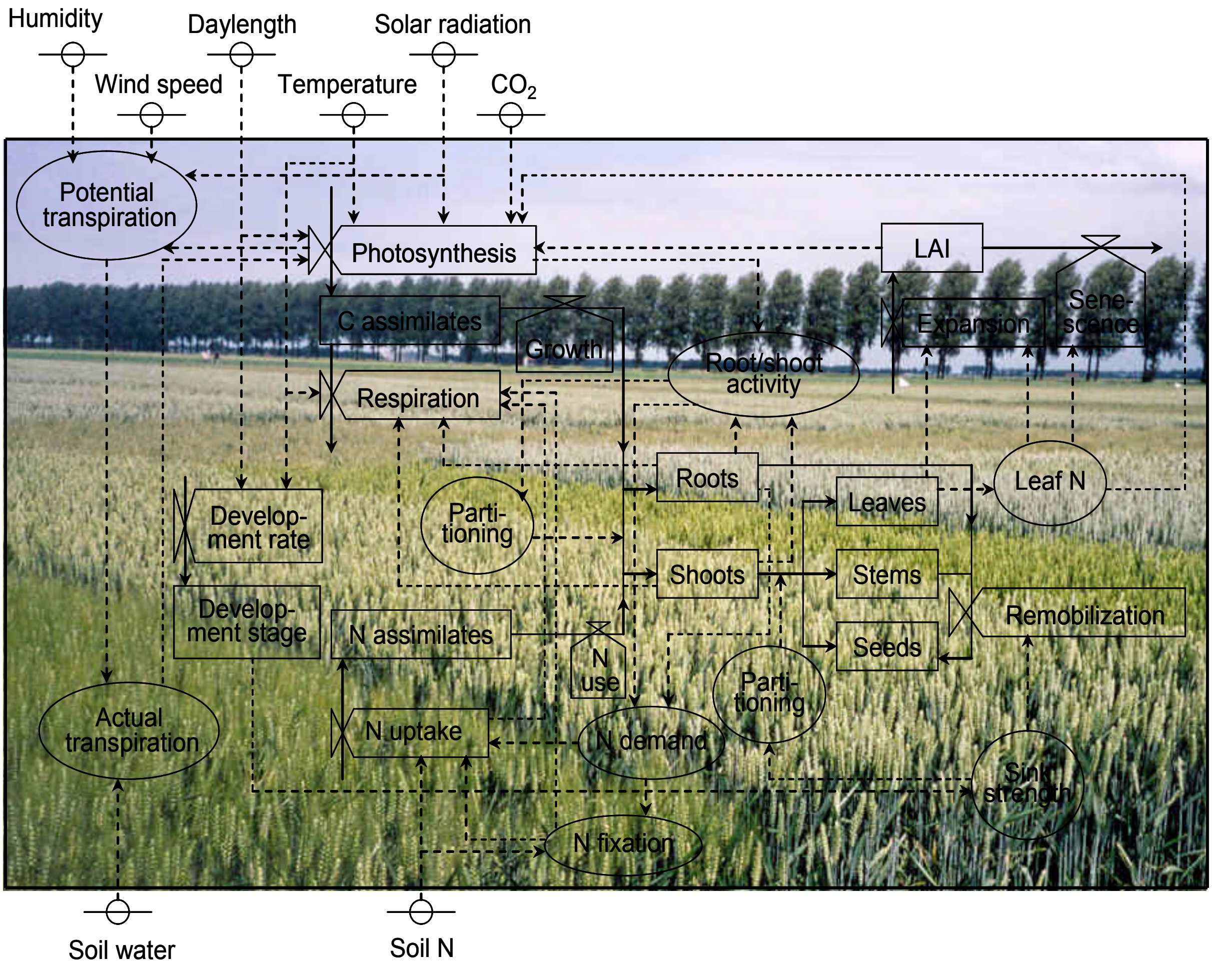
40 Years Theory and Model at Wageningen UR



40 Years Theory and Model at Wageningen UR

C.T. de Wit Graduate School for Production Ecology and Resource Conservation

Wageningen University and Research Centre

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40 Years Theory and Model at Wageningen UR

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On the occasion of the 40th anniversary
of the inaugural address of C.T. De Wit in 1968

Wageningen University and Research Centre, The Netherlands

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Introduction to 40 Years Theory and Model in Wageningen

On October 10^{th} 1968, Dr C.T. de Wit (Kees) gave his inaugural address as extraordinary professor in Theoretical Production Ecology (TPE). He was appointed in that position after a splendid scientific career in the research institutes of the Ministry of Agriculture. In his inaugural address, he explained how basic knowledge and insight in the basic disciplines could be used to strengthen the basis of Agricultural Sciences and to expand the possibilities that could be created for improvement of agro-ecosystems and explorative studies. In that way, he indicated how fundamental science can have a strong impact on policy and society. During De Wit's whole career that credo 'science for impact', now the motto of Wageningen UR, was present. In this Symposium, contributions will be presented to illustrate the way his vision 'Theory and Model' has been adopted and is used today. As a tribute to De Wit's scientific heritage, it will be demonstrated how his original ideas are still being applied by the third generation of scientists after his stimulating, original and excellent scientific work. The presentations will be at various scale levels as distincted in Theory and Model, and will vary from the more fundamental scientific approaches to the policy-oriented studies. A common thread is the scientific approach in building on basic principles that govern living systems, physical, chemical or biological in nature.

The four themes that were characteristic for TPE during many years are intertwined with the aggregation levels that are distinguished:

1. The basic physical, physiological and meteorological processes that occur in plants, soils and the atmosphere;
2. Crop growth under water- and nutrient-limiting conditions;
3. Pests, diseases and weeds, that may reduce crop yields;
4. Farming systems, agro-ecosystems and the interface with socio-economics.

In Theme 1, many studies have been done that have resulted in the tradition of crop growth models that integrate the basic physical, chemical and physiological knowledge in such a way that better understanding of growth and development of plants and crops was attained. In this Symposium, some typical examples of such studies based on better understanding of the genetic bases are presented. They build on the knowledge of the basic processes and use it to explore options for future plant types and to analyse the perspectives of for example typical C4-characteristics in C3 plants. The expectations are high, but counter-intuitively the real advantages are

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limited (Yin *et al.*). In the first theme of the former TPE department, also the promising study of De Groot on future energy systems should be placed. In his innovative study of 1965, 'Photosynthesis of leaf canopies', De Wit already introduced the concept of photosynthesis in an exceptional way. He made clear how physical processes (absorption of photons), depending on geometrical and optical characteristics of crops, determine the yield of the sun and how photochemical processes determine the transformation of irradiation in organic chemical compounds, which in biochemical processes are transformed into sugars, and then after many transitions into structural compounds.

The first step in the photosynthesis process could be used when energy gaining/solar energy harvesting is the aim (see De Groot) and the next steps in which sugars are synthesized are only needed when production of food or other products such as developed in the biobased economy is the aim. Therefore, it makes no sense to transform these compounds into fuel, thereby losing a lot of efficiency. De Wit's pragmatic approach was based on his conviction that theoretical production ecology should lead to better production systems, based on knowledge and insight. In this Symposium, that approach is also placed in perspective. Van Oijen and Scheffer indicate that theoretical ecology has other unexpected perspectives to offer as well. They demonstrate how theoretical ecologists may use models to analyse the possibilities of unexpected changes and how the original thoughts of Von Bertalanffy in his General Systems Theory may be used.

Most contributions in this Symposium are related to the earlier mentioned Theme 1. Basic phenomena are studied and will lead to better energy systems (De Groot), better plant systems (Yin), or better understanding of ecosystems (Van Oijen; Scheffer). De Wit and his successors established a strong tradition in this field that also formed the framework for many PhD theses. The models bridged the gap between basic processes and performance at systems level, they paved the way for explorative studies at plant, crop and ecosystem level and were instrumental in many, nowadays important, carbon balance studies.

In Theme 2, De Wit and his successors performed many studies in soil and water sciences and laid the basis for explorative land use studies. These studies were the basis of many World Food Security analyses, but also yielded detailed insights in the functioning of soils, as well as in the chemical, physical and biological processes. Many major programmes in developing countries were based on these analyses and paved the way for balanced and enlightened interventions, so strongly needed at this moment. In this Symposium, examples of studies in this field are not given but it goes without saying that especially in this field the De Wit School has made its impact.

In Theme 3, the studies on population dynamics and interactions between plants and crops and their threatening diseases and pests and weeds have laid the basis for an enriched ecological science. Pest and disease interactions, population dynamics, behavioural studies and many models on tritrophic relations were developed. They were first used to gain insight in the functioning of these agro-ecosystems and to understand how system performance is dictated by the response to environmental conditions. This insight was then used to develop Integrated Pest Management systems that were applied to minimize pesticide use and maximize biological control mechanisms. Counter-intuitively, many of these systems show much more stability at high production levels than at low production levels, where instability grows. In this theme, many students have worked and are still working at various places around the world. In this Symposium, a contribution from this theme is absent, but it is obvious that TPE studies in this field have strongly contributed to understanding of ecological processes through the combination of modelling and experimentation leading to the development of improved crop protection systems.

In Theme 4, De Wit's drive to contribute through his scientific analyses and studies to improvement of interventions and policy making was very present. In this Symposium, various studies at higher integration levels are presented as well as typical examples of upscaling (Meinke *et al.*; Opdam and Verboom). The need to be responsive to societal requests is illustrated, and the potential contribution of science to enrich the quality of policy making and decision making at higher integration levels is indicated. Especially in these cases, the scientific community is exposed to the criticism of those who cannot distinguish between explorative and predictive studies. The interface between science and policy is very present in studies in this theme. It requires a good positioning of the scientist. He/she should aim at being an honest broker and not an issue advocate or a pure scientist. The position of honest broker is difficult and urgently needed. In the 40 years of Theory and Model, De Wit and his successors have played a critical role in society to fulfil that role of honest broker. It has sometimes resulted in unjustified and unfair criticism, but that is the toll that has to be paid when scientific honesty, fairness and integrity are leading principles.

In the 40 years since the establishment of TPE, more than 150 PhD theses have been guided by De Wit and his successors. More than 2000 MSc students were supervised, at least 10 professors were born in TPE. Altogether, an impressive scientific contribution with a tremendous impact on science and society. The closure of TPE in 1998 has, also in hindsight, been a wrong decision of the Executive Board, but the creation and flourishing of the Graduate School Production Ecology and Resource

Conservation and various old and new Chair Groups participating in that School, show that the heritage of De Wit is alive and kicking in Wageningen and in other universities in the world.

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Harnessing solar energy for the production of clean fuels

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Mankind is urgently looking for a change towards a sustainable energy future by more efficient production and use of energy, by boosting renewables and by using domestic solar energy sources. Vigorous action will be needed if greenhouse gas concentrations are to be stabilized at a level that would prevent dangerous interference with the climate system. Governments are implementing legislation to increase the contribution of renewables. Despite these efforts, there is evidence that with current climate change mitigation policies and related sustainable development practices, global greenhouse gas emissions will continue to grow over the next few decades (IPCC, 2007).

Renewables address the problem of global warming through zero or near-zero net greenhouse gas emissions and can make major contributions to the security of energy supply and to economic development. Renewable energy technologies currently supply 13.1% of the world's primary energy supply, mostly in the form of hydro-power, biomass, and geothermal energy (IEA, 2007). The prime scarcity is not of natural resources nor money, but time. The shares of biomass, solar photovoltaic(s) and wind are increasing, while those of ocean, geothermal and concentrated solar power are decreasing. This reflects the evolving consensus among early adapters as to where the greatest potential is. The use of solar energy, either directly or from wind, is by far the most popular option. Decentralized energy from domestic sources directly addresses the need for energy security, economic prosperity and environmental protection.

In this context, solar energy is one of the major options as a sustainable fuel source that will allow a switch to a carbon-neutral energy economy. Electricity generation from solar energy is starting to spread in society, but it needs transport and storage to balance production and demand. At present, 70% of the worldwide energy use is based on fuels. The efficient conversion of solar energy into a useful fuel requires more research and development, in particular finding a fuel for a smooth transition to a carbon neutral transport sector is a difficult challenge. This sector is responsible for 25% of our energy use and has the fastest growing emission profile.

In a recent White Paper (ESF, 2006), a European task force assessed the research needs for clean solar fuels, starting from recent scientific progress in basic research in photosynthesis, a range of natural solar-to-fuel conversion processes that evolved 2.5

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billion years ago. Photosynthesizers such as plants and bacteria are abundant in the biosphere and use solar energy to make oxygen from water and convert atmospheric CO_2 into carbohydrates. They produced all the fossil fuels and fuel the current biosphere. Photosynthesis can also produce hydrogen.

The presentation will discuss promising routes to eventual full-scale commercial solar energy conversion directly into fuels (ESF, 2006). Dutch scientists want to capitalize on the recent scientific breakthroughs to learn from Nature how to harness solar energy for sustainable production of primary energy carriers like hydrogen from water or carbon-based fuels from CO_2 at an affordable cost and at much higher efficiency than is possible with biomass.

Potent novel technologies must be developed in order to be able to meet the challenge of mitigating climate change. This requires implementation of large-scale integrated research programs for production of biofuels from modified photosynthetic microorganisms and the development of chemical solar cells for fuel production. Both of these approaches have the potential to provide fuels with solar energy conversion efficiencies that are much higher than those based on field crops or forestry. In consequence, they could contribute substantially to sustainable economic growth and social stability.

Photosynthetic microorganisms can be optimized for the production of hydrogen and other fuels (biodiesel, etc.) with conversion efficiencies that are much higher than the current biomass production methods, based on modern systems biology and evidence-based modelling of the trajectory from photon to fuel (Figure 1). At the same time, they can produce valuable ingredients for food and feedstock. This will lead to the optimization of the processes through modelling-based synthetic biology methods.

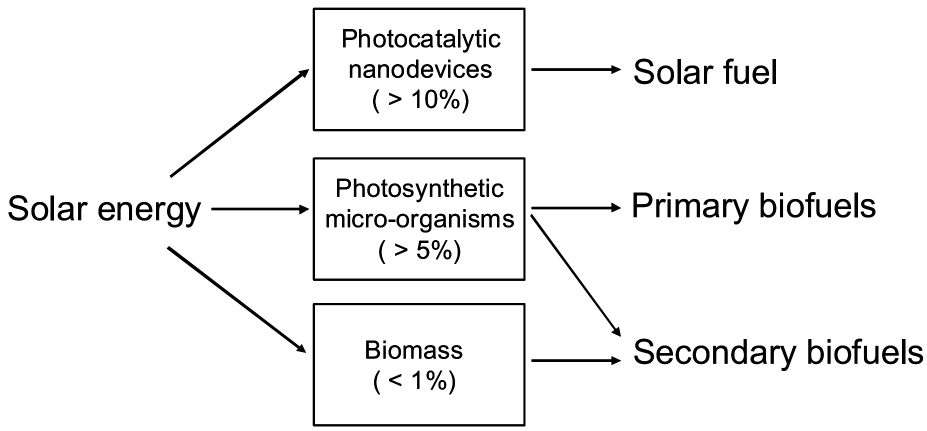

Figure 1. Schematic representation of pathways from solar energy to fuels. Micro-organisms can provide primary and secondary biofuels with efficiencies > 5%. The physical limit for artificial solar-to-fuel converters is above 10%.

In parallel to the biological route, the development of artificial solar-driven fuel production requires a series of fundamental and technological advances. Multi-electron redox catalysts must be developed; they must be coupled to photochemical elements, and all this governed by multiscale modelling. This will require physical and chemical research, often inspired by biological processes: biomimetic nanotechnology. Particular research efforts are required into finding new (photo)catalysts for water splitting, H_2 production and CO_2 reduction to produce liquid fuels such as methanol.

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Crop theory and model in the era of systems biology

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Mankind is facing several daunting global problems such as food security, climate change, and oil-reserve depletion. The real-world challenges for agriculture today are therefore, breeding for crop genotypes and expressing their potential in target (stressful) environments to produce sufficient quality food, feed, fibre and fuel, while maintaining the sustainability of agro-ecosystems and resource use. These goals can be achieved only via realizing phenotypes of complex traits at the level of the crop – the community of mutually interacting plants. We will discuss the necessity of integrating modern systems biology and traditional crop modelling in order to better assist in achieving the required crop phenotypes.

Systems biology

Systems biology was proposed (cf. Kitano, 2002) in the wake of the need for instruments to interpret, integrate and summarize large amounts of experimental data from modern high-throughput technologies in functional genomics. It aims to synthesize complex datasets from various genomic hierarchies (genome, transcriptome, proteome, metabolome) into useful mathematical models, and seeks to explain, in a quantitative manner, biological functioning in terms of 'how things work' in (sub-)cellular units. Similarly, 'plant systems biology' was defined (Minorsky, 2003), using computational approaches to predict a plant cell(ome) from underlying genomic understanding.

Systems biology, defined in this way, will facilitate the development of functional genomics as a scientific discipline, but, arguably, 'omics' has been driven more by novel experimental technologies than by holistic quantitative hypotheses. Therefore, the meaning of systems biology as a new scientific discipline is still under debate (Thomas, 2007; Bennett and Monk, 2008). Earlier, Hammer *et al.* (2004) argued that the current definition of plant systems biology not only largely overlooks the rich history of crop modelling, it is probably also not the best approach towards solving the real-world problems by improving crops for increased production – the ultimate goal plant systems biology (Minorsky, 2003) intends to achieve.

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Past experiences in crop modelling

Crop scientists have used systems analysis and systems modelling to investigate whole-crop physiology and crop ecology for decades. Dynamic crop growth models emerged in the mid-1960s with the pioneering work of De Wit (1965), who introduced Von Bertalanffy's systems theory and Forrester's dynamic model-simulation method into crop science. Crop modelling differs from empirical statistical analysis, just as systems biology differs from bioinformatics. In crop models, constituting elements and processes are put together in mathematical equations (*synthesis*). The rules by which the elements or processes interact give rise to systems behaviour and emerging properties, which may well be unexpected and even counterintuitive (*heuristics*). This heuristics, in turn, enhances the understanding of individual processes and improves the next-round modelling and the ability of the model in extrapolating information from one to another environment (*prediction*). Dynamic crop systems models have been used to support theoretical research and applied activities, via model-based systems *design*. In modelling at any level of layered biological systems (Passioura, 1979), the roles of systems modelling in *synthesis*, *heuristics*, *prediction*, and *design* should be recognized. Whilst crop models are considered by many to be matured enough for various agricultural applications, they still need to be upgraded to face new challenges in modelling gene-to-phenotype relationships (Yin *et al*., 2004).

Crop systems biology

Phenotypes at the crop level, irrespective whether they are related to yield *per se* or resource use efficiencies, are extremely complex, regulated by multiple interactive genes whose effects and expression may be highly dependent on environmental conditions and crop developmental stages. These phenotypes are achieved not only by molecular pathways, but also through multiple intermediate component processes and orchestrated feedback mechanisms, by intra- and inter-plant competition, and by interactions between stress factors. A change of one component may result in an often unexpected, but negative consequence on other components. On the basis of work from our group and others during the last decade (cf. Yin *et al*., 2004), we have recently argued that new initiatives for plant-based systems research should first draw on the existing crop modelling developments based on traditional sciences; at the same time, one should make use of modern genomics by parameterizing and redesigning some subroutines of crop systems models (Yin and Struik, 2007, 2008). We proposed a viable concept 'crop systems biology', in view of (*i*) the need to bring the information from functional genomics to the crop level, (*ii*) the need to better understand the organization of the whole crop and its response to environmental conditions, (*iii*) the need to fill the vast middle ground between 'omics' and relatively simple crop models, (*iv*) the concern about the lack of true biological mechanisms in many current crop models, and (*v*) the need to promote communications across scales. Crop systems biology aims at modelling complex crop-level traits relevant to global production of food, feed, raw materials and energy, via building the links between 'omics'-level information, underlying biochemical understanding, and physiological component processes. This concept is potentially promising to respond to real-world challenges in improving complex crop traits, such as grain yield and resource use efficiencies.

A 'road-map' of crop systems biology

To develop crop systems biology, it is necessary to map the organizational levels and the communication systems between these levels for the different key processes (Struik *et al*., 2007). Much of the fine detail may not be needed, and certain details of organization may be omitted as irrelevant or unnecessary, to develop a prototype model. Thus, crop systems biology models at this step may not necessarily be more complex in structure, nor in their computational requirement, than existing crop models. However, there is a need to more comprehensively synthesize the rich biological understanding of the functional relations between carbon and nitrogen metabolism, between sources and sinks, between shoots and roots, and between structural and non-structural components. For a comprehensive model that contains those capabilities, a modular design is needed to ensure that changes in or extensions of a sub-model will not affect other parts of the model. In relation to crop improvement, a key element would be to identify the mechanisms that are conservative in energy and water transfer and in carbon and nitrogen metabolism, and those that show genetic variation and are potentially amenable to selection and engineering. The prototype models should allow identification and quantitative assessment of specific metabolic pathways and processes that could be altered to achieve trait improvement.

There have been debates about whether it is necessary to create models that can describe a process at more than three scales, even if computational time would hardly be a constraint. The answer to this question depends on the research objective. A multi-scale model might be of little use in terms of *prediction* of crop-level phenotypes, because of its high input requirements that may add uncertainties to the model. However, such multi-scale models are very useful in terms of *heuristics* and systems *design*, since they should enable *in silico* assessment of crop responses to genetic fine-tuning under defined environmental scenarios, thereby being powerful tools in designing of and breeding for desirable genotypes and in engineering for complex crop traits.

Descending from the crop level to lower organizational levels is most likely to be done in a manner of one-process-at-a-time. First candidates are the most understood traits – flowering time and leaf photosynthesis. For more complex (and more yield-related) candidate traits/processes such as carbon-nitrogen assimilation interaction, structural-stem formation, and stress tolerance, it is essential to first understand and model the molecular-physiological basis of these traits/processes. The rich history of physiological and biochemical studies of these processes should provide the necessary information for the development of crop systems biology models. With the future development of functional genomics, combined studies of physiological components with gene expression profiles should illustrate the function of genes, biochemical pathways and cellular processes that are affected in a coordinated manner. Such studies should lay the groundwork for extending models to include regulatory networks and linkages among gene products, biochemistry and whole-plant physiology. Obviously, different developmental, temporal, spatial and structural scales are required for different components, pathways, and processes of the system. Ultimately, crop systems biology may develop into a highly computer-intensive discipline, and crop systems biology models will act as a predictive and heuristic engine and lead to innovations in designing crop improvement programmes.

Outlook

Manipulation of a relatively small number of genes (notably, dwarfing and photoperiod-insensitivity genes in many crops) has resulted in the first 'Green Revolution'. For the next 'Green Revolution' to happen, we have to deal with many genes as they work in concert. Therefore, an across-disciplinary systems approach is required. Molecular plant systems biology was proposed to possibly offer a fast way to solve some imminent food-, feed-, and energy-related, 'real-world' global problems (Minorsky, 2003). Although this approach and functional genomics might offer a few shortcuts, its proponents may have under-estimated difficulties of a successful programme to develop improved crop cultivars. Phenotypes at the crop level, even without biotic or abiotic stresses, are extremely complex. Alterations made at the genome level, though substantial, could have little effect on the crop-level phenotypes (Sinclair *et al.*, 2004). So, systems biology should not be considered the privilege of only those working on molecular, sub-cellular or cellular levels; instead, it can and should be applied across the whole spectrum of plant biological hierarchies. Although the importance of cross-disciplinary cooperation (between biology, mathematics, bioinformatics, chemistry, computer science, etc.) is well recognized, the existence of various biological scales has been less recognized. To allow systems biology to have significant impact on the next 'Green Revolution', the information from 'omics' should reach up to the crop level, and 'crop systems biology' should be established. Crop systems biology can narrow the genotype-to-phenotype gaps and enhance the link between traditional and modern sciences. For that to happen, it is necessary to continue the long-term, multi-disciplinary efforts towards crop improvement (Sinclair *et al*., 2004; White *et al*., 2004; Wollenweber *et al*., 2005), which should not be biased towards molecular approaches (Borrás and Slafer, 2008). In the meantime, a strong education programme is needed to foster the intellectual development of students to become crop scientists in the era of systems approaches.

Acknowledgements

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Considering plant structure in models of plant growth and development

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In plant production science, many different types of crop models are available. In general, these process-based models focus on functional aspects of the plants in the system. They simulate physiological processes and plant growth, taking into account factors affecting growth like ambient temperature, nutrients in the soil, and water availability, resulting in simulation output such as crop yield (Bouman *et al.*, 1996; Van Ittersum *et al.*, 2003). For many applications, process-based crop models have shown their value, and still do.

Nevertheless, there are many questions regarding plant and crop growth and development that could benefit from a modelling methodology that takes into account aspects of the spatial, three-dimensional structure of plants, also referred to as plant architecture. Examples of such questions include those related to the effects of manipulation of plant canopies (*e.g.*, pruning, harvesting), to competition phenomena between plants of the same or of different species, or to the plastic response of plant structure to environmental influences.

Functional-structural plant modelling (FSPM), a relatively young modelling methodology, builds upon the classical principles that have been implemented in the widely-used process-based crop models for decades, and adds the possibility of explicitly considering plant structure. The concept behind modelling development of plant structure has been described already quite some time ago (Lindenmayer, 1968; Prusinkiewicz and Lindenmayer, 1990), however, the link between the process-based and the structure-based approaches in agronomy and forestry is more recent (Perttunen *et al.*, 1996; Godin and Sinoquet, 2005; Vos *et al.*, 2007).

The FSPM approach to plant and crop modelling provides the framework to consider environmental influences on each component of the system, as well as mutual influences of structural components. The methodology builds on the principles introduced and established by De Wit and his colleagues, and implements these at the level of the plant organ, as opposed to the level of the plant canopy. The following section will describe two of the domains of application of this approach using examples of recent work conducted within WUR.

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Manipulation of crop canopies

The profit generated from production of cut roses (*Rosa hybrida*) strongly depends on the number of flowering shoots and the quality of the flowers and the stalks, over a prolonged period of time. Key factors affecting number and quality of flowers are the cultivation system and the plant manipulation strategy exercised by the grower: shoot bending, pruning, and harvesting. The plant manipulation strategy of a rose crop aims at (*i*) maintaining a sufficient number of leaves exposed to light in order to enhance growth and (*ii*) stimulating the emergence of new shoots ('bud break') from bud positions that yield high quality flowers.

Current plant manipulation strategies were developed empirically in practice. As rapid changes take place in cultivation technology and in cultivar characteristics, growers cannot simply apply experience gained in the past to a new cultivation technique or to a new cultivar. There is need for a more objective tool to guide growers in their decisions on plant manipulation.

An FSPM of rose growth and development is being developed (Buck-Sorlin *et al.*, 2007) that integrates several key aspects of the abovementioned framework; an example of the visual output is shown in Figure 1. The model contains well-established physiological concepts such as accumulation of thermal time, light interception, photosynthesis, and carbon distribution, in addition to structural concepts related to plant geometry and morphology.

Figure 1. Visualization of the simulated structure of rose; several plants growing on slabs are shown, each one having one developing upright flower shoot plus a bent shoot. The bent shoots are laid out into opposite directions. (G.H. Buck-Sorlin, unpubl.)

The FSPM aims at strengthening insight in bud break, focusing on the position of axillary buds in the plant structure, and on environmental cues (*e.g.* light) of bud break. The model calculates flower production (both quality and quantity) over time in relation to plant structure, plant manipulation and the glasshouse environment. Questions to be answered using this approach are related to the height at which shoots should be harvested, the added value of shoot bending on flower production, and the consequences of various pruning regimes. Additionally, an important aspect of simulating crop structure development is the ability to visualize this development, and use this visual output (Figure 1) to illustrate the effects of specific manipulation strategies on crop development, for both decision-support and educational purposes.

Intraspecific competition

Members of the Poaceae family have been rewarding subjects of research in the field of FSPM (Fournier *et al.*, 2007). Poaceae comprise important cereal crop species such as rice, wheat, and maize, and the plants usually exhibit a regular and co-ordinated development, making them particularly suitable for FSPM. In general, cereal crops grow at relatively high population densities and the individual plants are, therefore, experiencing a high degree of intraspecific competition (next to interspecific competition with weeds) for light, nutrients and water. Compared to solitarily grown cereal plants, crop cereals experience various competition effects, an important one of which is expressed in the number of tillers (side shoots) that the plant produces. For example, wheat plants grown at a low population density produce a high number of tillers, and *vice versa*. To a large extent, the number of tillers that a wheat plant produces can be traced back to the degree of intraspecific competition for light at the early stages of vegetative growth, when the axillary buds break and tillers are being formed.

To analyse competition between individual wheat plants in terms of their dynamics of axillary bud outgrowth, an FSPM of wheat was developed. The model accurately simulates development of wheat structure and important aspects of the light regime, such as light extinction by the canopy (see Figure 2) and the change in spectral composition of the light within the canopy, following scattering. Spectral composition is known to affect bud break in wheat, so this aspect of intraspecific competition was studied in detail (Evers *et al.*, 2007). Currently, the model is used to simulate photosynthesis and biomass allocation in the plant structure, aiming at understanding bud break from a carbon supply/demand point of view.

Concluding remarks

The FSPM methodology is still being heavily developed, but several mature applications have already been published. The approach is based on concepts and

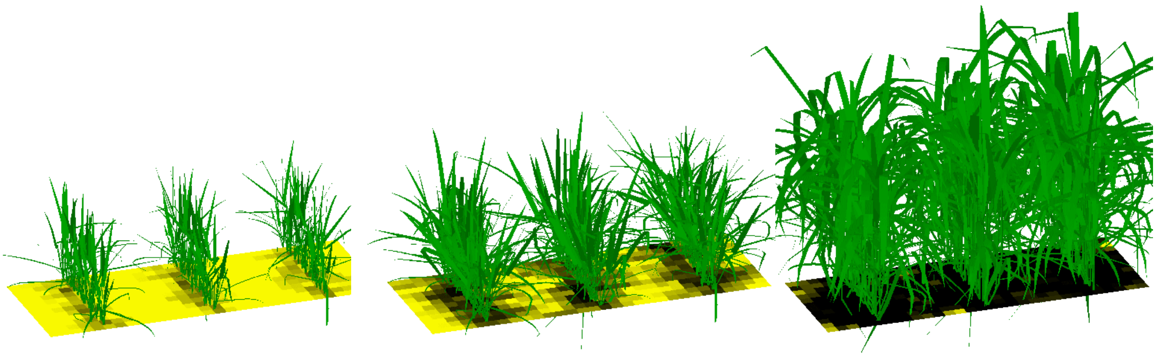

Figure 2. Visualization of three stages in vegetative wheat development. The colour of the soil elements represents the percentage of light that penetrated the canopy onto the soil element [ranging from black (0%) to bright yellow (100%)].

principles that date back to De Wit, and adds aspects of plant and canopy structure. In principle, FSPM can currently address similar issues as classical crop growth models, but offer particular advantage if plant structure needs to be taken into account for proper explanation of the phenomena under study. Additional benefits of the approach are the possibility to explicitly address internal transport in the structure as a co-explanatory variable for the behaviour of the system, and to generate convincing animations, a strong feature that can be used in extension and teaching.

Acknowledgements
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The (increasing) complexity of plant systems research and the use of models

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Introduction

Mathematical modelling has made a considerable contribution to plant and crop science in the past. It has improved the understanding of physiological processes and their relationships in determining responses at the system level. For the development of dynamic models, De Wit (1968) recommended to distinguish between two levels, the system level and the next lower (explanatory) process level. Crop models typically consider the processes of plant development, light interception, CO_2 assimilation and respiration, and the partitioning of biomass to plant organs and their growth. Including more detail at the process level ultimately increases model complexity and calculation time. Developments in computer science have progressively shortened calculation times and supported the consideration of more explanatory detail. This and the increasing complexity of problems to be addressed have resulted in the development of more complex models. Combining the demand for complex systems analysis considering multiple aims and scales (Figure 1) with the original ideas about effective modelling detail (De Wit, 1968) is difficult to realize in plant systems research and addressed in this paper.

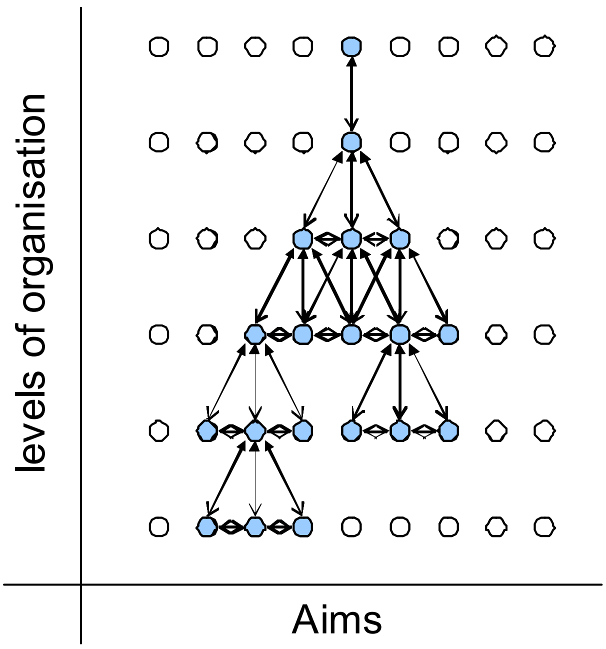

Figure 1. Schematic representation of a complex system with different aims and scales and a nested hierarchical structure (dark circles).

40 Years Theory and Model at Wageningen UR, Wageningen, The Netherlands, pp. 21-24.

Progress in plant/crop modelling

Crop modelling has progressed significantly, extending the considered factors (*e.g.*, water- and N-limitations, biotic and abiotic stresses, competition with other plants) and system properties (*e.g.*, product quantity and quality, morphological characteristics), and broadening the scales of application (from the detailed levels of systems biology to the coarse levels for climate impact assessment). Some emphasis has been on improving model structure based on physiological relationships (Yin and Van Laar, 2005). Scale-dependent changes in model structure and parameters are well understood for processes scaled up from the organ to the crop level, but are less clear for more detailed or coarser levels of organization.

Multi-aim and -scale modelling

Consideration of processes (and process detail) in a model, according to their relative importance for the systems' behaviour is the biggest challenge for modellers. For instance, photosynthesis is of key importance for growth in biomass, but inter-annual variability in biomass production and yield is often explained by other processes, *e.g.*, leaf area dynamics (Ewert, 2004). Accordingly, improving the modelling detail of photosynthesis will have little effect in terms of improving the results of system simulation. However, the relative (un-)importance of a specific process can change, depending on the factors considered and the scale of application. For instance, interactions between increasing atmospheric CO_2 concentration and tropospheric ozone or water limitation at the photosynthesis level can also be observed at the crop level. The significance of these effects often decreases at larger scales as other factors become more important such as farm characteristics and regional socio-economic conditions affecting crop management (Reidsma *et al.*, 2007). Several up-scaling approaches are available to account for these scale-specific factors (Ewert *et al.*, 2006), but their appropriate use is often not well understood.

Modelling for a range of aims and scales requires application of different models. Simultaneous modelling may require model linkages to account for dynamic feedback loops (Figure 1). If aims and scales vary with application, approaches are required that support flexible model linking. Several integrated assessment models (mainly in the field of climate change) have become available, following the idea of extending model applicability through model linking (Ewert *et al.*, in review). The resulting model composites are complex and often require expert groups to be run. Few examples are known [*e.g.*, SEAMLESS-IF, (Van Ittersum *et al.*, 2008)] where emphasis has been on frameworks to support flexible model composition depending on the problems at stake. Progress in computer science and software engineering (*e.g.*, object-oriented programming) supports the development of modular approaches for such flexible modelling frameworks that can assemble models according to changing modelling aims, also for plant systems research (Adam *et al*., in review).

Concluding remarks

Computer science and software engineering have enabled the development of dynamic simulation models; they may also support the development of approaches that are able to deal with problems of increasing complexity. In plant science, these modelling activities need to be supported by research on the structuring of systems into (physiologically) meaningful components and the development of appropriate scaling methods.

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Theory and models for managed ecosystems: From confusion to certainty and back again

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Introduction

'Theorie en Model' (T&M) appeared in 1968. It was the public lecture with which De Wit kick-started the development of process-based models for crops and other managed ecosystems. In many ways, De Wit's research programme, also called theoretical production ecology, has been highly successful. This contribution compares T&M and De Wit's research programme to other developments in theoretical ecology – and suggests one possible path for future development. The subject matter is very wide and the text only offers a personal, limited perspective.

The 1960s: a time of change

The end of the 1960s was a time of innovation in theoretical ecology. Besides T&M, many other landmark publications appeared, each stimulating a new research programme. The following five had a major impact:

- 1966 Optimal foraging theory (Emlen, 1966; MacArthur and Pianka, 1966)
- 1967 The theory of island biogeography (MacArthur and Wilson, 1967)
- 1968 Theoretical production ecology (De Wit, 1968)
- 1968 Energy flow in ecosystems (Odum, 1968)
- 1969 Meta-population ecology (Levins, 1969)

1969 also saw the publication of Ludwig Von Bertalanffy's 'General System Theory' (Von Bertalanffy, 1969), making his ideas about systems analysis more widely known among English readers.

It is unclear what caused this explosion of new approaches in theoretical ecology. It may have been the result of dissatisfaction with mainstream mathematical biology, with its focus on elegant, but perhaps oversimplified and data-poor mathematical modelling. Alternatively, the recognition that human beings affected their environment in surprising ways may have motivated a search for better understanding of ecosystems. And at least partly, scientific renewal was inspired by progress in information and computer science. In his pioneering work from 1968, Odum stated that "The growing importance of systems analysis and the use of computer models to simulate ecological functions are recognized as major areas of emphasis during the next decade". Whatever the main drivers were behind the divergence of theoretical approaches, they shared common aims of biological realism, and explanation of concrete data sets rather than general patterns. This approach strongly differed from much of the mathematical biology where biological realism was eschewed in favour of yet more subtle refinements of the logistic equation, SIR-models or predator-prey systems.

Obviously, the new approaches were not free from abstraction and idealization themselves. In many of them, something unobservable was presupposed: island biogeography assumed equilibrium, foraging theory assumed optimality, and Odum's programme assumed that energy availability was a more important constraint than matter. General System Theory (GST) was an exception in that it did not make strong assumptions: the idea that everything is a system of interacting parts is not contentious. When modelling systems, GST focused on their feedback structure. The great insight of Von Bertalanffy was that a view of the world as a hierarchy of systems dominated by feedbacks, could indeed explain much of the observed behaviour. However, Von Bertalanffy was still focusing on simplicity and elegant mathematics. In the socio-economic sciences, the systems view was progressing further in the direction of more detailed, realistic models with the work of Forrester (1961). His work, successful as it was, was hampered by the fact that in the socio-economic sciences experimental data are scarce and it is hard to define unambiguously what the key processes are. De Wit's programme would move further than all other innovators towards realism by combining the systems view of Von Bertalanffy with the empiricism of crop science.

With the classical methods still playing their part, and the new research programmes just starting up, there was a state of confusion: it was not clear in which direction theoretical ecology would evolve.

De Wit's research programme

Whereas most of the new theoretical ecology approaches focused on natural, unmanaged systems, De Wit's subject matter was managed ecosystems. In developing his research programme, De Wit used physics as an example to follow. He shared this outlook with the island biogeographers MacArthur and Wilson (1967) who, following R.A. Fisher, hoped for "a tradition of mathematical work devoted to biological problems, comparable to the researches upon which a mathematical physicist can draw … [pointing] to possible factors and relationships in the real world that would otherwise remain hidden and thus stimulates new forms of empirical research". Physics, as a scientific discipline, seemed a good example to follow. It showed how science could satisfy the intellectual curiosity of mankind by discovering laws of nature, with those laws also being useful in practical applications like engineering and technology.

In T&M, De Wit referred to physics as the "search for processes and mechanisms that control phenomena and the reduction of these relations to a minimal number of laws" [my translation]. This quotation might explain one of the strengths of De Wit's research programme: he put the search for controlling processes and mechanisms first, not the postulation of overarching principles or universal patterns of behaviour. Premature abstraction was to be avoided. Already in T&M, De Wit listed concrete processes to be simulated in crop models: photosynthesis, respiration, growth, phenology, root uptake – and these are still prevalent in models today. This focus on concrete, measurable processes guaranteed a close link with empirical disciplines, from soil science to plant physiology and micrometeorology. Research results from these disciplines were directly useable by the modellers and model results could help explain observations, and not just qualitatively. This was theoretical science not being afraid to get its hands dirty. The research programme that followed brought great clarity to the theoretical analysis of managed ecosystems.

Of course, crops are ideal subjects for such process-based ecosystem modelling. They are more homogeneous than most natural ecosystems and more amenable to experimentation – permitting the required data to be collected. If anywhere, theory for living systems that was both rigorous and realistic seemed possible in crop science. However, models needed to be built before theory could be derived and De Wit chose the right tools for model development. Like Odum (1968, quoted above), he advocated computer simulation in T&M. And with remarkable early insight – not shared by all modern modellers – he added sound methodological advice, *e.g.*, the need to restrict the number of integration levels in individual models.

By the end of the 1970s, De Wit's programme had already advanced remarkably (de Wit *et al.*, 1978). It seemed to be on its way to becoming the dominant approach in the study of managed ecosystems. Looking back at this early period, British modeller John Thornley stated that "De Wit pioneered crop modelling, and his intellect, experience and insight give his contributions and views unique weight and authority" (Thornley, 1998). Competing classical ecological methods and models received less acclaim: according to a 1988 survey of the historically most influential theoretical models in ecology, no data "support the predictions of the equations" (Hall, 1988). Despite this, at many universities, mathematical modelling remained the norm – with little application to new data. Computational methods were introduced, such as cellular automata and Lindenmayer systems, but to process-based modellers these methods seemed to produce form but no substance.

In contrast, the models originating from De Wit's programme addressed ever more real-world issues in agriculture, such as pathosystems, weed infestations, drought, etc. Much of this work is recounted in recent reviews (Bouman *et al*., 1996; Van Ittersum *et al*., 2003).

With respect to modelling managed ecosystems, it seemed that from among the many approaches, the right one had been found.

Limitations of process-based modelling

As mentioned above, physics was paradigmatic for De Wit, and the hope was that the process-based models would lead to theory. The shining example was the discipline of mechanics, with its small set of deterministic laws. De Wit's research programme did retain this idealistic flavour: the idea persisted that some universal set of process descriptions could be found that would apply to all crops and that only needed to be reparameterized whenever a new crop was to be simulated. The aim was to define the processes in such a way that the rate-determining parameters would be universal constants, only dependent on the genetic characteristics of the crop. Such universal constants were never found. When measurements were taken in real systems, the parameters showed variability within species and over time (*e.g.*, Meinke, 1996). The attempt to ascribe the variation to measurement problems failed, when it turned out that even under controlled conditions no universal values were found. It became clear that the predictive capacity of the process-based models was less than had been expected.

A problem with the process-approach is of course that we can always hope to find our universal constants just one level deeper. Unfortunately, such reductionism quickly runs into the 'curse of dimensionality' when the degrees of freedom expand with every extra layer we examine. In fact, even if we could go all the way down to physical constants, parameter value uncertainty would remain. For example, Newton's constant of gravitation, G, is only known to a precision of 0.01% (NIST, 2008). As mentioned above, De Wit in fact already warned against an overly reductionist approach when he stated that models should not aim to bridge more than two integration levels. Despite that warning, we still see biochemical photosynthesis modules in ecosystem models and much concomitant parameter tuning.

The realism and pragmatism of De Wit's research programme also had other downsides. The "reduction of relations to a minimal number of laws" (T&M) has been all but given up. Perhaps no such laws exist in biology (Lawton, 1999), but without basic theory to guide us, the limitations of any single modelling method may be overlooked. A considerable number of phenomena are difficult or impossible to simulate with the detailed process-based models. These include adaptation (Van Oijen and Levy, 2004), chaotic dynamics, threshold behaviour, changes in biodiversity and the switching of ecosystems between multiple stable states. Some of these phenomena are more common on the pages of theoretical journals than in the real world, but not all of them are, and even the rare ones are important whenever they do occur. A very stimulating inaugural lecture by theoretical biologist Hogeweg (1992) – which can be seen as a counterpoint to T&M – suggests that we may be blind to real phenomena if we don't have the 'search images' produced by simple mathematical models to make us notice them. But, if we are to once more include the full range of available ecological models in our studies, are we then not back in the state of uncertainty that we found ourselves in at the end of the 1960s?

Statistical physics as a new role model?

The question is whether the lack of universal constants invalidates De Wit's research programme. Perhaps all that is needed is a modification of methods and aims. It may be time to embrace the lack of certainty rather than strive for universals. This might mean that we should use another branch of physics as our role model: not mechanics but statistical mechanics.

Statistical mechanics accepts the existence of underlying deterministic laws, but acknowledges that the underlying system state (the 'microstate' of particle positions and velocities) can never be fully known, preventing the direct application of the laws. Acknowledging our incomplete information about microstates, statistical mechanics represents that uncertainty through probability distributions. Information about the macrostate, such as mean kinetic energy (temperature) is used to constrain the distributions. Edwin Jaynes (1957) showed how the simple procedure of maximizing uncertainty within given informational constraints, *i.e.* the statistical inference principle of maximum entropy, suffices to derive the key principles of equilibrium statistical mechanics and explain its link with the macroscopic theory of thermodynamics.

It remains to be seen whether all of this translates well from statistical physics to a statistical ecology of managed ecosystems, but there are some encouraging developments. Clearly, ecosystems are not in equilibrium (they would be dead), but Jaynes' work has recently been extended to non-equilibrium statistical dynamics (Dewar, 2003). Using Jaynes' information theory approach, Dewar has shown that systems in steady state converge to a condition of constrained maximum entropy production (Dewar, 2003, 2005), and he showed how the informational approach helps explain the dynamics of species abundance in ecosystems (Dewar and Porté, 2008).

The assumption of steady-state remains a restrictive one, and the main benefit from the statistical mechanics paradigm may actually come from its methodology rather than its results. Statistical mechanics is little more than applied probability theory (Jaynes, 2003), and the feasibility of a probabilistic framework for parameterization and comparison of different process-based models of managed ecosystems has recently been demonstrated, using forests as an example (Van Oijen *et al*., 2005). We now have a rigorous method for using data to help assign plausibility to different models and, for each of the models, to different parameter values – all by means of Bayesian updating of probability distributions.

The feasibility of such probabilistic modelling frameworks suggests that uncertainties about modelling approaches and theory may indeed have returned, but that we now have methods to accommodate them.

Outlook

It seems that no simple laws will be derived from process-based modelling of managed ecosystems, but simple laws will not be generated by other approaches either. It is also unlikely that we will find process descriptions that yield universal rate parameter values. Model predictions will therefore remain uncertain. That uncertainty must be quantified, if models are to be practically useful, but we have the required probabilistic tools. Given the limitations of each individual modelling method, it will be advisable to tackle ecological problems by multiple models, originating from different paradigms. This might lead to a future of ecological modelling where different schools of thought remain in existence, but learn from each other each time the different approaches are used on the same ecological problem.

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Ecological models as a bridge between spatial ecology and societal decision-making

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In the last decades of the 20th century, the increasing understanding of the impact of land use change on ecosystems has resulted in a policy response to explicitly include spatial conditions in biodiversity conservation planning. This shift presented a major challenge to ecology. Understanding the interaction of many spatially separate units of ecosystems introduced much more complexity: an extra level of spatial scale, an explicit spatial context for studying the interactions between pattern and process, and a key role for chance processes. Further complexity was added by extending the ecological system with a social component: decision-making on the design of ecological networks. This required that scientists also understand how information about the complex system can be simplified to play a role in negotiation processes about landscape change. Ecological models play a key role in both, the understanding of the interaction between biodiversity and regional patterns of ecosystems and as a bridge between science and society.

But let's go back to the days of C.T. De Wit and other founding fathers of modern life sciences. All the more complex models used today evolved upon the fundaments laid in those days, the simple mechanistic models developed to link basic processes to patterns. For theoretical ecology, Robert MacArthur probably was the equivalent of Kees De Wit for production ecology. His simple models and hypotheses have inspired generations of scientists, and his theory of island biogeography is still influential today. During the 1960s, Robert MacArthur had difficulty getting his papers published in peer-reviewed journals. His truly innovative ideas were often perceived as wrong, and his often contra-intuitive results were based upon fuzzy or incomplete mathematics and oversimplified and limited data (Fretwell, 1975). Some contemporaries even called him a charlatan; others called attention to some of his mistakes (Fretwell, 1975). Were those models correct? Does it matter if they were not? Even if some of the work of 40 years ago is considered 'wrong' in the light of current knowledge, it certainly was not done in vain. First, it stimulated discussion and inspired others to prove – or falsify – the results of the theoretical models. Second, it introduced a way of thinking in which *e.g.* equilibria, disturbance, stochasticity and thresholds played a role. MacArthur was the first to discuss the relation between biodiversity and ecosystem stability.

Although there are many similarities between MacArthur and De Wit, there are also important differences. Whereas MacArthur was not very interested in resource conservation (Fretwell, 1975), De Wit was not only driven by the desire to understand processes and patterns, but also to apply this knowledge in production ecology and resource conservation. Partly thanks to him, Wageningen has a unique place in the international scientific community. Unique is the long history of interaction with stakeholders (long before this word became popular) and the focus on problem-driven research, together with the fact that in this part of the world, problems related to resource ecology and landscape science simply tend to be bigger and more urgent because of the high population density and the intensive economic activity. This combination of factors has led to a flourishing local scientific community that, at least when it comes to landscape science, is highly respected internationally. This is illustrated for example by the fact that the International Association of Landscape Ecology (IALE) World Congress 2007 was held in Wageningen. Building upon the work and principles of founding fathers such as De Wit and MacArthur, inspired by stakeholders and urgent emerging societal problems, Wageningen has become a world player.

This brings us back to the topic of this presentation: ecological models as a bridge between spatial ecology and societal decision-making. Ecological models are used in a variety of ways. First, models can help to understand how things work; how processes link to patterns. This is the case for both the more general, simple models from the 1960s and the more realistic, complex models developed later upon these fundaments. For example, the National Ecological Network (NEN or EHS) is based upon the notion of ecological networks as a concept and early work on metapopulation models (*e.g.*, Verboom *et al.*, 1991). Second, models are used to derive thresholds, procedures and rules of thumb. As an example, we refer to the work of Verboom *et al.* (2001) (the key patch approach) and Vos *et al.* (2001) (the ecologically scaled landscape indices approach). These tools, based upon both, modelling and data analysis, are being used in landscape planning and assessments – not the complex models themselves (Opdam *et al.*, 2008). Third, simple tools and spatial concepts based upon these thresholds and rules, are used in the decision support cycle. This takes place when different spatial plans, or scenarios, are assessed, as in environmental impact assessments, but more and more also when stakeholders discuss options for solving a spatial planning problem. An example, elaborating on these metapopulation models and derived tools, is described by Opdam *et al.* (2003). The spatial concept of ecosystem networks now is emerging in spatial planning. We begin to understand its role in integrating ecosystem functions, in linking the interests of actors in collaborative planning, and in incorporating biodiversity in multifunctional land use planning (Opdam *et al*., 2006, Termorshuizen *et al*., 2007, Opdam and Steingröver, 2008, Nassauer and Opdam, 2008). Thus, in all three cases, but in three distinct ways, models serve as a bridge between spatial ecology and societal decision-making.

But, although in the fields of landscape ecology and landscape design models already play an important role, there remains more work to be done. Some challenges for the near future are: (1) Understanding the impacts of climate change on biodiversity, and designing adaptation measures. We cannot stop climate change but we can adapt the landscape (Opdam and Wascher, 2004); the models and methods developed in the 20th century were not designed to deal with increasing levels of environmental fluctuations, such as droughts and heavy rainfall, nor are the ecological networks designed for ecosystems shifting to the north. (2) Assessing and predicting impacts of land-use change and climate change on resilience and ecosystem functioning/ ecosystem services (Vos *et al*., 2009). Since we will have to deal with major changes in our ecosystems due to, among others, climate change, an important question, going back to the original work of MacArthur and others, is: how does biodiversity relate to ecosystem stability, can ecosystems function when species become extinct or are replaced by other species, and do the most important ecological processes and functions remain intact? (3) Dealing with uncertainty in complex models and model chains. Since complex problems require complex tools, uncertainty in model outcome is an important issue (Verboom and Wamelink, 2005). For example, changing rainfall patterns influence groundwater dynamics; this in turn affects vegetation dynamics and consequently animal populations and entire communities. Yet, models tend to have a high level of uncertainty, so when using chains of coupled models, can we still make predictions? Is it true that the ranking of scenarios is far more robust than individual outcomes? (4) Using models in the planning process with stakeholders and in decision support. This requires that scientists also understand how information about the complex system can be simplified to play a role in negotiation processes about landscape change (Opdam *et al*., 2008).

We conclude that over the past 40 years, starting with more fundamental scientists such as De Wit, unravelling basic and general processes in the life sciences, Wageningen has become a centre of problem-driven science that could successfully build upon the developed concepts and insights. Now, a new generation of scientists is emerging that specialize in participative research, making the concepts and knowledge available for non-scientists within the interactive participative planning process with stakeholders. In all these types of research, models play an important and multifaceted role.

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Modelling that bridges scales and connects disciplines

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Crop science is in a state of flux, caught up in 'tensions of scale'. These tensions arise from the attempts to address 'top-down' issues such as global change impacts with 'bottom-up' solutions such as biotechnology. The rapidly changing global environment impacts on the management of farms, fields, crops and plants. However, as the resolution of spatial scale increases, these global impacts are increasingly difficult to quantify. Similarly, rapid biotechnological developments provide new insights and skills at the molecular, genome and cell levels, but with decreasing spatial resolution, environmental interactions increase, making it often difficult to quantify the impact of biotechnology at crop, field, farm or regional levels. Attribution of cause and effect becomes increasingly intractable as the scale difference between the issues and the proposed technological solution increases. Correctly matching problems of societal importance with science-based solutions is a challenge that requires good, quantitative modelling at all scales.

Recent increases in commodity prices have resulted in a renewed interest in agricultural production. So much for the good news. We are now faced with substantial increases in food prices in developed countries and looming food crises in developing countries, particularly in Africa. This comes at a time when western consumers are looking increasingly towards carbon-neutral energy sources to maintain their lifestyles, while many parts of the world, particularly in the tropics and subtropics are rapidly running out of fresh water.

Many solutions for these global problems are perceived to be plant-based, a fact that gave rise to the term 'bio-based economy'. It is paramount that this 'new' economy be implemented sustainably by harnessing the environmental benefits that plants and plant production can provide, while minimizing their potential downsides. To realize a sustainable, bio-based economy requires innovative scientists, that understand how plants and plant systems function, how they can be managed and how new, plant-based technologies can be integrated into our existing agro-ecosystems. Such scientists need to have strongly developed systems-analytical skills and the ability to understand and respond to stakeholder needs. Although biotechnology promises a wide range of technical innovations that could provide partial solutions to

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some of these problems, such technical innovations need to be assessed against their socio-economic feasibilities, *i.e.* they need to be assessed in terms of their broader environmental, economic and social consequences (Meinke and Stone, 2005; Richards *et al*., 2008). Such assessments require 'systems thinking' – the ability to quantitatively think through the consequences of proposed systems changes.

Systems thinking acknowledges that in dynamic systems, components interact, creating behaviours and outcomes that can be very different from viewing these components in isolation. Systems thinking places equal importance on understanding dynamic relationships between parts as on understanding the parts themselves. The system of interest needs to be viewed and evaluated holistically, including all the linkages and interactions between system components. For agro-ecosystems it is particularly important to identify the leverage points where management can influence systems behaviour. Successful technological innovations need to go hand-in-hand with appropriate risk management and *ex-ante*, model-based evaluation of such technology × management interactions. Frequently, model output is used to evaluate alternative management options or technologies probabilistically (*e.g.*, Hayman *et al*., 2007; Landis *et al*., 2008). Used in such a way, models then become essential tools for operational risk management (Meinke and Stone, 2005).

Agricultural systems bear many of the hallmarks of complex, adaptive systems (CAS) that generally have three key characteristics: (*i*) order emerges rather than being predetermined, (*ii*) the history of the system is largely irreversible, while (*iii*) the system's future can only be predicted probabilistically (Dooley, 1997). Cause and effect relationships become increasingly intangible as a system becomes more complex and open[1] (Nelson *et al*., 2007). In extreme cases, there may be 'no scientific basis on which to form any calculable probability whatever. We simply do not know!' (Keynes, 1937, p. 214). For plant-based systems, which are generally regarded as intermediate in terms of their complexity and openness, effective integration across various scales is further challenging due to their intrinsic interdisciplinarity (ranging from genetics, molecular biology, plant physiology to plant nutrition, soil sciences, hydrology and social sciences, to name just a few disciplines). This is further complicated by the frequent lack of empirical data needed to test hypothetical options. Under such circumstances, models can often replace traditional, *in vivo* approaches to data collection (*i.e.* experimentation) with *in silico* approaches that enable a rapid *ex-ante* assessment of the likely outcomes of alternative management or decision options. In keeping with C.T. De Wit's philosophy, such an *in silico* approach complements and adds value to experimental approaches that will, nevertheless, remain essential, at

[1] In contrast to closed systems, open systems interact and exchange flows/information with their external environment.

all aggregation levels of the system. System modelling allows us to ask the critical 'what if'-questions needed to investigate the impact of choices made in agro-ecosystems management.

The emphasis of the Centre for Crop Systems Analysis (CSSA) is on improvement and innovation of plant production at various levels of integration; from genotypes to cropping systems (including the human dimension). The Centre also contributes to assessments of risks arising from climate variability and climate change. The Centre's core expertise is in the quantification of complex and often non-linear interactions between plants (or genotypes), management and the environment (G×M×E) using model-based approaches. This knowledge is integrated via sophisticated modelling tools to generate insights into complex system interactions (*e.g.*, biochemical modelling of C3 and C4 photosynthesis under stress; predicting phenotypic expressions to multiple traits in breeding programmes; optimizing crop management via functional-structural plant modelling; quantifying G×M×E interactions in a changing world).

The Centre's experimental and modelling research assists in analysing and developing sustainable and profitable plant production chains and cropping systems in temperate, sub-tropical and tropical regions. These systems also include grassland systems managed for animal or biomass production and for nature management. The Centre is addressing these issues under five themes or 'signature projects' that exemplify the research approach:

(1) Crop systems biology

The new discipline of crop systems biology is challenged to (a) bring the information from functional genomics to the crop level, (b) introduce true biological mechanisms in many current crop models, (c) better understand the organization of the whole crop and its response to environmental conditions, (d) fill the vast middle ground between '-omics' and crop physiology using models, and (e) promote communication across scales. As a discipline, crop systems biology simulates complex crop-level traits relevant to global food production and energy supply by linking 'omics'-level information, biochemical understanding, and crop physiological component processes. For instance, Yin and Struik (2008) showed that a successful genetic modification to equip the rice plant with C4 photosynthesis would enable it to substantially increase biomass production. This modelling work entailed incorporating equations for C3 and C4 photosynthesis, combined with a stomatal conductance model, into the mechanistic crop model GECROS. They further found that the grain yield advantage of C4 rice (average 23%) varied considerably, depending on climatic conditions and would be considerably less than the 50% hoped for by Mitchell and Sheehy (2006). Essential in crop systems biology is to properly map the organization levels and the communication systems between these levels for the different key processes, from the molecule or gene, all the way up to the crop (Hammer *et al*., 2006). Modelling tools based on crop systems biology can generate important crop physiological insights and lead to investigation of important societal issues, such as improving food security or Zn supply for human nutrition in rice-based diets (*e.g*., Jiang *et al*., 2008). Further, systematic evaluation at this level of integration can also contribute to scientific debates such as the recent emergence of 'plant neurobiology' that Struik *et al*. (2008) helped to put into perspective.

(2) Virtual plant modelling

Plants respond to their environment by adapting their functions (*e.g*., light interception, photosynthesis, transpiration, N allocation) as well as their structure or architecture (*e.g*., buds either break or remain dormant; size, shape and orientation of organs). Functional-structural plant models (or virtual plant models), are models explicitly describing the development over time of the 3D architecture or structure of plants as governed by physiological processes which, in turn, are driven by large scale environmental factors (Vos *et al*., 2007). Such models offer options to develop a coherent research programme aiming at advancing plant (or genotype) × environment × management interactions. They show promise as (a) a research tool in plant sciences, (b) a new tool supporting plant management decisions and (c) a support tool in plant breeding through exploring morphological and functional aspects of plant ideotypes. For instance, Evers *et al*. (2007) developed a 3-D wheat model in which local light interception determines the outgrowth of a tiller, providing feedback mechanisms between organ and whole crop phenomena of growth and development. Such models can then be used to investigate, for instance, competition for resources. In the case of intercropping, different crops can act competitively and synergistically – at the same time! The net result can only be assessed *in silico*. For instance, the (partial) shade provided by different companion crops generally reduces overall biomass accumulation of the understory crop, but can also lead to quality improvements (*e.g*., coffee) that might (in economic terms) more than compensate for the loss in production volume.

(3) Designing climate-robust cropping systems

The impact of climate change on many natural and managed systems is now beyond doubt (Rosenzweig *et al*., 2008). Amongst the managed systems, agro-ecosystems arguably are among the most climate-sensitive sectors in our global economy. Many developing countries remain heavily dependent on agriculture for national income, food security and employment, while agriculture occupies a special place in the national psyche of many developed nations (Meinke *et al.*, 2007). Hence, any effort to reduce the vulnerability of this sector to climate-related risks is likely to lead to considerable global benefits, both economic and social. Specifically, targeted adaptations to continuing climate changes are urgently needed (Howden *et al.*, 2007). Particularly in developing countries, farmers' coping capacity is limited by (a) lack of resources and (b) lack of knowledge. This research is designed to allow practitioners and policy makers to negotiate policy and management responses from a position of knowledge rather than from ignorance (ensure that policy intent and management practices are aligned; avoid or discourage 'perverse' policy incentives such as subsidizing poor or unsustainable management practices). This theme also aims at reducing costs associated with risks and change management by supporting informed decision making; and at increasing enterprise profitability and environmental performance through early assessment of management alternatives. Research includes investigation of better and more relevant ways to use new and enhanced climate information (including climate forecasts; *e.g.*, Lo *et al.*, 2007; Maia *et al.*, 2007). It also considers natural resource implications in conjunction with impacts on crop production and quality and deals with farm-enterprise issues in addition to crop and cropping systems issues (*e.g.*, Nelson *et al.*, 2007). Although technological progress in one discipline can sometimes trigger quantum leaps (*e.g.*, the introduction of synthetic fertilizer or genetic engineering for conferring trans- or cisgenic pest resistance to crops), in most cases multidisciplinary problems require multidisciplinary solutions and a focus on integration of disciplinary-based science (Howden *et al.*, 2007).

(4) Ecology of mixed plant systems

Modern, mechanized agriculture has largely led to monocultures, often associated with low biodiversity and sub-optimal resource use efficiency. The recent emergence of the misguided use of cereals such as maize as a supposedly 'economically viable' resource for ethanol production has increased this pressure considerably (Landis *et al.*, 2008). There is ample evidence that systems that are more diverse, *e.g.*, agroforestry systems, mixed grass swards or (relay) intercrops, are more productive than monocultures, because they are better able to capture the available resources (Zhang *et al.*, 2008). Further, plant mixtures have been shown to be more resilient to biotic stresses arising from pests and diseases (Wolfe, 2000) and abiotic stresses such as climate variability (including low-frequency fluctuations). Nevertheless, contrary to Eastern countries, such as China, mixed plant systems are rarely exploited in the west, with grass-clover mixtures in organic agriculture a notable exception. Mixing perennial species in cropping systems can increase robustness against biotic threats, reduce erosion, make the landscape more attractive, provide ecosystems functions, such as biological pest control, and possibly sequester carbon. Despite available evidence from case studies, the generic understanding of resource use in mixed cropping systems is incomplete and there is limited capacity to calculate, explain and predict the benefits of mixtures compared to single species. Potentially negative side effects of mixed cropping on the ability to use crop rotation as an effective tool for the management of soil-borne pests need to be resolved. Mixed systems may be indispensable in order to meet the rapidly increasing demand for multifunctional use of the available land. This highlights an important knowledge gap that can be filled by proper combination of *in vivo* and *in silico* experimentation of mixed plant systems.

(5) Interactions between natural and social sciences

None of this work would be complete or even make sense without the appropriate so-called 'beta-gamma integration', *i.e.,* strong and active links with social sciences that ensure the relevance and social value of the research. These interactions are essential to ensure that possible, technical innovations are also socio-economically viable and will eventually be implemented to the benefit of stakeholders (*e.g*., Richards *et al*., 2008). Although this theme is a major and essential underpinning activity for all the other research themes, it is also designed to investigate major activities on, for instance, the agronomic and social aspects of informal seed systems on several continents (*e.g*., Bishaw, 2004), gender issues in participatory plant breeding (Galie', 2008), impact of HIV/AIDS on agriculture (*e.g*., Akrofi *et al*., 2008), farmer-managed biodiversity (*e.g*., Kudadjie *et al*., 2007; Zannou *et al*., 2007), wild-gathered foods (*e.g*., Challe and Struik, 2008), economic and spatial analysis of seed-, soil- and air-borne diseases (*e.g*., Breukers *et al*., 2006; Skelsey *et al*., 2008). Social sciences in combination with systems modelling can create 'social capital' by (a) upscaling from an understanding of crop physiological responses to field-scale environmental conditions and (b) downscaling from an understanding of global climatic conditions to 'quantities' that really matter to farmers: farm income and the long-term sustainability of their resource base (Meinke *et al*., 2006).

Simulation modelling provides an effective means of bridging disciplinary divides by creating new insights and helping decision makers at all scales to evaluate alternative options. This means that stakeholders can engage in informed discussions about these alternative options, negotiate an outcome desirable for all involved, and then engage in a process of innovation by design. To be most effective, modelling should be conducted in an open, transparent and participatory style that creates legitimacy for the approach and fosters global collaboration and communication.

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Stochastic events can trigger large state shifts in ecosystems with reduced resilience

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In the early times of the Department of Theoretical Production Ecology, one of De Wit's opinions was that for an ecosystem to be amenable to modelling, it had to be 'repeatable', so that he had serious doubts about the possibilities to model natural ecosystems that supposedly are 'unique', contrary to agro-ecosystems that typically *are* repeatable. In this contribution, we will show that modelling is also a useful tool in increasing insight in and explaining the behaviour of natural ecosystems.

The notion that ecosystems may switch abruptly to a contrasting alternative stable state emerged from work on theoretical models (Holling, 1973; May, 1977). Although this provided an inspiring search image for ecologists, the first experimental examples that were proposed were criticized strongly (Connell and Sousa, 1983). Indeed, it appeared easier to demonstrate shifts between alternative stable states in models than in the real world. In particular, unravelling the mechanisms governing the behaviour of spatially extensive ecosystems is notoriously difficult, as it requires the interfacing of phenomena that occur on very different scales of space, time, and ecological organization (Levin, 1992). Nonetheless, recent studies have provided a strong case for the existence of alternative stability domains in various important ecosystems (Scheffer *et al*., 1993; Van de Koppel *et al*., 1997; Nystrom *et al*., 2000; Carpenter, 2001). In this contribution, we concentrate on observed large-scale shifts in major ecosystems and their explanations. After sketching the theoretical framework, we present an overview of results from different ecosystems, highlight emerging patterns and discuss how these insights may contribute to improved management.

Theoretical framework

Ecosystem response to gradually changing conditions

External conditions to ecosystems such as climate, inputs of nutrients or toxic chemicals, groundwater reduction, habitat fragmentation, harvest, or loss of species diversity often change gradually, even linearly, with time (Vitousek *et al*., 1997; Tilman *et al*., 2001). The state of some ecosystems may respond in a smooth continuous way to such trends (Figure 1a), others may be quite inert over certain

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ranges of conditions, responding more strongly when conditions approach a certain critical level (Figure 1b). However, a crucially different situation arises when the ecosystem response curve is 'folded' backwards (Figure 1c). This implies that for certain environmental conditions the ecosystem has two alternative stable states, separated by an unstable equilibrium that marks the border between the basins of attraction of the alternative stable states.

The presence of alternative stable states has profound implications for the response to environmental change. When the ecosystem is in a state on the upper branch of the folded curve it can not pass to the lower branch smoothly. Instead, when conditions change sufficiently to pass the threshold ('Saddle-node' or 'fold' bifurcation), a 'catastrophic' transition to the lower branch occurs. Note that when one monitors the system on a stable branch prior to a switch, little change in its state is observed. Indeed, such catastrophic shifts occur typically quite unannounced, and 'early warning signals' of approaching catastrophic change are difficult to obtain. Another important feature is that in order to induce a switch back to the upper branch, it is not sufficient to restore the environmental conditions of before the collapse. Instead, one needs to go back further, beyond the other switch point, where the system recovers by shifting back to the upper branch. This pattern in which the forward and backward switches occur at different critical conditions is known as *hysteresis*. The degree of hysteresis may vary strongly even in the same kind of ecosystem. For instance, shallow lakes can have a pronounced hysteresis in response to nutrient

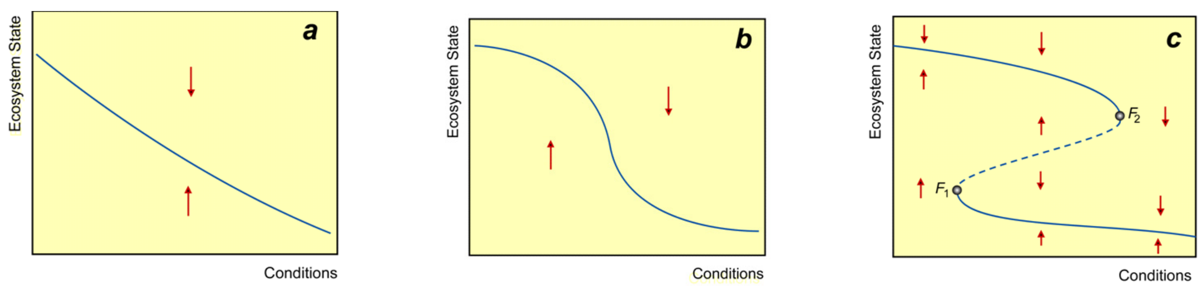

Figure 1. Schematic representation of possible ways in which ecosystem equilibrium states can vary with conditions such as nutrient loading, exploitation or temperature rise. In panels a and b only one equilibrium exists for each condition. However, if the equilibrium curve is folded backwards (panel c) three equilibria can exist for a given condition. It can be seen from the arrows indicating the direction of change, that in this case equilibria on the dashed middle section are unstable and represent the border between the basins of attraction of the two alternative stable states on the upper and lower branches. Modified from Scheffer *et al*. (2000).

loading, whereas deeper lakes may react smoothly (Carpenter *et al*., 1999). A range of mathematical models of specific ecological systems with alternative stable states has been published.

Effects of stochastic events

In the real world conditions are never constant. Stochastic events such as weather extremes, fires or pest outbreaks can cause fluctuations in the conditioning factors (horizontal axis) but often affect the state (vertical axis) directly, for instance by wiping out parts of populations. If there is only one basin of attraction, the system will settle back to essentially the same state after such events. However, if there are alternative stable states, a sufficiently severe perturbation of the ecosystem state may bring the system into the basin of attraction of another state. Obviously, the likelihood of this to happen depends not only on the perturbation, but also on the size of the attraction basin. In terms of stability landscapes, if a valley is small, a small perturbation may be enough to displace the ball far enough to push it over the hill top resulting in a shift to the alternative stable state. Following Holling (1973) we use the term '*resilience*' here to refer to the size of the valley or 'basin of attraction' around a state which corresponds to the maximum perturbation that can be taken without causing a shift to an alternative stable state.

In systems with multiple stable states, gradually changing conditions may have little effect on the state of the ecosystem, but nevertheless reduce the size of the attraction basin. This loss of resilience makes the system more fragile in the sense that it can be easily tipped into a contrasting state by stochastic events. Such stochastic fluctuations may often be externally driven. However, they can also result from internal systems dynamics. The latter can happen if the alternative attractors are *cycles* or *strange attractors* rather than equilibria. On a strange attractor, a system fluctuates chaotically, even in the absence of an external stochastic forcing. These fluctuations can lead to a collision with the boundary of the basin of attraction, and consequently induce a switch to an alternative state. Models indicate that such 'non-local bifurcations' (Kuznetsov, 1995) or 'basin boundary collisions' (Vandermeer and Yodzis, 1999) may occur in ocean-climate systems (Rahmstorf, 1995) as well as various ecosystems (Rinaldi and Scheffer, 2000). In practice, it will often be a blend of internal processes and external forcing that generates fluctuations (Ellner and Turchin, 1995) which can induce a state shift by bringing systems with reduced resilience over the boundary of an attraction basin. Obviously, in view of these permanent fluctuations, the term 'stable state' is hardly appropriate for any ecosystem. Nonetheless, for the sake of clarity, we use 'state' rather than the more correct term 'dynamic regime'.

Emerging patterns

Case studies on various ecosystems, such as lakes, coral reefs, woodlands, deserts and oceans all suggest shifts between alternative stable states (Scheffer *et al*., 2001). Nonetheless, proof of multiplicity of stable states is usually far from trivial. Observation of a large shift per se is not sufficient, as systems may also respond in a non-linear way to gradual change if they have no alternative stable states (Scheffer, 1998). Also, the power of statistical methods to infer the underlying system properties from noisy time series is poor (Carpenter and Pace, 1997; Ives and Jansen, 1998; Carpenter, 2001). On the other hand, mere demonstration of a positive feedback mechanism is also insufficient as a proof of alternative stable states, as it leaves a

Table 1. Characteristics of some major ecosystem state shifts and their causes.

	State I	***State II***	***Events inducing shift from I to II***	***Events inducing shift from II to I***	***Suggested main cause of hysteresis***	***Factors affecting resilience***
Lakes[1]	Clear with submerged vegetation	Turbid with phyto-plankton	Herbicide plant kill Pesticide *Daphnia* kill High water level	Fish kill Low water level	Positive feedback in plant growth Trophic feedbacks	Nutrient accumu-lation
Coral reefs[2]	Corals	Fleshy brown macro algae	Hurricane Coral kill Pathogen Sea-urchin kill	unknown	Unpalatable adult algae prevent coral recoloni-zation	Nutrient accumu-lation Climate change Fishery
Woodlands[3]	Herbaceous vegetation	Woodlands	Fires Tree cutting	Pathogen grazer kill Hunting grazers	Positive feedback in plant growth Inedible adult trees	Over-grazing Climate change
Deserts[4]	Perennial vegetation	Bare soil with ephemeral plants	Climatic events Overgrazing by cattle	Climatic events	Positive feedback in plant growth	Climate change
Oceans[5]	various	various	Climatic events	Climatic events	physical	Fishery Climate change

[1]Carpenter *et al*. (1999); Scheffer *et al*. (1997); [2]Done (1991); Knowlton (1992); McCook (1999); [3]Walker (1989); Dublin *et al*. (1990); [4]Hoelzmann *et al*. (1998); Jolly *et al*. (1998); [5]Hare and Mantua (2000)

range of possibilities between pronounced hysteresis and smooth response, depending on the strength of the feedback and other factors (Scheffer, 1998). Indeed, the strongest cases for the existence of alternative stable states are based on combinations of approaches, such as observations of repeated shifts, studies of feedback mechanisms that tend to maintain the different states, and models showing that these mechanisms can plausibly explain field data.

Although the specific details of the reviewed state shifts differ widely, an overview (Table 1) shows some consistent patterns: (1) The contrast among states in ecosystems is usually due to a shift in dominance among organisms with different life forms. (2) State shifts are usually triggered by obvious stochastic events such as pathogen outbreaks, fires or climatic extremes. (3) Feedbacks that stabilize different states involve both biological and physical-chemical mechanisms.

Perhaps most importantly, all models of ecosystems with alternative stable states indicate that gradual change in environmental conditions such as human-induced eutrophication and global warming may have little apparent effect on the state of these systems, but still alter the *stability domain* or *resilience* of the current state and hence the likelihood that a shift to an alternative state occurs in response to natural or human-induced fluctuations.

Implications for management

Ecosystem state shifts can cause large losses of ecological and economic resources, and restoring a desired state may require drastic and expensive intervention (Maler, 2000). Thus, neglect of the possibility of shifts to alternative stable states in ecosystems may have heavy costs to society. Due to hysteresis in their response and the invisibility of resilience itself, these systems typically lack early warning signals of massive change. Therefore, attention tends to focus on precipitating events rather than on the underlying loss of resilience. For example, gradual changes in the agricultural watershed increased the vulnerability of Lake Apopka (Florida, USA) to eutrophication, but a hurricane wiped out aquatic plants in 1947 and probably triggered the collapse of water quality (Schelske and Brezonik, 1992); gradual increase in nutrient inputs and fishing pressure created the potential for algae to overgrow Caribbean corals, but overgrowth was triggered by a conspicuous sea urchin disease outbreak that released algae from grazer control (Nystrom *et al*., 2000); and a gradual increase in grazing decreases the capacity of Australian rangelands to carry the fires that normally control shrubs, but extreme wet years trigger the actual shift to shrub dominance (Walker, 1993; Tongway and Ludwig, 1997).

Not surprisingly, prevention of perturbations is often a major goal of ecosystem management. This is unfortunate, not only because disturbance is a natural component of ecosystems which promotes diversity and renewal processes (Holling and Meffe, 1996; Paine *et al*., 1998), but also because it distracts attention from the underlying structural problem of resilience. Indeed, the main implication of the insights presented here is that efforts to reduce the risk of unwanted state shifts should address the gradual changes that affect resilience rather than merely control disturbance. The challenge is to sustain a large stability domain rather than to control fluctuations. Stability domains typically depend on slowly-changing variables such as land use, nutrient stocks, soil properties and biomass of long-lived organisms. These factors may be predicted, monitored and modified. In contrast, stochastic events that trigger state shifts (such as hurricanes, droughts or disease outbreaks) are usually difficult to predict or control. Therefore, building and maintaining resilience of desired ecosystem states is likely be the most pragmatic and effective way to manage ecosystems in the face of increasing environmental change.

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C.T. De Wit (1924-1993)

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Kees (Cornelis) De Wit grew up in a rural village in the eastern part of The Netherlands, and spent most of World War II as a farm laborer. This aroused his interest in the complexities of farming and in farmers and was to guide his professional career. He completed his studies after the war with a PhD thesis ('A physical theory on placement of fertilizers', 1953). His subsequent employment at the Ministry of National Planning of the Union of Birma laid the foundation for his strong commitment to agriculture in developing countries.

After his return in 1956, De Wit was employed at the Institute for Biological and Chemical Research on Field Crops and Herbage (IBS) and its successor, CABO (Centre for Agrobiological Research), and in the next decade produced some of his most influential papers: 'Transpiration and crop yields' (1958), a major re-interpretation of crop water use data, based on a physical analysis of canopy processes; 'On competition' (1960), describing in physical and mathematical terms the interactions between plants of different species; 'Ionic balance and growth of plants' (1963), elaborating on the chemical composition of plants and the crucial role of anion/cation balances; 'Photosynthesis of leaf canopies' (1965), introducing the brute force of the computer in crop physiology; and 'A dynamic model of the vegetative growth of crops' (1971), the first publication on crop growth simulation. These publications are still widely quoted and constitute significant steps in the progress in agricultural science.

De Wit was appointed professor at Wageningen Agricultural University in 1968 to create the Department of Theoretical Production Ecology. Through its research and teaching (De Wit (co-)supervised 32 PhD theses), under his strong leadership, systems analysis and modelling gained a firm footing in the agricultural research community. 'No simulation without experimentation', and later also the reverse, were among his most vivid expressions, always presented with characteristic conviction. He was the initiator of the series 'Simulation Monographs' (Publisher Pudoc, Wageningen) that in the 1970s and 1980s formed the major outlet for publication of models of agricultural production systems.

In the eighties, as member of the Dutch Scientific Council for Government Policy (WRR) and the Technical Advisory Committee (TAC) of the CGIAR, De Wit either initiated or took a very active part in discussions on environment, sustainability and development. For him, these appointments were challenges to combine biophysical and social sciences at a scientific and at operational level. His continuing innovative efforts yielded a critical review of the consequences of the Common Agricultural Policy of the European Union (1988), a new approach to multi-stakeholder planning of land use and agricultural development (1988), an unconventional view on ‘Resource use efficiency in agriculture’ (1992) and an innovative transparent methodology for priority setting in international research (1992).

De Wit’s scientific qualities, his keen interest in human beings, deep feelings of justice and equality, his informality and his very original, sharp and systematic mind made him welcome, unavoidable and outstanding in any meeting. He received the Wolf price of the State of Israel, the ‘Nobel Price for Agriculture’, in 1983/4.
His approach to science has formed the starting point for many of the recent developments in the international science community, both within and outside agriculture.

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