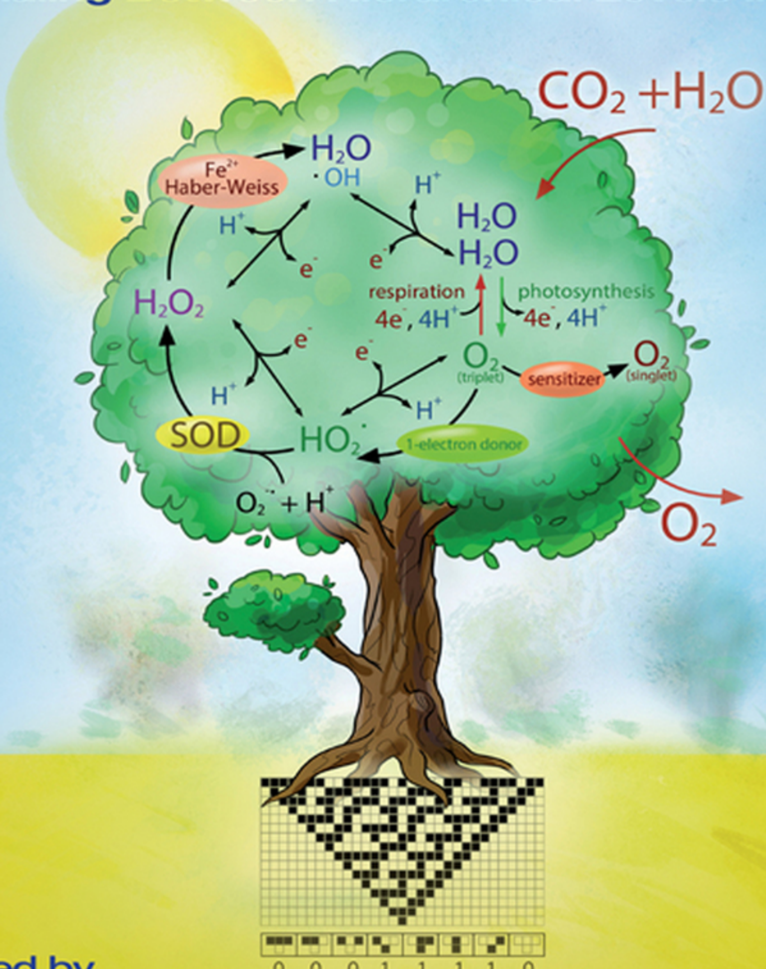
REACTIVE OXYGEN SPECIES

Signaling Between Hierarchical Levels In Plants



Edited by
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Scrivener Publishing

WILEY

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This edition first published 2017 by John Wiley & Sons, Inc., 111 River Street, Hoboken, NJ 07030, USA and Scrivener Publishing LLC, 100 Cummings Center, Suite 541J, Beverly, MA 01915, USA

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Wiley Global Headquarters
111 River Street, Hoboken, NJ 07030, USA

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Library of Congress Cataloging-in-Publication Data
ISBN 978-1-119-18488-1

Cover image courtesy of Suleyman I. Allakhverdiev
Cover design by: Kris Hackerott

Set in size of 11pt and Minion Pro by Exeter Premedia Services Private Ltd., Chennai, India

Printed in the USA

10 9 8 7 6 5 4 3 2 1

Contents

Abstract

Reactive oxygen species (ROS) play different roles in oxidative degradation and signal transduction in photosynthetic organisms. This book introduces basic principles of light-matter interaction, photophysics and photosynthesis to elucidate complex signaling networks that enable spatiotemporally directed macroscopic processes. Reaction schemes are presented for the formation and monitoring of ROS and their participation in stress signal transduction pathways within prokaryotic cyanobacteria as well as from chloroplasts to the nuclear genome in plants. Redoxregulated systems, mitogen-activated protein kinase cascades and transcription factor networks play a key role in ROS-dependent signaling systems in plant cells and for their spatiotemporal morphology and lifespan. ROS are understood as bottom up messengers and as targets of top down communication in plants. The role of the chemical environment in introducing genetic diversity as a prerequisite for efficient adaption is elucidated. Finally, it is suggested how the presented concepts can be used to describe other biological principles and multiscale hierarchical systems in society, politics and economics.

We hope that this book will be an invaluable reference source for university and research institute libraries, as well as for individual research groups and scientists working in the fields. It will be helpful not only for photo–biophysicists, biochemists, and plant physiologists, but also for a wider group of physicists and biologists. Lastly, and most importantly, it will serve to educate undergraduate, graduate and post-graduate students around the world.

Foreword 1

This book introduces basic principles of light-matter interaction, photophysics and photosynthesis in a brief manner in order to elucidate complex signaling networks that enable spatiotemporally directed macroscopic processes. The roles of reactive oxygen species (ROS) are explained both as bottom up messengers and as targets of top down communication. Starting with Hermann Haken's Principles of Synergetics, the role of ROS is investigated in order to explain emergent phenomena that occur during light-driven chemical reactions. Rate equations are used to describe energy transfer processes in photosynthesis, nonlinear phenomena that fill up energy reservoirs, and drive forces that are able to control macroscopic dynamics. The second chapter describes the basic principles of the light reaction in photosynthesis from light absorption to the storage of free Gibbs energy in the form of energy rich chemical compounds. The roles of different processes that support light energy transduction, on the one hand, and non-photochemical quenching, on the other hand, are elucidated with special focus on the context of a highly adapted system that has developed as an advanced structure for energy conversion during evolution in its local environment. Rate equations are not only used to understand optical transitions, excitation energy and electron transfer processes, and chemical reactions but are used to much more generally describe information processing in complex networks.

In the third and fourth chapters, the messenger role of ROS is described including formation, decay, monitoring and functional role of ROS – mainly H_2O_2, $^1O_2$, $O^{\bullet}{}_2^{-}$ – in both oxidative degradation and signal transduction during exposure of oxygen-evolving photosynthetic organisms to oxidative stress. These chapters focus on phenomena and mechanisms of ROS signaling. Reaction schemes are presented for the for mation and monitoring of ROS and their participation in stress signal transduction pathways, both within prokaryotic cyanobacteria as well as from chloroplasts to the nuclear genome in plants. It is suggested that redox-regulated systems, mitogen-activated protein kinase cascades, and transcription factor networks play a key role in the ROS-dependent signaling systems in plant cells and for their spatiotemporal morphology and lifespan.

Vladimir A. Shuvalov,
Academician (Russia)

Foreword 2

Reactive oxygen species (ROS) play different roles in oxidative degradation and signal transduction in photosynthetic organisms. Since modern microscopic, genetic, and chemical techniques for ROS detection and controlled generation have improved significantly in recent years, our knowledge of the complex interaction patterns of ROS has significantly increased. This book introduces basic principles of light-matter interaction, photophysics and photosynthesis in a brief manner in order to generally elucidate complex signaling networks that enable spatiotemporally directed macroscopic processes. ROS are understood as bottom up messengers and as targets of top down communication. Reaction schemes are presented for the formation and monitoring of ROS and their participation in stress signal transduction pathways, both within prokaryotic cyanobacteria as well as from chloroplasts to the nuclear genome in plants. It is suggested that redox-regulated systems, mitogen-activated protein kinase cascades, and transcription factor networks play a key role in the ROS-dependent signaling systems in plant cells and for their spatiotemporal morphology and lifespan.

Rate equations are used to explain the dynamics of excitation energy and electron transfer during light-driven reactions. Energy transfer processes and subsequent chemical reactions in photosynthesis are nonlinearly coupled. They fill up energy reservoirs and drive forces able to control macroscopic dynamics.

Photosynthetic organisms (as all organisms) represent highly adapted systems that have developed advanced structures for energy conversion during evolution in their local environment. Basic principles of evolution as the continuous adaption to environmental constraints are derived from considerations based on state transitions as basic theory and ROS as an example for a chemical reaction partner that contributes to selection and mutation. It will be shown that the structure of the environment mainly allows for genetic diversity as a prerequisite for efficient adaption and that mutations are of minor relevance in that context.

Finally, it is suggested how the presented concepts can be used to describe other biological principles and multiscale hierarchical systems in society, politics and economics.

This book is intended for a broad range of researchers and students, and all who are interested in learning more about the most important global process on our planet – the process of photosynthesis.

Tatsuya Tomo,
Professor (Japan)

Preface

To my family and my friends
Franz-Josef Schmitt

To my mother, my wife and my son
Suleyman I. Allakhverdiev

This book introduces basic principles of light-matter interaction, photophysics, and photosynthesis in a brief manner in order to elucidate principles of complex signaling networks that enable spatiotemporally directed macroscopic processes. We will start with random walk processes typically used to describe excitation energy transfer in plant lightharvesting complexes and later focus on coupled systems such as the communication network of reactive oxygen species (ROS) which are embedded into the plant metabolism and enable an information transfer from molecules to the overall organism as a bottom up process. In addition the microscale dynamics always accepts signals on the bottom level that can be understood as a top down communication. One example is the activation of genes by ROS caused by macroscopic events like strong sunlight or atmospheric variations that activate a change in composition of the microscopic environment by producing new proteins.

Typical bottom up processes are cascades that start with gene activation and protein translation regulating plant growth and morphology. Top down messengers triggered by macroscopic actuators like sunlight, gravity, environment or any forms of stress, on the other hand, activate gene regulation on the molecular level and therefore concern the dynamics of single molecules under the constraints of macroscopic factors. In this book the generation and monitoring as well as the role of ROS in photosynthetic organisms as typical messengers in complex networks are primarily treated in a scientific manner. All findings are supported by our own research results and recent publications. Additionally, the principles of top down and bottom up messaging are presented in the form of a philosophical discussion.

The first chapter focuses on a theoretical approach according to the Principle of Synergetics (Haken, 1990) to understand coupling, networks, and emergence of unpredictable phenomena. The approach is used to model light absorption, electron transfer and membrane dynamics in plants. Special focus will be placed on nonlinear processes that form the basic principle for the accumulation of energy reservoirs and on the formation of forces that are able to control the dynamics of macroscopic devices.

The formalism of rate equations is presented as a general scheme to formulate dynamical equations for arbitrarily complex systems. Key is the definition of "states" as an intensity level or a pattern that carries a certain amount of information, and their dynamics which are assessed by evaluating the probability of transfer from one state to another. In fact, rate equations are not only used to describe energy transfer processes in photosynthesis but in many systems, for instance, optical transitions, particle reactions, complex chemical reactions and more general information processing in complex networks. Rate equations are also used to describe complex systems such as sociological networks.

The second chapter describes the basic principles of the light reaction in photosynthesis from absorption to the storage of free Gibbs energy in the form of energy rich chemical compounds. The roles of different processes that support light energy transduction, on the one hand, and non-photochemical quenching, on the other hand, are elucidated with special focus on the context of a highly adapted system that has developed as an advanced structure for energy conversion during evolution in its local environment.

In the third chapter the formation, decay, monitoring, and the functional role of ROS – mainly H_2O_2, $^1O_2$, $O^{\bullet}{}_2^-$ are described and the fourth chapter especially focuses on the messenger role of ROS. The ambivalent picture of oxidative degradation and signal transduction during exposure of oxygen-evolving, photosynthetic organisms to oxidative stress isteluci-dated. Both degradation and activation are important mechanisms of ROS signaling. Reaction schemes are presented for the formation and monitoring of ROS and their participation in stress signal transduction pathways both within prokaryotic cyanobacteria as well as from chloroplasts to the nuclear genome in plants. It is suggested that redoxregulated systems, mitogen-activated protein kinase cascades and transcription factor networks play a key role in the ROS-dependent signaling systems in plant cells and for their spatiotemporal morphology and lifespan.

Chapter five focuses on evolution. It is emphasized that mainly the local environment of evolving organisms enforces directed evolution resulting in quick changes of the phenotype if the genetic diversity of the organisms is large enough. In that sense leaps in evolution necessarily follow volatile changes of the environment. It might be possible that ROS are the most important driving forces in evolution.

The last chapter finally offers a glance at how the described concepts can be used to describe other biological principles and multiscale hierarchical systems in society, politics and economics. The book is intended for a broad range of researchers and students, and everyone who is interested in learning about the most important global process on our planet – the process of photosynthesis. We would like to believe that this book will stimulate future researchers of photosynthesis and lead to progress in our understanding of the mechanisms of photosynthesis and their practical use in biotechnology and in human life.

We express our sincere gratitude to the two referees: the Academician of the Russian Academy of Sciences (RAS) Prof. V.A. Shuvalov and Prof. T. Tomo of Tokyo University of Science, Tokyo, Japan. We are extremely grateful to Corresponding Member of RAS Vl.V. Kuznetsov, Corresponding Member of RAS A.B. Rubin, and Professors D.A. Los, A.M. Nosov, V.Z. Paschenko, A.N. Tikhonov, G.V. Maksimov, V.V. Klimov, A.A. Tsygankov, and Drs. V.D. Kreslavski, S.K. Zharmukhamedov, I.R. Fomina, J. Karakeyan for their permanent help and fruitful advice. We are also indebted to Professors T. Friedrich, N. Budisa, P. Hildebrandt, L. Kroh, H.J. Eichler, Drs. M. Vitali, V. Tejwani, C. Junghans, N. Tavraz, J. Laufer, and J. Märk from TU Berlin and Drs. E.G. Maksimov and N. Belyaeva from Moscow State University, Prof. J. Pieper from University of Tartu, Prof. H. Paulsen from Johannes Gutenberg-Universität Mainz, Prof. F. Zappa and Dr. D. Bronzi from Politecnico di Milano, and Prof. R. Rigler, Drs. J. Jarvet, and V. Vukojević from the Karolinska Institute in Stockholm.

We express our deepest gratitude to Russian Science Foundation (№ 14-04-00039) and the German Research Foundation DFG (cluster of excellence “Unifying Concepts in Catalysis”) and the Federal Ministry of Education and Research for funding bilateral cooperation between Germany and Russia (RUS 10/026 and 11/014). We acknowledge COST for financial support in the framework of COST action MP1205. We thank F. Schmitt for preparing Figs. 4, 5, 7, 10, 11, 18, 27A, 50, 51, 71, 75, 79 and 80. Further gratitude belongs to M. Nabugodi and J.M. Zinn for proofreading of the manuscript. F.-J. Schmitt especially thanks Joachim Herz

Stiftung and Stifterverband für die Deutsche Wissenschaft for the fellowship IGT-educationTUB.

We are grateful to **Scrivener Publishing**, **Wiley and Izhevsk Institute of Computer Sciences** for their cooperation in producing this book.

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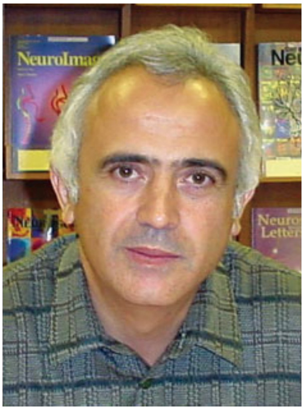

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1
Multiscale Hierarchical Processes

Träumen wir uns für einen Moment in einen zukünftigen Zustand der Naturwissenschaft, in dem die Biologie ebenso vollständig mit Physik und Chemie verschmolzen sein wird, wie in der heutigen Quantenmechanik Physik und Chemie miteinander verschmolzen sind. Glaubst du, dass die Naturgesetze in dieser gesamten Wissenschaft dann einfach die Gesetze der Quantenmechanik sein werden, denen man noch biologische Begriffe zugeordnet hat, so wie man den Gesetzen der Newtonschen Mechanik noch statistische Begriffe wie Temperatur und Entropie zuordnen kann; oder meinst du, in dieser einheitlichen Naturwissenschaft gelten dann umfassendere Naturgesetze, von denen aus die Quantenmechanik nur als ein spezieller Grenzfall erscheint, so wie die Newtonsche Mechanik als Grenzfall der Quantenmechanik betrachtet werden kann ?

Werner Heisenberg (1901–1976),
Deutscher Physiker (Heisenberg, 1986)

Multiscale hierarchical processes are understood as information transduction in networks which are hierarchically structured. The most simple assumption might be a house which is structured into rooms, rooms are structured into furnishings but also people that move from one room to another. Of course cupboards and chairs, computers and TVs as well as human beings are hierarchically structured in a somehow comparable way. We would call our house a hierarchically structured system. If information flows from one room to another – and everyone would agree that this is the case when people live in that house and move objects or direct information – we can speak about hierarchical processes. These processes might comprise the information conveyed by the parents that the food is prepared which leads to a movement of the children towards the kitchen and the covering of the table by dishes, not to mention all the processes that are correlated with eating and enjoying the wonderful meal.

If we agree that the type of hierarchical structure might additionally vary if elucidated from different aspects we speak about multiscale hierarchical processes. Such different aspects can be aspects of spatial organization as it is the case in our example, the house. But in addition also other, for example temporal, organization principles are possible. To summarize all these organization principles we generalize the hierarchical systems to multiscale hierarchical systems housing the dynamics of multiscale hierarchical processes.

Living systems are always spatially hierarchically organized: in this case molecules are the basic entities that form genes and proteins as an intermediate structure on a mesoscale. The proteins aggregate in a quaternary structure to form higher ordered systems that do not necessarily need to be stable in time. The network of interacting proteins is in its turn forming a metastructure that can be understood as a network formed from single proteins. However, also on the temporal scale multiscale hierarchical processes arise. For example, a reaction scheme may represent the dynamics of the chemical reaction of two compounds on the temporal microscale. However, if a certain threshold of concentration of its output is present, another chemical reaction may start and is therefore triggered by the first reaction scheme. Long-term effects like the active movement of our extremities, circadian rhythms, the growth of an organism and senescence are typical examples of processes that change their appearance over time and are therefore a hierarchical metastructure that arises on the network of microscale processes.

1.1 Coupled Systems, Hierarchy and Emergence

Naturally, coupled systems are generally nonlinear. That is always the case if two compounds form a special reaction pathway that is not possible if only a single compound is present. If two molecules of two different compounds interact, then the reaction is bilinear or bimolecular, which is a nonlinearity. If two molecules (or two photons) of the same kind are able to reach a state that is not accessible by a single molecule (or photon) then the outcome is typically in a nonlinear dependence on the input. One prominent example of nonlinear optics in physics is the two photon absorption where the absorbing state is reached by interaction of two photons with the ground state within a certain time interval. If the photon density is too low for that to happen then the output is zero, but when the photon density increases the probability for the two photon absorption increases with the square of the photon density. Therefore two (or more) photons are needed to activate a state transition. Only spontaneous population and depopulation of certain states, which is not the typical situation for characteristic biochemical reactions, are truly linear. If several molecules of one or several compounds have to interact within a certain time interval, then the reaction scheme is nonlinear and characterized by the typical mathematical problems and challenges of nonlinear systems.

Photosynthesis is a truly nonlinear reaction as at least eight photons have to be absorbed by two different photosystems to split two molecules of water and release one molecule of oxygen. Photon absorption drives an electron transfer in photosynthesis. However, the involved molecules are reduced and/or oxidized by more than one electron and the coupled proton transfer again forms ATP from ADP and phosphate in a nonlinear process. Biochemistry is truly a hierarchy of nonlinear processes.

The "cycles" of nonlinearities that form the overall, hierarchical structure also include loss processes. After photon absorption excitation-energy can be lost and the following electron transfer processes are likewise restricted by loss processes that limit the production of one molecule of oxygen with a demand of at least 11–12 photons. Other sources report 60 photons per molecule glucose (Häder, 1999; Campbell and Reece, 2009) which would equal 10 photons per molecule glucose according to the basic equation of photosynthesis understood as the light-induced chemical reaction of water with carbon dioxide to glucose:

$$12\,H_2O + 6\,CO_2 \xrightarrow{h\cdot\nu} C_6H_{12}O_6 + 6\,O_2 + 6\,H_2O \qquad \textbf{chemical equation 1}$$

The energetic stoichiometry of light and dark reactions in photosynthesis are again discussed in chap. 4.4.1 as well as in the literature (Häder, 1999). This also features discussions of coupled reaction schemes like the proton assisted electron transfer (Renger, 2008, 2012; Renger and Ludwig, 2011). This question shall therefore not be discussed here in more detail. The basic principles of the photosynthetic light reaction are presented in chapter two.

Here we primarily intend to elucidate the highly nonlinear character of photosynthesis. Indeed, the nonlinearity of photosynthesis goes far beyond this discussion. If one regards the hierarchy of the spatiotemporal order of a plant as an overall reaction system, one could ask how many photons are involved in the construction of a new leaf. Analyzing the biomass of a dried leaf, which is strongly dependent on the organism, we might look at, say, 100 mg and find that the fixation of an order of 10^{21} carbon molecules was necessary with a corresponding nonlinear response of a new “leaf” to more than 10^{22} absorbed photons. That means absorption of 10^{22} photons finally leads to the spontaneous appearance of a single “leaf”. Of course these photons have to be absorbed within a certain time interval. If illumination stays under a certain threshold, nothing happens, but if bright sunlight, sufficient day length and adequate temperature trigger the mechanisms correctly in spring, leaves might appear proportional to “packages” of 10^{22} absorbed photons. In this sense, the process might seem to be a linear response, but it is surely not and stops completely after a short growth period when new priorities like the production and storage of biomass take over in summer.

Even if we understand this reaction as a subsequent construction which can be analyzed step by step, it might still be a matter for discussion whether this reductionism leads to the loss of information and prevents our overall understanding of the growth of a plant (Heisenberg, 1986). After all, we have the appearance of one single leaf after the absorption of 10^{22} photons if we work as a pure phycisist who did not learn the details of biochemistry and does not know anything from gene activation and proteomics.

Our first identified nonlinear system (the water splitting and oxygen evolution) forms the trigger or the “input” for processes that are highly nonlinear themselves since they require several molecules of glucose, ATP or NADH to drive the production of one single further unit like for example a whole cell. We have a complicated spatiotemporal network of nonlinear systems that are coupled to nonlinear networks on the next hierarchically higher “level”. In this way, the complexity of the overall system, the plant, arises. However, if only bottom up processes from the molecular interaction on the single molecule level are taken into account, then reductionism will fail to explain the details of the plant’s morphology and lifespan.

Therefore it might still be wondered, like Heisenberg did in his book *Der Teil und das Ganze* (Heisenberg, 1986), whether we can expect that a possible picture of a plant as an organism understood in full detail will still use the language of physics or whether this picture will require that we formulate its propositions with novel approaches. Of course, taking the view of a physicist, the formalism that enables a scientist to understand an organism in detail and therefore enables the possibility to simulate the response of the system to a parameter change will be understood as a novel formalism. Therefore, Heisenberg's skepticism might not necessarily lead to the termination of actual scientific approaches. It is more likely that in the future science will overcome actual limitations as it has always done in the past: by inventing new approaches, new languages and more computational power. Current novel, highly-funded activities in the field of synthetic biology give rise to the hope that at least the composition of a single working cell from its basic chemical compounds will soon be possible.

Outputs of highly nonlinear reaction schemes function as substrate for highly nonlinear processes – on a hierarchic order of the scaling. In fact, interaction partners, cofactors, substrates, a series of several molecules or whole reaction networks, and even time can be a nonlinearity or a nonlinear scaling factor if there exists a feedback parameter that influences the dynamics in such way that it is no longer dependent on the substrate in a purely linear manner. Mathematical and physical representations of quite simple nonlinear systems show that the dynamics of such systems can change extremely if one parameter only changes slightly. This is called "chaotic behavior" or simply "chaos".

In contrast to the fact that nonlinear systems typically respond with chaotic behaviour, such coupled nonlinear structures can also be stable. Stability can arise from chaos. The chaotic behaviour of simple reaction schemes and the complexity that arises as well as the simplicity that arises from a complex pattern were topics in a broad series of literature that flourished 15–20 years ago (Gell-Mann, 1994; Cohen and Stewart, 1997; Wolfram, 2002). These excellent research books show how simple rules lead to complex structures and/or mathematically analyze chaos in deep detail using a scientific procedure.

At this point we might go a step backwards and focus on our initially introduced question how complex phenomena can arise from simple processes and how a hierarchical organization might deliver patterns with novel properties. It helps also to understand principles of self-similarity and macroscopic structuring arising from simple rules for single (chemical) reactions. Stephen Wolfram´s book *A New Kind of Science* deals with such an approach to motivate rise and decay of complex macroscopic patterns from simple rules on the microscale.

He works with so called "cellular automata" that define rules how to color a square in dependency of neighbouring squares. Programming such rules he found that the computer starts to draw interesting patterns and complex networks that arise even if the underlying rule is the most possible simple one working with black and white squares only.

Stephen Wolfram's underlying aproach is clearly bottom up. The concept of cellular automata explains complex patterns and their self-similarity by basic rules that the smallest entities in the concept have to follow. From the simple rule that determines in which color neighbouring squares on a white sheet of paper have to be imaged he can principally generate any desired pattern while discussing complexity, spatial and temporal hierarchies in the structures and the phenomenon of emergence.

Figure 1 is a computation of a simple rule, called "rule 30" by Wolfram with the commercial program Mathematica® also invented by Wolfram and distributed by Wolfram research. Wolfram has invented the concept of cellular automata that propose certain rules for the generation of binary two dimensional (or also more complicated) patterns of elementary cells only from the information content of neighbouring cells. Some selected rules as published in (Wolfram, 2002) are shown in Figure 2.

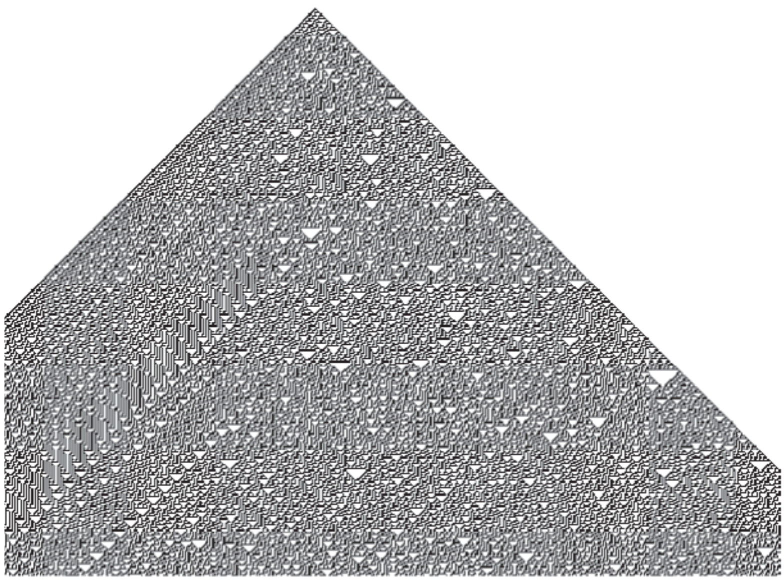

Figure 1. Mathematica® simulation according to "rule 30" (see Wolfram, 2002 and Figure 2) with 400 lines/iteration cycles. The image is cut asymmetrically at the left and right side.

Cellular automata generate patterns starting with a single black elementary cell in the middle of the first line on a white sheet of paper. The rule delivers the information how the neighbouring elementary cells in the next line have to be colored. The output of the rules indicated in

Figure 2 is shown in Figure 3. Some of these rules generate quite boring patterns like rule 222 which forms a black pyramid and rule 250 forming a chess board pattern (see Figure 2 and Figure 3). However, there exist rules that generate complicated patterns with typical properties of self-similarity. For example rule 30 (see Figure 1, Figure 2 and Figure 3) iteratively generates white triangles standing on the top with varying size (albeit with a limited size distribution).

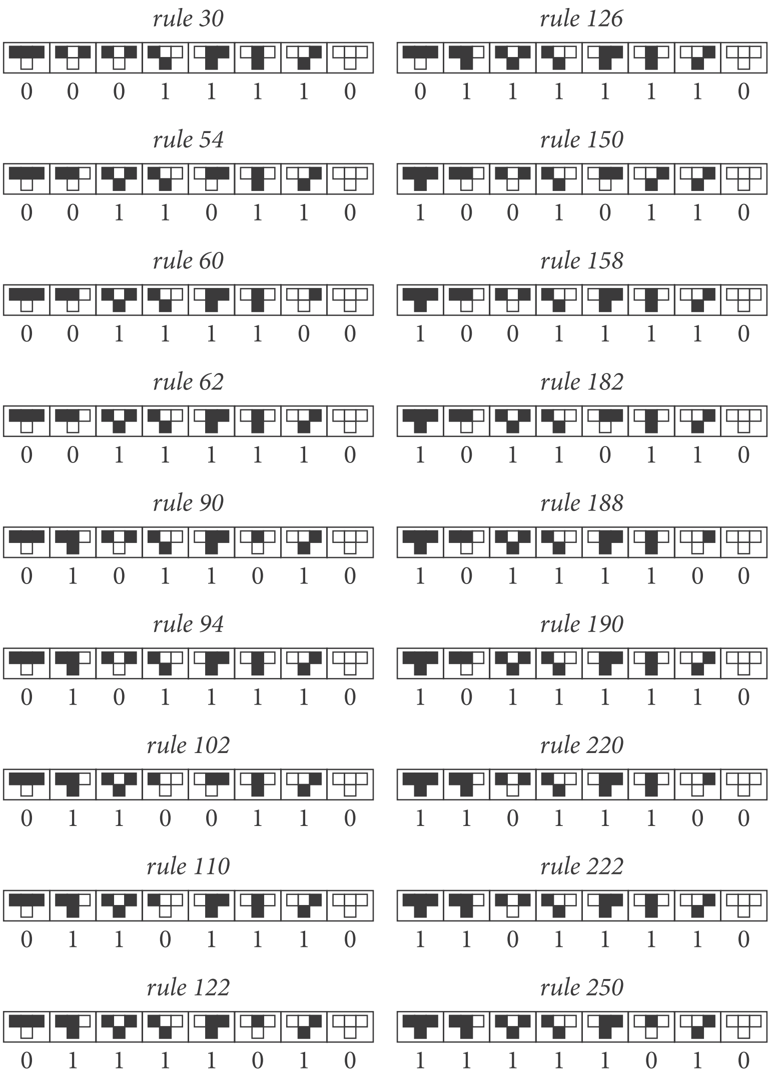

Figure 2. Typical rules for cellular automata according to Wolfram (Wolfram, 2002). Image reproduced with permission.