A SPECTRUM OF ECOLOGICAL STUDIES

# 生态学文集

## 贺钟章成教授80华诞

In honour of Professor Zhong Zhangcheng at his 80th birthday


主编
Editors-in-chief

董鸣 Dong Ming

维尔格 M. J. A. Werger



西南师範大學出版社
SOUTHWEST CHINA NORMAL UNIVERSITY PRESS

A SPECTRUM OF ECOLOGICAL STUDIES

# 生态学文集

## 贺钟章成教授80华诞

In honour of Professor Zhong Zhangcheng at his 80th birthday


主 编

Editors-in-chief

董 鸣 维尔格

Dong Ming M. J. A. Werger



西南師範大學出版社

SOUTHWEST CHINA NORMAL UNIVERSITY PRESS

**图书在版编目(CIP)数据**

生态学文集/董鸣主编.—重庆:西南师范大学出版社,2009.9
ISBN 978-7-5621-2850-2

Ⅰ.生… Ⅱ.董… Ⅲ.生态学—文集
Ⅳ.Q14-53

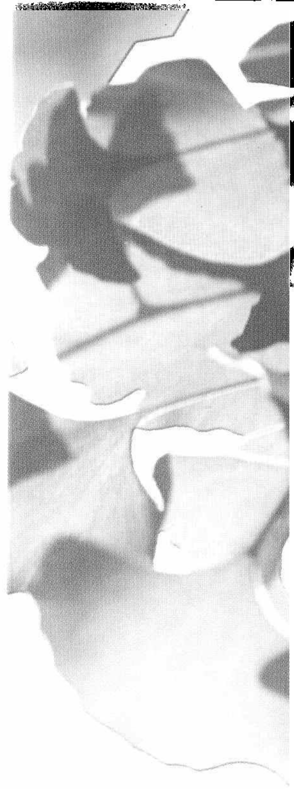
中国版本图书馆 CIP 数据核字(2009)第 140711 号

**生态学文集**

主　　编:董　鸣　M. J. A. Werger
责任编辑:杜珍辉
封面设计:戴永羲
出版发行:西南师范大学出版社
　　　　(重庆·北碚　邮编 400715)
网　　址:www.xscbs.com
经　　销:新华书店
印　　刷:四川外语学院印刷厂

开　　本:889mm×1194mm　1/16
印　　张:22.125
字　　数:750 千字
版　　次:2009 年 10 月第 1 版
印　　次:2009 年 10 月第 1 次印刷
书　　号:ISBN 978-7-5621-2850-2

**定价:58.00 元**



钟章成教授长期担任本科生、硕士生和博士生的教学工作。从1979年开始招收硕士生，至今已有20届52名（其中荷兰硕士生1届2名）。1990年至今招收博士生17届22名（其中荷兰博士生3届3名），荷兰博士后1名。其学生中已有26人提升为教授或研究员，25人提升为副教授，10人担任博士生导师，并有高校（含厅局级）正副校级干部各2人，杰出青年基金获得者1人。55年来从事生态学和植物种群生态学的研究，独编或主编专著9余部，主要有《植物生态学研究进展》、《常绿阔叶林生态学研究》、《常绿阔叶林生态系统研究》、《植物种群生态适应机理研究》、《三峡库区消落带生物多样性与图谱》、《中华人民共和国植被图》（常务编委）、《自然环境保护概论》、联合主编《植物生态学》教材1部等。在国内外著名学术刊物独立或合作发表论文200余篇。专著《常绿阔叶林生态学研究》1989年获四川省科技进步二等奖，并获国家教委自然科学专著优秀奖。《常绿阔叶林生态系统研究》于1994年获国家教委科技进步三等奖。《植物生态学研究进展》于2001年获中国高校科学技术二等奖。《植物种群生态适应机理研究》于2003年获教育部国家自然科学推荐二等奖。《自然环境保护概论》专著1988年获四川省环保科技一等

奖。《中国植被》获国家自然科学二等奖（参编）。自1985年以来先后主持国家自然科学基金重点项目《植物种群生态适应机理研究》，国家自然科学基金项目：《亚热带常绿阔叶林乔木配置的生理生态研究》、《攀援植物行为生态学研究》、《植物种群在重庆石灰岩地区植被恢复中的功能作用》，国家教育部重点科学技术项目《四川亚热带常绿阔叶林生态系统研究》和《木本药用植物拟种群理论与生物技术开发研究》。还主持国际合作项目荷兰WOTRO基金《毛竹生态学研究》和《中国乔木树种修枝—生长和分配》，国务院三峡办《三峡库区消落区生态环境问题—生物多样性研究》和《重庆石漠化地区植物种群动力学原理》等17个主要科研项目。

鉴于在教学和科研上的贡献，他于1991年获得首批国务院政府特殊津贴，同年获四川省优秀研究生导师称号，1993年获曾宪梓教育基金会高等师范院校教师二等奖，1996年获香港柏宁顿（中国）教育基金会第二届孺子牛金球奖荣誉奖，1997年获重庆市首届科技先进工作者称号，2000年10月获荷兰乌德勒支大学国际勋章，2000年被推荐为中国科学院院士有效候选人。

# 前言

此书是专为祝贺钟章成教授80华诞的，绝大多数著者，与我一样，是钟章成教授的研究生。此书仍为包容性较大的“文集”类，不仅可有研究论文、综述和评述等科学研究惯常所用的文体，也可有杂感和心得等别样的文章，使得无论是否从事生态学研究工作的钟先生的弟子们和同事们都有机会参与进来。此书的另一主编是荷兰乌德勒支大学（Utrecht University，the Netherlands）教授维尔格博士（Prof. Dr. Marinus Werger）。我们曾共同主编了《生态学文集——贺钟章成教授70华诞》一书。维尔格教授是荷兰皇家科学院院士，国际著名的生态学家、与钟章成教授保持着近30年的长期合作，联合开展生态学研究和研究生培养，他们是老朋友、老伙伴。自1983年以来，他们在西南师范大学（即西南大学）和乌德勒支大学共同指导了多名中国籍和荷兰籍的研究生。维尔格教授也是1990年到1994年间我在荷兰攻读博士学位时的导师。

在1966年至1976的10年间，中国经历了那场史无前例的“文化大革命”。其间，中国的生态学发展，与其它学科门类一样，经历了长达10年的中断！文化大革命结束后，满目疮痍、百废待兴的中国迎来了“科学的春天”；1978年开启的划时代的“改革开放”，也开启了中国科技发展的大时代。这为包括生态学在内的科学的快速发展和走向世界提出了急切的要求，提供了绝佳的机遇，注入了强劲的推力。中国生态学学会于1979年11月宣告成立，生态学在中国开始加速发展。“十年文革”后幸存的科学家们，多数学成于“文革”前，其时他们已年逾中年或老年。面对着国内的10年学术停滞和国际的10年学术快速发展，他们在10年业务赋闲后，历史地担负起发展科学和培养人才的双重重担。他们为再造中国科技体系，尤其是再造中国科技队伍，做出了历史性贡献。

钟章成教授就是他们中杰出的一员！其时，钟先生已年近五旬，正值人生的巅峰年华，他远见卓识、锐意求索，他思维敏捷、作风踏实、思路开放，他精心组织科研、细心教书育人、悉心打造团队，他广泛而持续地开展国际国内合作，他待人热情、笃定、真诚。从钟先生1954年研究生毕业后执教于当时的西南师范学院算起，迄今，他教学和科研已达55年；从钟先生1979年招收第一届硕士研究生算起，迄今，他指导生态学研究生已整整30年。钟先生业已培养毕业20名博士和55名硕士，输送到不同的国家，服务在多个领域。

钟章成教授是我国植物生态学发展的早期推手之一。在半个多世纪的时间里，他和他的团队在植物种群生态学研究中、在西南地区植被生态、植被地理和植被制图研究中，在常绿阔叶林生态系统研究中，在污染防治与生态保育的研究中，在以“三峡库区”为主要对象的生态系统生态学研究中，在植物适应生态学和恢复生态学研究中，取得了一系列重要成果。

钟先生曾先后长期担任西南师范学院和后来的西南师范大学的生物系主任、西南

师范大学校长；曾先后长期担任四川省生态学会理事长、重庆（直辖）市生态学会理事长，曾先后担任中国生态学学会的理事、常务理事和副理事长。钟先生在耋耄之年仍担任中国生态学学会的顾问和种群生态学专业委员会主任，仍然活跃于科研和教学前线。这不，2009 年的 6 月 5 日～ 6 月 8 日，钟先生率 14 人之队，考察川西北山区的马脑壳金矿。他健步登临海拔 4000 多米的现场，实地研讨马脑壳金矿的矿山生态修复与生态保育的对策。我有幸随先生前往，时值我作为钟先生的硕士研究生毕业四分之一世纪之际，参与其中，再受师教，感触良多，获益丰厚！

本书收录了钟章成教授的研究生们和同事们的部分成果，以为读者提供生态学知识的方式，着意于对钟章成先生的礼赞。

礼赞钟先生培养研究生的 30 年！

礼赞钟先生教学科研的 55 年！

礼赞钟先生绚丽人生的 80 年！

同时，本书也礼赞与钟先生同时代的生态学前辈们所经历的大时代！

生态学思想古来有之，然而作为一门学科，生态学却是年轻的。生态学伴随着人类社会的发展而发展；人类在发展自己的同时，改变着自己所属的自然，自然的改变返回来又深刻地影响着人类发展。生态学正呈现出前所未有的繁荣，同时也面临着前所未有的挑战。严峻的挑战来源于生态学理论体系发展的自身要求，也来源于人类对环境、经济和社会可持续发展的急切需要。生态学界从未像现在这样深入地开展理论研究，更从未像现在这样注重实践，致力于诸如全球变暖、生物多样性丧失、生物入侵、环境破坏和资源锐减等人类共同面对的重大问题的解决。本书含两篇，共 44 篇文章。第一篇为生态学案例，包括 28 篇文章，涵盖分子生态学、生理生态学、个体生态学、种群生态学、群落生态学和生态系统生态学等各个层次上的基础研究和应用基础案例研究；第二部分为生态学综论，包括 16 篇文章，较广泛地综合论述了涉及到生态恢复/重建、生物入侵、生物多样性保育、污染的生态治理、生态规划与设计、环境管理和生态旅游等方面的研究进展和新的想法，也包括在与生态学交叉中发展事业的体验。美国南弗罗里达水域管理区（South Florida Water Management District）的缪世利博士为此书作跋，绵阳师范学院的苏智先博士为此书作后记，他们也都是钟先生早年的研究生。本书适宜于生态学及其相关专业的科研和技术人员、大专院校师生使用、阅读；对生态学的科学普及也有重要价值。

在编辑过程中，编委会成员齐心协力，高效工作，分工负责各章的同行评审，编辑小组在具体编辑工作付出了心血。借此机会向本书的所有著者、审者和编者表示衷心感谢！

在编辑过程中得到钟章成先生的悉心指导，特表深深的谢意和敬意！

董鸣

**中国科学院植物研究所**

**2009 年 6 月 15 日，北京香山**

# Preface

This book is for the celebration of the 80th birthday of Prof. Zhong Zhangcheng. Most authors of most chapters of this book, include myself, were directed by Prof. Zhong for their Master degree and /or PhD degree. This book not only collected academic research articles, reviews and overviews, but also essays and stories, providing all his students and colleagues with an opportunity to join in. Another editor-in-chief of this book is Prof. Dr. Marinus Werger, who is an ecologist at Utrecht University, the Netherlands and a member of Royal Netherlands Academy of Art and Sciences. Prof. Werger and Prof. Zhong are old friends and partners who have had a 30-year long cooperative relationship in ecological research and joint-directing of postgraduate students. In 1999, Marinus and I, as editors-in-chief, compiled the book *A Spectrum of Ecological Studies— in honour of Professor Zhong Zhangcheng* at his 70th birthday. Prof. Werger was also my supervisor/promoter during my study for my PhD degree at Utrecht University, the Netherlands from 1990 to 1994.

From 1966 to 1976, China experienced the unprecedented 'Cultural Revolution'. The development of ecology in China, like other disciplines of sciences, was interrupted for ten years. After the Culture Revolution, the country was devastated and it has come up with the "Spring of Science" and the "Reform and Opening" policy carried out in 1978 started a new era of development of sciences in China. This led to an urgent demand for high-speed development of sciences and technologies, including ecology, in China and for their linkage to the world, providing a great opportunity for changes and infusing strong vigor into the development. Ecological Society of China (ESC) established in November 1979 and ecology was developing rapidly in China. The scientists survived from the Culture Revolution all achieved high academic fame before it and as a decade passed, they are already in their middle-aged or elder. Facing the stagnation of the domestic academic research and the rapid development of sciences around the world, they, after leaving the research front for a decade, had to take the historic responsibility of both the development of sciences and the education of experts in their own research field. They greatly contributed to reconstruction of the whole Chinese scientific and technological system, in particular, to reconstruction of the academic research team.

And Prof. Zhong Zhangcheng is one of these outstanding scientists. At that time, Prof. Zhong was in his late 40s, the peak years of life, and he was farsighted, sagacious, open-minded and full of passion as well as putting great effort on research, teaching and research team building. He continued to carry out wide-ranging domestic and international academic cooperation and he was enthusiastic, determined and sincere. Prof. Zhong has taught and done academic research for more than 55 years since 1954 when he graduated, as a postgraduate and started working at Southwest China Normal College. Since Prof. Zhong's first postgraduate student enrolled in 1979, thirty years have passed, so far he has successfully directed 20 PhD students and 55 Master Students who are working in different countries in different professions.

Prof. Zhong is one of the pioneers in development of plant ecology in China. In more than half century, he and his team have achieved a series of important scientific results in the researches on plant population ecology, vegetation ecology, geography and mapping of vegetation of the southwest China, evergreen broadleaved forest ecosystems, prevention and cure of pollution, ecological conservation, ecosystem ecology of Three Gorges Reservoirs Region, plant adaptive ecology and restoration ecology.

Prof. Zhong has successively served as the dean of the biological department of Southwest China Normal University, the president of Southwest China Normal University, chairman of the Ecological Society of Sichuan, chairman of Ecological Society of Chongqing and member, executive member and vice chairman of ESC. Now in his 80s, he still act actively both in research and teaching frontier as well as undertaking the consultancy of ESC and serving as the director of the plant population ecology section of ESC. From June 5～8, 2009, he has led a team of 14 people investigating the Horse Head gold mine located in the northwest part of Sichuan Province. He easily ascended to the scene situated over 4000 meters above see level and carried out a on-spot investigation to find the solution to the prevention and cure of pollution and ecological conservation of Horse Head gold mine. In 1984, I graduated as one of his Master Degree students. So far, quarter century has passed. It was my pleasure to join his team this time and I had plentiful feelings and much profit. Be my teacher, he again has taught me a lot!

This book includes part of the scientific research results of Prof. Zhong's postgraduates and colleagues which are compiled in the way aiming at providing basic ecological knowledge to the readers and serve as a special gift for his 80th birthday.

Give praise to Prof. Zhong for his directing postgraduate students for 30 years!

Give praise to Prof. Zhong for his carrying on teaching and researching for 50 years!

Give praise to the marvelous 80 year life of Prof. Zhong!

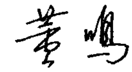
Meanwhile, this book also gives praise for the epoch that all ecologists of Prof. Zhong's generation have experienced.

The thought of ecology has a long history. However, as a discipline of sciences, ecology is young. Associated with the evolution of the modern human society which constantly alters the attributes of the nature, ecology never stops its own development. On the other hand, the changes of the nature have a profound impact on the development of human society, especially in modern times. Ecology is showing prosperity as never before, but is facing unprecedented challenges. Severe challenges not only come from the need for development of the ecological theoretical framework, but also from the increasing demand of human beings on sustainable development in terms of economy, society and the environment. Ecology and ecologists are going more deep into theoretical framework and paying more attention to on practice than ever, as to addressing big issues we are facing, such as global warming, loss of biodiversity, biological invasions, environmental destruction and declining of resources. The book contains 44 chapters belonging to 2 parts. The first part is ecological case studies including 28 chapters, involving in molecular ecology, physiological ecology, autecology, population ecology, community ecology and ecosystem ecology. The second part is an overall review of ecology which is composed of 16 chapters. This part is an extensive description of the current progresses and new ideas related to ecological restoration/reconstruction, biological invasion, the conservation, prevention and cure of pollutions, ecological planning and design, environment management and eco-tourism. It is also contains experiences of career due to combining with ecology. The postscripts of this book are written by Dr. Miao Shili, a professor working in South Florida Water Management District, USA, and Dr. Su Zhixian a professor at Mianyang Normal College, China. They are postgraduates directed by Prof. Zhong during 1980s. The book applies to the researchers doing ecological studies and university and college students majoring in ecology and ecology-related disciplines. It also has great value on the popularization of ecology.

During the editing, all the members of the editorial committee have put great effort in it, worked effectively and sufficiently together and each division is responsible for the peer review process of the chapters. I would like express my gratitude to all the authors, reviewers and editors of the book!

Many thanks and great respect to Prof. Zhong for his advices during the editing of the book!


**Dong Ming**



**Institute of Botany, Chinese Academy of Sciences**

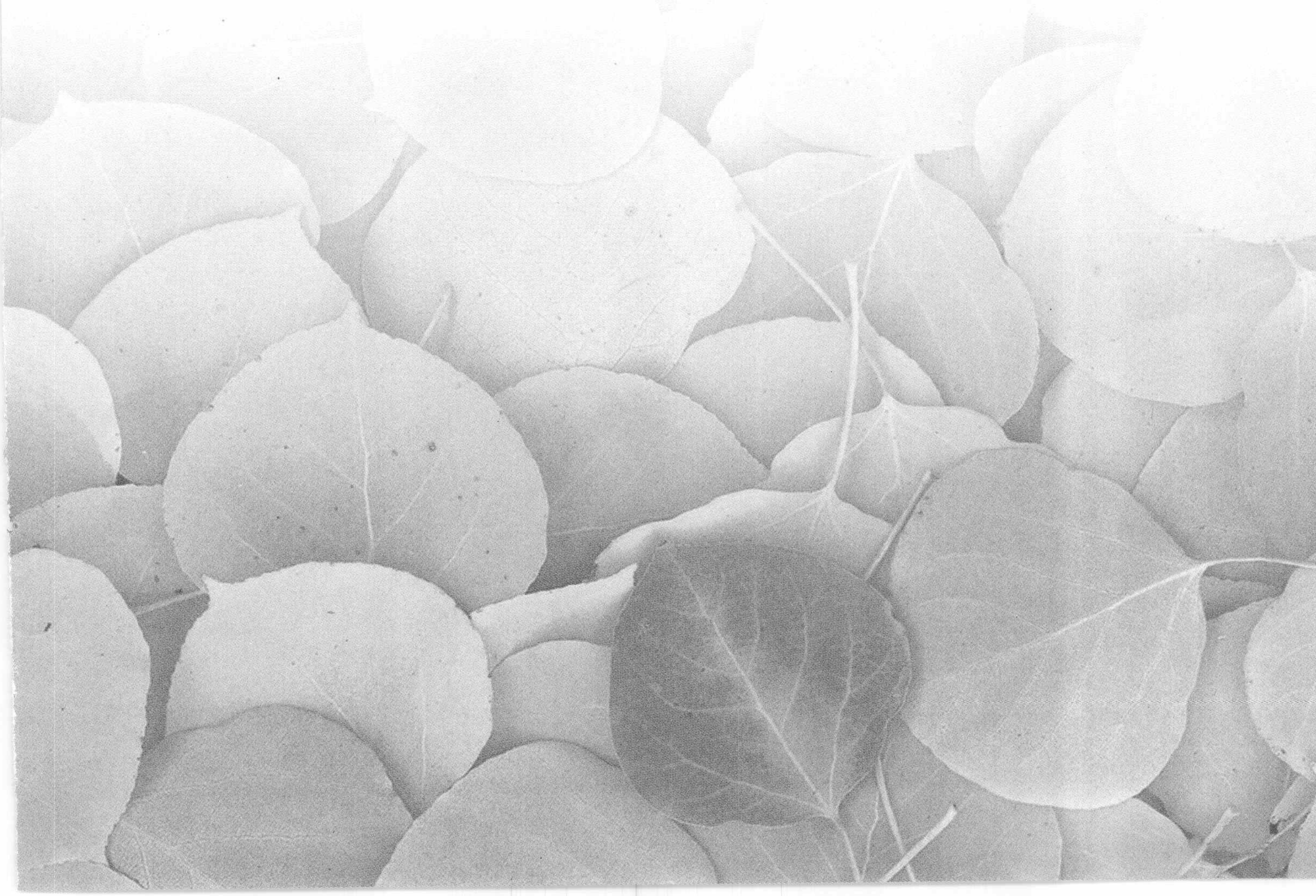
15 **June** 2009, **Mt. Fragrance, Beijing**

# 目录

## 第一篇　生态学案例

## 第二篇 生态学综论

# 第一篇 生态学案例



# Differences in reproduction time allows multi-species co-existence in oscillating patterns

Tessa E. Pronk[1,2], Feike Schieving[2], Heinjo J. During[2], Marinus J. A. Werger[2]*

(1. *Integrative Bioinformatics Unit / Computer Systems Architecture group, Faculty of Science, University of Amsterdam, Kruislaan* 403, 1098 *SJ Amsterdam, the Netherlands*; 2. *Plant Ecology group, Utrecht University, Sorbonnelaan* 16, 3584 *CA Utrecht, the Netherlands*)

**Abstract**: Species can coexist at non-equilibrium circumstances, for instance, by oscillations in population densities or chaos, caused by non-linear responses of species to their environment. We analyzed whether plant genotypes that vary in their timing of reproduction can coexist under equilibrium or non-equilibrium circumstances when competing for light. We used a game theoretical approach, based on a biologically mechanistic model of plant growth.

In our model, the genotype switching to reproduction slightly later than its competitor attained a higher fitness. This caused a succession from early switching genotypes to those switching later to reproductive investment. However, there were cyclic opportunities for extinct genotypes that switch early to reproduction to re-establish and grow into the community. The cause was that genotypes that switched very late produced relatively very little seed because of an overinvestment in vegetative growth; especially when competing against individuals of the same genotype. Because the very early switch genotypes could establish, circumstances were such that other extinct switch genotypes could re-enter the vegetation as well. In this way the diversity of genotypes was maintained over time by temporal oscillations of genotype abundances.

We show that within a model, an externally undisturbed plant community can produce its own temporal cyclic or chaotic disturbances to promote diversity, rather than converge to a stable equilibrium when competing for light. Cyclic fluctuations in species composition can occur in a model community of plants sharing the same growing season and that are limited just by light as a single resource.

**Keywords**: Game theory; Light interception; Cyclic; Annuals; Coexistence; Temporal; Mechanistic Model; Oscillations; Reproduction

## Introduction

In community ecology, many studies try to unravel the mechanisms by which species-rich communities overcome the competitive exclusion principle[1]. In most of these studies stable coexistence is considered, e. g. in communities or populations that are at equilibrium. As an alternative, however, the non-equilibrium view was proposed[2~4]. It was predicted that it is possible that mechanisms that promote coexistence at non-equilibrium will prove to be most important for the maintenance of diversity. Aside from regular disturbances that can create circumstances for species to coexist, species can coexist at non-equilibrium circumstances by non-linear responses that cause oscillations in population densities or chaos[2,3]. So far, well-known examples can be found in the oscillating populations in trophic food-webs such as predator-prey systems[5], where predator, prey, and food source are dependent on the other for their survival. Aside from such dependence, non-hierarchical competitive relationships between species can cause species to coexist on a limited number of resources[2]. Kerr et al. [6], for instance, modeled and tested empirically the coexistence of a system of paper-rock-scissors[7]. Species coexisted when interaction and dispersal was local and thus they emphasize, that spa-

* Corresponding author

tially restricted patterns also may lead to coexistence of species. Similarly, species limited by one resource only may coexist indefinitely if they partition the growing season and each is active only in its "own" part of that season[8]. Huisman and Weissing[2], on the other hand, found oscillating patterns in their model for well-mixed plankton species, on the basis of competition for three or more different resources. This was under the condition that species differed in their required resource ratio. Within oscillations, circumstances for growth differed and species with different requirements for growth found a window of opportunity. In their study, more species could coexist than there were limiting resources [2,9]

We investigate whether or not in a system with one limiting resource coexistence of species is possible. We study this in virtual, competing, annual plants that differ in the timing of reproduction, just as species do in real communities. In this study we assume that in plants there is a trade-off between the production of vegetative parts and seed production. We also assume that the amounts of seed production and photosyntetic carbon gain are strongly correlated. Model studies have indicated that, to maximize seed mass yield, plants should show a sharp transition between the vegetative and reproductive phases of growth[10,11]. One would assume that the allocation scheme determining reproductive output is subject to strong selection because reproductive output is one of the main determinants of fitness[12]. Under strong selective pressure, all plants might be expected to evolve towards a single or at most a few optimal reproductive allocation schemes[10,13]. However, this is only the case in a system where reproductive performance is not affected by the presence of competitor plants. Competitive optimization sensu Anten [14] leads to a delayed switch from growth to reproduction. But whether or not this leads to a single switch time from growth to reproduction is still an open question. In natural vegetation stands, however, often large numbers of plants with widely different timings of the transition to reproduction coexist[15].

Because a large investment in seed mass implies a low investment in vegetative mass and hence competitive strength, reproduction and competitiveness are closely related. As plants mostly do grow in close proximity to each other, competition will often play a role in affecting the fitness of plants with different growth strategies[16]. Part of the variability in reproductive allocation between genotypes may therefore stem from the influence of competition.

When, as is the case in the direct competition for light[14], the success of a genotype depends on the strategies of the other genotypes present, game theory is an appropriate tool to assess the possibilities for different genotypes with their particular traits to persist[16,4]. Also in the research of timing issues, game theory has often been successfully applied[17]. Whereas most modeling studies on the selection for traits concentrate on the dynamics at plant or even population level, we explicitly include allocation patterns within a plant as the basis for competition. Plants thus grow on the basis of intrinsic allocation trade-offs. The size and leaf area distribution of a plant and that of neighboring plants during growth explicitly determines a plant's resource capture[18,19]. This puts each plant into a direct game theoretical context. In addition, on a population level, plants on average will change their seed production as the total composition of the vegetation changes and thus the frequency of encounters with other plant types change. This puts the populations in a game theoretical context as well. Plants in our model are competing for light as a single limiting resource.

An important finding of this study is that competing annual plants that differ in the timing of reproduction do not necessarily converge towards a single evolutionary stable strategy without external disturbances. Populations of plants with different strategies are able to generate their own variability and show cyclic behavior. In this self-organizing model vegetation, multiple genotypes differing in their switch to reproduction find temporal opportunities to perform well so that the diversity of genotypes over a period of time is maintained.

# 1 Methods

## 1.1 The plant growth model

To simulate the fitness and growth of competing plants that switch to reproduction at different moments in time, we used a mechanistic plant growth model. The model is described in detail in Appendix A[20]. Only a brief description of the most important features of the model is given here.

Plants grow within a fixed area of ten by ten centimeters, referred to as a cell. Only plants that share such a cell compete (i. e. plants in separate cells do not compete). However, plants are able to disperse their seeds into other cells between growing seasons. Plants are annual and die at the end of the growing season. The growing season is 365 days, with a seasonal course of the light climate, as it would occur in a temperate region (Equation A14).

As we want to compare plants with respect to their timing of the switch to reproduction, other characteristics are held equal amongst plants. Each plant starts with an initial leaf area, root mass and height (Table A1 in the Appendix). All plants have a parabolic distribution of leaf area over their height [19,21] (Equation A1). Light interception is modeled following Beer's law [22] (Equations A5-A7 Appendix) and the light response of photosynthesis is described by a non-rectangular hyperbola[23]. To obtain daily gross photosynthesis per plant, leaf photosynthesis is integrated over canopy depth and over the day (Equation A10). Part of the assimilate pool thus obtained is spent on the maintenance respiration of structural mass (Equation A9).

In the vegetative phase of growth, a plant invests a fixed proportion of its net photosynthetic production in height (i. e. stem mass). When growing in height, the leaves at the base of the plant are discarded while leaves at the top are newly produced, according to the leaf distribution (Equation A1). Whatever of the net photosynthetic production is left after height growth is invested in leaf and root mass, divided between these structures in some constant proportion. If at any time the carbon that is spent for maintenance and height growth exceeds the carbon income, leaf and root mass are shed and the retracted carbon from these leaves and roots is used to make the carbon balance equal to zero. If either leaf or root mass is zero grams or less, the plant is considered dead.

## 1.2 The switch to seed production

The model plants have a clear switch from vegetative growth to seed mass production. After the switch, the plants no longer grow in height or leaf mass, but all available carbohydrates are invested in seeds. Seed production continues to the end of the growing season. All seeds stay on the plant until the end of the growing season. At the start of the new growing season, all old plants are removed, the seeds are redistributed over the cells and germinate. We assume, that switching time is genotype-specific. To evaluate the consequences of the timing of a switch to seed production, we distinguish ten genotypes which differ in their timing of this switch during the simulated growing season (top part of Table 1).

### 1.2.1 Simulations with isolated plants

First we simulate the growth and seed production of plants of the different switch genotypes (Table 1) without competition in a cell, for a single growing season.

### 1.2.2 Simulations with competing plants

To simulate the competition between plants that grow up together, we let the different switch genotypes (described in Table 1) grow in pairs within a cell, in every possible combination of genotypes. The seed mass produced by the plants in each pair at the end of the 365-day simulation is put into a 'pay-off matrix'[24,25] (see Table 1).