中华农业科教基金资助图书

大豆高光效育种

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内 容 简 介

本书是作者课题组30年来在承担国家“六五”、“七五”、“八五”、“九五”科技攻关计划、国家自然科学基金及“973”项目（光合作用高效转能机理及其在农业中的应用）期间对大豆产量形成的光合生理生化特性、光合作用遗传控制和遗传传递规律及高光效种质遗传改进等进行深入研究的成果，并汇以一些有关文献综述成册。全书共分10章，主要内容包括光合作用研究的最新进展、高光效大豆的光合生理生化特性及光合作用的遗传和种质改进等，提出大豆籽粒产量的提高主要取决于光能的截获、光能转换效率、CO_2 同化效率及光合产物在籽粒中的高比例分配。

本书在通过增强 C_3 作物本身固有类似 C_4 光合途径运转、改善 C_3 作物光能利用效率方面提出了新的观点，即通过遗传改进可以使 C_3 作物的内源类似 C_4 途径潜力大幅度提高。

本书指出大豆非叶器官——豆荚具有良好的光合结构与功能，在高产条件下，应充分发挥这些器官的光合功能，提高大豆整体的光能利用效率。

本书就选育出的高光效种质哈79-9440、哈82-7799等和高光效品种黑农39、黑农40、黑农41等及建立一套行之有效的选育高光效品种的生理生化指标及高光效高产育种体系作了详细阐述。

本书指出，通过有性杂交和人工诱变或基因工程，修饰某些光合基因，均可将多项高光效生理功能整合到高光效大豆品种中，特别是 C_3 作物中固有 C_4 途径酶的高效表达，可能是提高 C_3 作物光合效率的新突破点。

本书可供大豆或其他作物的遗传和育种研究工作者、教师和学生参考。

Supported by the Science and Technology Program of the 6th, 7th, 8th, and 9th National Five-Year-Plan, the National (China) Natural Science Foundation, and the "973" project, we conducted studies on soybean breeding for high photosynthetic efficiency in the past 30 years. The book summarized the achievements of our studies on biochemical and physiological characterizations of photosynthesis in relation to yield, the genetic control of photosynthesis, and the principles of inheritance and the genetic improvement of high photosynthetic germplasm. Relevant updates in this research field were also included. This book consists of ten chapters. The main contents cover the current advances in the studies of the photosynthetic process, physiological and biochemical characterization of photosynthesis in soybean varieties of high photosynthetic efficiency, genetic control of photosynthesis and germplasm improvement, and etc. We showed that the increase in soybean yield is mainly depended on the efficiency of solar energy capturing and transfer, the efficiency of CO_2 assimilation and the high proportional distribution of assimilation products in seeds.

The book put forward a new idea on enhancing the C_4 analogous pathway in C_3 plants to increase photosynthetic efficiency. We suggest that the potential of the C_4 analogous pathway in C_3 plant could be improved genetically.

The book also illustrated that soybean non-leaf organs possess intact photosynthetic structures and functions. To achieve high yield, the photosynthetic functions of those non-leaf organs are functioning to increase photosynthetic efficiency of the whole soybean plant.

In soybean breeding program, we successfully developed germplasms and cultivars of high photosynthetic efficiency, including Ha79-9440, Ha82-7799, Heinong39, Heinong40, Heinong41, and etc. We also formulated physiological and biochemical parameters for developing soybean cultivars with high photosynthetic efficiency as well as effective breeding strategies and methodologies for high photosynthetic efficiency and high yield.

The book pointed out that many physiological functions can be integrated into soybean cultivars with high photosynthetic efficiency by sexual crossing, artificial mutation, or genetic engineering. Increasing the expression of intrinsic C_4 enzymes may represent a new breakthrough to increase photosynthetic efficiency in C_3 plants.

The book is a reference to geneticists, plant breeders, and teachers and students in this field.

序　一

大豆是我国的重要油脂和蛋白的来源，近年总产徘徊在 1 800 万 t 左右，尚不及国内需求之半。通过大规模扩种增加产量是不现实的。因此，主要的努力应该放在提高单产上。我国大豆单产只有美国的 65％左右，潜力是巨大的。

大豆产量的 90％来自光合作用，因此提高光能吸收、传导、转化的效率是提高单产的根本。黑龙江省农业科学院大豆研究所与中国科学院植物研究所的育种与生理学科的研究人员正是看准了这一方向坚持不懈、持之以恒，经过二十多年两个学科、两代人之间的合作，开创性地育出了黑农 39、黑农 40 和黑农 41 等高光效大豆品种（种质），并已大规模推广种植，为我国大豆单产的提高做出了贡献。研究成果获得 2005 年黑龙江省科技进步一等奖，可喜可贺。

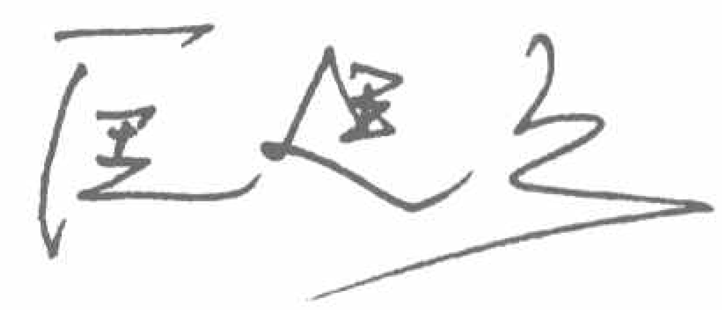
本书总结了大豆高光效育种的艰苦历程和成功经验，但其意义远不止于此。我认为广大农学、生物学工作者至少可以从本书中获得以下三点启迪：

第一，自主创新，敢为人先。二十多年前大豆高光效育种国内外尚无成功的先例，也无技术路线可循，本项目的研究人员勇于探索，在实践中探求可行的技术途径，一步步摸索前进，终于创造出大豆高光效育种的可行模式。

第二，学科交叉，密切合作。遗传育种与作物生理两大学科的研究思路、研究方式、应用技术都有很大差别。参加的工作人员在工作中互相学习，互补短长，融为一个集体。尤为难能可贵的是在长期合作中互谦互让，从未发生名利的纷争。

第三，学术突破，值得借鉴。大豆高光效育种中的主要学术突破

是充分筛选C_3植物大豆固有的C_4代谢途径在结荚、鼓粒期强表达的种质特性与其他优良特性整合于高产品种之中，并取得成功，是前人不曾报道过的。这一尝试可为其他作物育种引以为鉴。

中国科学院院士、欧亚科学院院士 

2006 年 12 月 29 日

Preface one

Soybean is an important source of dietary oil and protein in China. In recent years, the annual production of soybean in China is around 1.8 million tons, providing less than half of the national demand. It is impractical to extend the acreage of soybean cultivation. Therefore, major efforts should be placed on the increase of unit production. Unit production of soybean in China is only about 65% of that in the USA, suggesting a high potential for improvement.

Photosynthesis provides 90% of the yield of soybean. Enhancement in the efficiency of absorption, transduction, and transformation of light energy should be the foundation to increase unit production. Working toward this end, breeders and physiologists from Institute of Soybean Research at Heilongjiang Academy of Agricultural Sciences and Institute of Botany at the Chinese Academy of Sciences persistently and unyieldingly conducted their collaborated researches for more than 20 years. The combined efforts of researchers from two generations and two research areas successfully produced several soybean varieties (germplasms) exhibiting high light utilization efficiency, including Heinong39, Heinong40, Heinong41, etc. These varieties have been popularized and contributed to the increase in the unique production of soybean in China. I congratulate their achievements that led to a First Class Award of Heilongjiang Science and Technology Advancement Award Scheme in 2005.

This book summarized the difficult path and successful experience during the long process of the trial and error attempt by the authors. Furthermore, researchers in the field of agronomy and biological sciences could also be inspired in three aspects:

First: innovation and originality. There was no successful national or international example for such breeding strategy twenty years ago when the researchers launched this program. Without any prior footprint to follow, the researchers bravely searched for new path. Step by step, they ultimately accomplished a workable model for breeding of soybean for high light utilization efficiency.

Second: cross-discipline and deep collaboration. There were major differences in the research strategies, methodologies, and technologies between breeding geneticists and crop physiologists. The participating researchers successfully integrated their expertises. During the prolonged collaboration period, a strong team spirit was exhibited.

Third: breakthrough in science. The major breakthrough of soybean breeding for high light utilization efficiency lied in the selection of high native C_4 activities during early and late podding stages, together with other elite traits to integrate into the breeding program. Such unprecedented success should be exemplary to other crop breeding programs.

Kuang T.-Y.

Dec. 29, 2006

序二

大豆是我国产量最多的油料作物，也是人体重要蛋白质来源和畜牧业饲料蛋白的来源。当前我国大豆产需缺口巨大，2005 年我国大豆总产量 1 750 万 t，而进口量达 2 659 万 t。国外进口量为国内产量的 1.52 倍，是我国进口量最大的农产品。随着全面小康的实现，我国对大豆的需求量将会进一步增加。依靠扩大种植面积增加大豆产量是有限的，大豆的主要出路是大幅度提高大豆单产以满足社会对大豆的需要。

植物干重 90%～95%是来自光合作用，光合作用的产物是作物产量形成的重要基础，提高大豆单产关键在于提高大豆的光能利用效率和协调碳氮代谢功能。为此，1976 年黑龙江省农业科学院大豆研究所与中国科学院植物研究所合作开展了大豆高光效育种的研究。经 30 年的努力，在大豆高光效育种理论和实践上取得了重要的原始创新成果。本书是汇总了杜维广研究员课题组 30 年来所取得的主要成果，并结合目前国内外相应研究工作的进展而编辑出版的。

该书详细地介绍了光合作用的基本理论和基础知识，大豆高光效育种的遗传生理基础和高光效的光合生理基础，大豆光合作用与根瘤固氮的关系，高光效育种高产理论，高光效品种（种质）选育及转基因植物研究的最新成就。

该书在通过增强 C_3 作物本身固有类似 C_4 光合途径运转，改善 C_3 作物光能利用效率方面提出了新的观点，并进行了实践探索。该书在高光效的光合生理基础方面做了较系统深入的研究，发现大豆叶片及豆荚具有类似 C_4 途径，提出了光合碳同化酶系活性高效表达促进光能高效转换的生理机制。该书在过去大豆常规育种实践基础上，创造

了独有的育种与基础生物学科紧密结合的范例，建立了大豆高光效高产育种体系及高光效育种理论，育成了高光效品种（种质），这些研究结果表明：由此创造出的C_4途径酶系超水平表达的C_3植物与转C_4酶基因具有异曲同工、殊途同归的效果。这一经验可供参考借鉴，推而广之。该书还关注到转基因植物研究等方面的最新进展。该书基本反映了目前国内外大豆高光效育种研究的进展，很值得一读。

本书对于从事大豆或其他作物遗传和育种研究工作者、农业和生物科技工作者、教师和学生都有重要的参考价值。本书的出版是黑龙江省农业科学院大豆研究所与中国科学院植物研究所多年合作的结晶，是学科交叉共同研究的硕果，它必将促进作物遗传育种学科的发展。

俄罗斯及印度农业科学院院士、原中国农业科学院院长
国立俄罗斯莫斯科季米里亚捷夫农业大学农学博士 王连铮

2006年12月29日

Preface two

Soybean has the highest production among all oil crops in China. It is also an important source of dietary proteins for human consumption and husbandry. At present, there is a large gap between the need and the supply of soybean in China. In 2005, the locally produced and imported soybean totaled 1750 and 2659 million tons, respectively. The amount of imported soybean was 1.52 times of the local production. Following the actualization of a fairly prosperous society in China, there will be a further increase in the national need for soybean. Increasing production by expanding acreage is limited by the available land resources. Therefore, the best strategy to fulfill the need of soybean is to increase unit production.

About 90%~95% of the plant dry weight is coming from photosynthesis. The products from photosynthesis determine the final crop yield. The key to increase unit production is to enhance the efficiency of photosynthesis and coordinate carbon and nitrogen metabolism. In 1976, the Institute of Soybean Research at Heilongjiang Academy of Agricultural Sciences and the Institute of Botany at the Chinese Academy of Sciences initiated a collaborated research on the breeding for soybean of high photosynthetic efficiency. In the past 30 years, significant and original results were obtained in both theoretical and application aspects. This book is a collection of the major contributions made by Prof. DU Weiguang's group over the last 30 years, together with the current progresses in other relevant researches performed in China and worldwide.

This book detailed the basic theory and knowledge on photosynthesis, the genetic and physiological bases of breeding for soybean of high photosynthetic efficiency, the relationship between photosynthesis and nodular nitrogen fixation in soybean, the theoretical principles for high yield and high photosynthetic efficiency breeding, the screening of soybean germplasm and the researches using transgenic approaches.

In this book, novel theoretical contributions were made on the enhancement of native C_4 - like photosynthetic pathway in C_3 plants, supporting by corresponding experimental data. Through systematic researches of the physiological bases of high photosynthetic efficiency, C_4 - like pathways were found in leaves and pods of soybean. This finding led to a theory of increasing photosynthetic efficiency by enhancing the isozyme activities in the photosynthetic carbon assimilation pathway. Based on the traditional soybean breeding practice, the book provided a unique example to the integration between breeding and knowledge from basic biological sciences. Through this integration, a novel breeding and theoretical system for high photosynthetic efficiency and high yield has been established. Accordingly, soybean germplasms of high photosynthetic efficiency have been generated. These results illustrated that manipulation of isozymes in C_3 plants and introduction of C_4 genes by transgenesis should have similar effects. This concept can be further elaborated and applied to other crops. This book also concerned the recent development of transgenic crops. Current developments of national and worldwide researches on breeding for soybean of high photosynthetic efficiency were also included.

This book is a valuable reference to researchers, teachers and students in the field of genetics and breeding of soybean and other crops. This book signified a major achievement of the long-term collaborated research between the Institute of Soybean Research at Heilongjiang Academy of Agricultural Sciences and the Institute of Botany at the Chinese Academy of Sciences. This book is a product of the integration among different disciplines in science. It will certainly promote the development of crop genetics and breeding researches.

Wang Lianzheng

Dec. 29, 2006

绪　言

作物科学家们深知作物产品最终来自将根部吸收的养分通过叶绿体光合作用形成的光合产物。光能是地球上食物能源的终极来源。随着人口的大量增长，可用耕地面积的大量缩减，只有靠提高单位面积产量来增加总产，因而提出了超高产育种和超高产栽培的要求。许多人并不同意“超高产”的说法，因为产量的高低始终是相对的，高于现在的产量称为超高产，那么高于未来的就要称为超超高产了。这里我们姑且把超高产理解为一种动态的概念，未来的超高产和现时的超高产有不同的含义。实现超高产有赖于单位面积上光能利用效率的提高，包括光能截取的提高和光合效率的提高。因此，作物科学家提出了株型和群体结构的最优化问题。20 世纪的绿色革命便是围绕株型带动光能利用效率而展开的。

“七五”、“八五”和“九五”期间，国家委托南京农业大学大豆研究所主持“大豆新品种选育技术”攻关课题，针对国内大豆育种的实际情况和国内外差距，育种计划包括新品种选育及相关的基础研究两方面，兼顾近期目标和长远要求，总体上分为三个层次。第一层次为直接服务于当前生产的高产、稳产大豆新品种选育，要求选育出分别适于全国各主要大豆产区，综合性状优良，比当地推广良种增产10%以上的新品种；第二层次为优质与抗病虫大豆新品种选育，一方面提供品种、品系直接为生产和进一步选育服务，另一方面促成在全国建立品质及抗病虫育种的较为系统、科学的研究体系及重点单位，扭转此方面的薄弱环节；第三层次为大豆育种应用基础和技术的研究，包括高产品种理想型及其生理特性和主要经济性状的鉴定技术、种质筛选创新及遗传与选育两个方面，为远期的高产、优质、多抗育

种准备必要的方法和材料。其中高产品种理想型及其生理特性是计划中的重要内容，本书的作者因擅长于大豆高光效研究而承担了这方面的工作。参加全国性的育种攻关，推动了大豆高光效研究与育种工作的紧密结合。

本书作者近30年来长期致力于大豆光能利用效率及其育种应用的研究，在解释自然现象和选育高光效品种方面均有所建树。在此基础上他们将前人已经建立的基本知识和自己的研究成果综合起来，写成这本专著《大豆高光效育种》。全书共分十章，在介绍光合作用基本原理的基础上，重点阐述了大豆光合速率与产量的各种可能的关系，大豆高光效育种有关的遗传和生理生化基础，高光效大豆的光抑制和耐光氧化特性，大豆 C_3 代谢的 C_4 途径，大豆非叶器官的光合作用，大豆光合作用与根瘤固氮的关系，大豆产量界限与高光效育种，以及 C_3 大豆的遗传改进等。显然上述内容具有作者本身研究的特点，尤其关于 C_3 大豆的 C_4 途径和非叶器官光合作用的探讨提供了提高大豆光能利用效率的新理解和新途径。

将大豆光合作用和提高光能利用效率的育种相结合起来是这本书的特色。尽管有些内容还具有初步结果的性质，有待继续深入，但这是一次非常有益的尝试，它将推动大豆光合生理与大豆高产育种及高产栽培的进一步结合。希望在本书基础上光合生理科学工作者为育种学家们和栽培学家们提供进一步探索理想株型和群体结构及其育种与栽培调控的途径和理论依据。

中国工程院院士，原南京农业大学校长 盖钧镒

2006年12月29日

Preface

Crop materials are coming from soil nutrients absorbed via roots and photosynthetic products assimilated in chloroplasts. Light is the ultimate energy source of the Earth. The growing global population has led to a severe reduction of arable lands. To increase total yield, an elevation in unit production is essential, leading to a strong demand in "super-high yield" breeding and cultivation. Many scientists disagree with the "super-high yield" concept since yield in always a relative term. If we define "super-high yield" as an immediate targeted yield higher than the current one, any further increase in yield in the future will become "super-super-high yield". Therefore, "super-high yield" should be treated as a dynamic concept that covers different criteria in the present and the future. To achieve the goal of "super-high yield", the light utilization efficiency per acreage should be increased; this involves improvements in both light capturing capacity and photosynthetic efficiency in plants. Therefore, crop scientists proposed to optimize the plant morphology and the population structure. The "Green Revolution" in the last century was harvested on the utilization of plant morphologies that led to an enhancement of light utilization efficiency.

During the 7th, 8th, and 9th Five-Year-Plan of China, the Central Government commissioned a key topic "New Technology for Breeding New Varieties of Soybean" to the Institute of Soybean Research at Nanjing Agricultural University. Based on the actual situation in China, the task was to reduce the technological gap in soybean breeding between China and the international scientific communities. The research program included the breeding for new soybean varieties as well as conducting relevant basic researches. Considering both short-term and long-term goals, this program was conducted at three levels. The first level was to directly serve the production needs by generating new soybean varieties that were of high and stable yield and could adapt to the environments of major soybean cultivation regions. These new varieties exhibited overall elite traits and attained at least 10% increase in yield compared to local popularized varieties. The second level was to breed for soybean varieties of high quality and multiple resistances to pests and pathogens. On one hand, these new varieties provided genetic resources for breeding programs useful for direct soybean production. One the other hand, this nationwide and systematic effort also helped to establish standardized research systems and target research units for related studies. The third level was to perform basic researches and develop technological platforms related to soybean breeding and its applications. This included two aspects: (1) to identify ideal phenotypes and physiological traits for breeding of high yield varieties and to establish technologies to examine major economic traits; and (2) to perform innovative germplasm screens and related genetic analyses and breeding studies. This provided the necessary genetic materials and technologies for the long-term breeding task to produce soybean varieties of high yield, high quality, and multiple resistances. Among these, ideal phenotypes for high yield and the related physiological characteristics were crucial parts in the overall research program stated above. The authors of this book, experts in high photosynthetic efficiency in soybean, were responsible for this part of research. Participating in the key task force of the nationwide soybean breeding program, they successfully established a link between the basic research in high photosynthetic efficiency and the soybean breeding program.

The authors have been working in the area of light utilization in soybean and related breeding for more than 30 years. They made significant contributions to both the understanding of this natural phenomenon and breeding for high light utilization varieties. Combining the results of their own works and the findings by other pioneer scientists in the field, the authors published this book "Breeding for Soybean of High Light Utilization Efficiency" . The book consisted of 10 chapters. Based on the fundamental principles of photosynthesis, the possible relationship of photosynthetic rate in soybean and the final yield was addressed. This book also explained the genetic, physiological, and biochemical bases of breeding for soybean of high light utilization efficiency. Other related topics were also discussed in individual chapters, including the characteristics of photo-inhibition and photo-respiration in soybeans of high light utilization efficiency, the C_4 pathway in the C_3 plant soybean, photosynthesis in soybean organs other than leaves, the relationship between nodular nitrogen fixation and photosynthesis in soybean, the upper limit of soybean yield potential and light utilization efficiency, and the genetic improvement of the C_3 plant soybean. The above contents highlighted the research expertise of the authors. In particular, the chapters on C_4 pathway in the C_3 plant soybean and the photosynthesis in non-leaf organs in soybean have shed light to new understandings and new pathways to enhance light utilization efficiency in soybean.

A link between photosynthesis in soybean and soybean breeding for high light utilization efficiency is a distinct feature of this book. Although some findings are still preliminary and require detailed follow-up investigations, it is a meaningful attempt. This work will promote further integration among the studies of physiology of soybean photosynthesis and breeding and cultivation programs for high yield soybean. I hope that based on the initial effort of this work, physiologists in the field of photosynthesis will provide breeders and cultivators more useful information on the ideal phenotypes, population structures, and strategies and theoretical bases for breeding and cultivation.

Junyi GAI

Dec. 29, 2006

编著者的话

高产稳产始终是作物育种追求的目标。为了提高 C_3 作物大豆单位面积产量，人们在不断地探索中。作物干物重 90%～95%是通过光合作用过程合成的，因此光合作用是提高大豆产量的重要因素。随着作物 C_4 途径和光呼吸的发现，人们越来越认识到提高光能利用率大幅度提高产量尚有巨大潜力。于 1976 年始，黑龙江省农业科学院大豆研究所有幸与中国科学院植物研究所合作，开展了大豆高光效育种的研究。经 30 年的探索和追求，取得了“大豆光合特性研究和高光效种质哈 79－9440 的发现”、“大豆高光效育种生理遗传基础及高光效种质遗传改进”、“高光效大豆品种选育及高光效的光合生理基础”，并选育出具有自主知识产权的高光效高产大豆新品种黑农 39、黑农 40 和黑农 41 等重大创新成果。提高 C_3 作物的光合效率是人们多年的梦想，近年来我们发现大豆等 C_3 植物具有类似 C_4 途径，为大幅度提高 C_3 作物的光能利用效率带来曙光。虽然，在追求大幅度提高大豆产量的科研道路上我们踏出一条大豆高光效育种的研究之路，但这条路尚有漫长艰难的路途要走，实现追求的梦想尚需不懈的努力。本书只是将我们课题组（王育民、戈巧英、匡廷云、杜维广、李卫华、张桂茹、陈怡、郝廼斌、栾晓燕、徐继、满为群、谭克辉）（以姓氏笔画为序）的研究成果和前人的研究成就综合撰写成文，提供农学界同仁们作进一步研究的参考。

我们十分感谢农业部、科技部、国家自然科学基金委员会等有关部门和同仁们的关怀与支持，也非常感谢中华农业科教基金会接受了编著者的申请，并给予资助。承蒙盖钧镒院士、苗以农教授对本书的审阅和修改，香港中文大学林漢明教授对书中英文部分的审核，使我

们研究工作的智慧和汗水得以表达。

在本书出版之时，谨向本书所引用过的论文和著作的作者、同仁们表示谢意，并恳请广大读者对拙著不吝赐教。

编著者

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