Achievements and Prospects of Soybean Molecular Design Breeding in China: Postprint

Authors: Tian Zhixi, Baohui Liu, Yang Yanping, Li Ming, Yao Yuan, Xiaobo Ren, Xue Yongbiao

Date: 2023-03-19T00:00:00+00:00

Abstract

Soybean is an important oil and grain dual-purpose crop and the primary source of high-quality protein for humans and feed protein for livestock, occupying a significant position in China's grain structure. At present, China's breeding technology is predominantly based on conventional breeding, with soybean scientific research and production levels significantly lagging behind those of the United States. Through the implementation of the Strategic Priority Research Program (Category A) of the Chinese Academy of Sciences, "Innovative System for Molecular Module Design Breeding", several high-yield and high-quality molecular modules have been identified, the module coupling effects of some important agronomic traits have been elucidated, a batch of excellent soybean germplasm materials have been created, multiple high-yield and high-quality primary module soybean new varieties have been successfully cultivated, and a soybean molecular module design breeding system has been preliminarily established. In the future, efforts should continue to strengthen systematic evaluation, mining, utilization, and creation of germplasm resources, promote the construction of independently integrated public databases, improve data sharing mechanisms, vigorously carry out research on breakthrough technologies for high and stable yield of soybean and soybean meal alternative feed, accelerate the construction of molecular design breeding and artificial intelligence breeding innovation systems, cultivate breakthrough soybean new varieties, develop green and efficient cultivation techniques, enhance China's soybean self-production capacity, and alleviate the soybean demand gap.

Full Text

Update and Perspectives on Soybean Molecular Module-based Designer Breeding in China

Authors: TIAN Zhixi[1]*, LIU Baohui[2], YANG Yanping[3], LI Ming[1], YAO Yuan[4], REN Xiaobo[4], XUE Yongbiao[1]

[1] Institute of Genetics and Developmental Biology, Chinese Academy of Sciences, Beijing 100101, China

[2] Northeast Institute of Geography and Agroecology, Chinese Academy of Sciences, Harbin 150081, China

[3] Center for Documentation and Information, Chinese Academy of Sciences, Beijing 100190, China

[4] Bureau of Major R&D Programs, Chinese Academy of Sciences, Beijing 100864, China

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Abstract

Soybean is one of the most economically important leguminous seed crops that provide the majority of plant proteins, and more than a quarter of the world's food and animal feed. At present, soybean breeding technology in China mainly relies on conventional breeding, and the levels of both fundamental study and production lag behind those of the United States. Supported by "Innovative System of Designer Breeding by Molecular Modules," one of the strategic priority research programs of the Chinese Academy of Sciences, Chinese soybean scientists have dissected several important molecular modules controlling yield and seed quality, revealed the coupling mechanisms of diverse molecular modules, bred a series of designer soybean varieties for field tests or regional trials, which together establish the first-generation molecular module-based designer breeding systems in soybean. In the future, we should continue to strengthen germplasm resources evaluation and exploitation system, promote autonomy public database building, improve the data sharing mechanism, vigorously develop breakthrough technologies for high and stable yield soybean and for soybean replacement feed crops, speed up the molecular design breeding and artificial intelligence breeding systems, cultivate breakthrough soybean varieties, and develop green and efficient cultivation techniques. With these studies, it is expected to enhance soybean production capacity and relieve the soybean demand gap in China.

Keywords: soybean, breeding technology, molecular module-based designer breeding, molecular module, module coupling and assembly

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Current Status of Soybean Industry and Research in China

Soybean serves as a primary source of edible oil and feed in China, and the country has long been the world's largest consumer of soybean products, including soybean oil and soybean meal. In 2017 alone, China consumed 17.4 million tons of soybean oil, accounting for 30.9% of global consumption, and 74.07 million tons of soybean meal, representing 31.7% of the global total . As an important food and cash crop, soybean provides abundant high-quality oil and protein resources for human consumption. With population growth, rising living standards, and changing dietary structures, China's demand for soybean has increased annually, leading to increasingly prominent supply-demand contradictions.

Prior to 1995, China was a net exporter of soybean. However, after adjusting its import-export policies in 1995 to increase imports and reduce exports, China became a net importer for the first time, with import volumes rising year by year. Imports exceeded 10 million tons in 2000, surpassed 50 million tons in 2010, and reached 95.53 million tons in 2017. Currently, China's dependence on foreign soybean exceeds 87%, making it the world's largest soybean importer. In 2017, the majority of imports originated from Brazil (53%), the United States (34%), and Argentina (7%) .

China's soybean production and research levels lag significantly behind those of the United States. Since 1978, Chinese soybean breeders have developed over 1,800 new varieties through continuous efforts, achieving four to five generations of variety replacement and increasing soybean yield by 140%. However, a substantial gap remains compared to major foreign producers. The average soybean yield in Brazil, the United States, and Argentina has already exceeded 3,000 kg/ha (equivalent to 200 kg/mu), while China's average yield has long hovered around 120 kg/mu. In recent years, China's soybean research capabilities have improved notably, but still fall considerably short of U.S. standards. A bibliometric analysis of SCI papers on soybean research from 1916 to 2017 reveals that the United States holds absolute dominance in both quantity and quality, accounting for 44% of global publications. All top 10 institutions by publication volume are U.S.-based, and the U.S. leads in highly cited papers, representing over half of the top 10% most-cited articles worldwide. The U.S. also ranks first in authorized soybean-related invention patents. Analysis of core soybean patents shows that key technologies are primarily controlled by American companies such as Monsanto and Dow-DuPont, which achieve monopoly over the industrial chain source through control of seed technology. While U.S. breeding companies have already adopted molecular breeding, China still relies primarily on conventional breeding methods, lagging behind in breeding efficiency and precision improvement of specific traits.

Achievements in Soybean Molecular Module-based Designer Breeding

Through the implementation of the Chinese Academy of Sciences' Strategic Priority Research Program (Category A) "Innovative System of Designer Breeding by Molecular Modules," China has made significant progress in molecular module identification, coupling effect analysis, and breeding of primary molecular module varieties, establishing a preliminary soybean molecular module-based designer breeding system. Related research findings have been published in prestigious international journals including *Nature Biotechnology*, *Nature Genetics*, and *Molecular Plant*, with over 20 invention patents applied for and granted.

Molecular Module Identification Soybean is a photoperiod-sensitive short-day plant, which limits its cultivation regions. Collaborative work by the Kong Fanjiang and Liu Baohui team from the Northeast Institute of Geography and Agroecology, the Tian Zhixi team from the Institute of Genetics and Developmental Biology, and the Hou Xingliang team from the South China Botanical Garden led to the cloning of the long-juvenile gene *J*. Mutant alleles of this gene can delay flowering time under low-latitude (short-day) conditions, increasing yield by 30-50% compared to wild-type. Functional analysis revealed a soybean-specific genetic network model for photoperiod-regulated flowering: PHYA(E3E4)-J-E1-FT. Population genetic analysis identified at least eight loss-of-function allelic variations of the *J* gene in low-latitude-adapted soybean varieties. This research provides crucial theoretical foundations for soybean production in tropical regions and was published in *Nature Genetics* in 2017[1]. The findings were highlighted in review articles in *Nature Plants* and *Chinese Bulletin of Botany*, which noted that the results "open a door for revealing and applying soybean adaptation theory in tropical regions," and the work was selected for the *Compilation of Excellent Achievements from NSFC-funded Projects (Volume VII)*.

Hundred-seed weight is an important yield component trait in soybean, regulated by multiple genetic loci, yet few studies have cloned genes controlling this trait or investigated the molecular mechanisms of seed development. The Zhang Jinsong and Chen Shouyi team from the Institute of Genetics and Developmental Biology, in collaboration with the Man Weiqun and Lai Yongcai teams from the Heilongjiang Academy of Agricultural Sciences, performed whole-genome resequencing and QTL analysis of a recombinant inbred line population derived from wild soybean ZYD7 and cultivated soybean HN44. They identified a superior allele for hundred-seed weight, *Glyma17g33690* (*PP2C*), originating from wild soybean. The mechanism involves interaction with brassinosteroid (BR) signaling pathway transcription factors (such as GmBZR1), which are activated through dephosphorylation to promote downstream gene expression controlling seed size, thereby increasing seed weight. Population genetic analysis revealed that nearly 40% of cultivated soybeans lack the *PP2C-1* genotype, and introducing this genotype into varieties lacking this locus could further improve yield. These results were published in *Molecular Plant* in 2017[2]. Additionally, the He Chaoying team from the Institute of Botany, in collaboration with Northeast Agricultural University, identified *GmWRKY15a* through QTL analysis of a cross between cultivated soybean SN14 and wild soybean ZYD0006, combined with differential expression gene mapping. Variation in CT repeat numbers in the non-translated region affects its expression level and likely relates to seed size and domestication. This work represents the first discovery of a WRKY transcription factor regulating soybean seed size, providing new insights into soybean domestication processes. The findings were published in *Journal of Experimental Botology* in 2017[3].

Leaf petiole angle in soybean affects canopy structure, photosynthetic efficiency, and ultimately yield, representing an important agronomic trait. However, the regulatory mechanisms controlling petiole angle remain unclear. The Feng Xianzhong team from the Northeast Institute of Geography and Agroecology, in collaboration with the Chinese Academy of Agricultural Sciences and Purdue University, identified the *GmILPA1* gene controlling soybean leaf petiole angle by analyzing the *gmilpa1* mutant with increased petiole angle. This gene encodes an APC8-like protein that functions by interacting with GmAPC13a to form a complex. Expression analysis revealed that *GmILPA1* is primarily expressed in cells at the base of leaf primordia, likely controlling pulvinus morphology by promoting cell proliferation and differentiation. These results were published in *Plant Physiology* in 2017[4].

Soybean is a major oil crop, and seed oil content is one of its most important quality traits. Artificial selection during domestication has continuously increased soybean seed oil content. The Tian Zhixi team from the Institute of Genetics and Developmental Biology and the Wang Wen team from the Kunming Institute of Zoology performed deep resequencing and genomic analysis of 302 representative soybean accessions, identifying 121 strong selection signals during domestication and 109 during variety improvement. Further analysis revealed that at least 96 selection signals were associated with oil-related traits, indicating that oil traits have undergone strong artificial selection, forming a complex network system that jointly regulates oil metabolism and causes variation in oil-related traits among different germplasms. This study also mapped important molecular modules controlling key agronomic traits, such as *E1* for flowering time, *Dt1* for growth habit, and *T* for pubescence color, laying an important foundation for research on regulatory networks of soybean agronomic traits. The findings were published in *Nature Biotechnology* in 2015[5] and selected for the *Compilation of Excellent Achievements from NSFC-funded Projects (Volume VI)*. Furthermore, the Zhang Jinsong and Chen Shouyi team constructed a gene co-expression network for soybean seed oil content through transcriptome analysis, identifying the seed-preferred transcription factor *GmZF351* encoding a tandem CCCH zinc finger protein during the rapid oil synthesis period. Functional analysis showed that overexpressing *GmZF351* significantly increased oil content in transgenic *Arabidopsis* and soybean seeds. Population genetic analysis revealed that *GmZF351* underwent artificial selection during domestication, with its haplotype originating from wild soybean type III, which is associated with high gene expression, promoter activity, and oil content. This research is of great significance for improving soybean quality and value, and was published in *Plant Physiology* in 2017[6].

Through the "Innovative System of Designer Breeding by Molecular Modules" program, researchers have also mapped several molecular modules related to flowering time and branching, such as *QNE1*, *qFT12-1*, and *TMS22*. Additionally, important progress has been made in understanding legume-specific gene loss and the evolution of important gene families[7-13], exploring their roles in soybean domestication and laying theoretical foundations for subsequent molecular module mining and designer breeding.

Molecular Module Coupling Effects for Important Soybean Traits The coupling of different complex traits is a key scientific question in molecular designer breeding. Yield, quality, and other traits are mostly complex traits controlled by multiple genes. Due to pleiotropy and genetic linkage drag, some traits show coordinated variation across different materials and breeding progeny, presenting coupling correlations. Deciphering the genetic regulatory networks underlying trait coupling and identifying key regulatory units are crucial for molecular designer breeding. The Tian Zhixi team from the Institute of Genetics and Developmental Biology, in collaboration with teams including Wang Guodong, Zhu Baoge from the same institute, and Zhang Zhiwu from Washington State University, conducted multi-year, multi-location observations of 84 yield and quality traits across 809 soybean cultivars. They found varying degrees of correlation among different traits. Using genome-wide association analysis, they systematically scanned the genome for regulatory loci of all 84 traits, identifying 245 significant association loci. Linkage disequilibrium analysis among these loci revealed that 115 could be linked together, forming a complex multi-trait, multi-locus regulatory network that connects 51 observed traits and well explains the coupling relationships between different traits. Within this network, 23 association loci serve as important nodes, playing key regulatory roles in the formation of different traits. This study provides an important theoretical foundation for soybean molecular designer breeding and is of great significance for improving soybean quality and yield. The research was published in *Genome Biology* in 2017[14].

Breeding of Primary Molecular Module Soybean Varieties The four-seed-pod molecular module *ln* can increase seed number per pod and has been widely applied in breeding high-yield soybean varieties in Northeast China, though its application in the summer soybean production areas of the Huang-Huai-Hai region remains limited. The Zhu Baoge and Tian Zhixi teams from the Institute of Genetics and Developmental Biology introduced the superior *ln-C* allelic variant (molecular module) into the widely planted chassis varieties "Zhonghuang 13" and "Kedou 1" that lack this module, successfully breeding five new summer soybean lines and varieties with significantly increased four-seed-pod ratio and yield: "Kedou 15", "Kedou 16", "Kedou 17", "Kedou 18", and "Kedou 30". Multi-year evaluations at various planting scales in Suzhou and Huaibei (Anhui) and Xihua (Henan) demonstrated that these five new lines achieved actual yields of 3,105.0 kg/ha, 2,965.2 kg/ha, 3,141.0 kg/ha, 3,000.5 kg/ha, and 3,034.5 kg/ha, respectively, representing yield increases of 9.3%, 7.83%, 10.6%, 8.24%, and 8.62% compared to local check varieties (the respective chassis varieties). The four-seed-pod ratio increased by 15.2%-21.47%. These materials are currently undergoing national or provincial regional trials. Notably, the new variety "Kedou 17" completed all procedures for Henan provincial trials in 2017 and was approved by the Henan Provincial Crop Variety Approval Committee on March 13, 2018, with an average yield of 3,215.55 kg/ha in two years of regional trials (5.07% higher than the check "Yudou 22") and 3,034.8 kg/ha in production trials (6.11% higher than the check). The variety has been transferred to Anhui Yongmin Seed Company for commercial development and application, with import registration applied for in Anhui Province. It has been demonstrated on over 10,000 mu in Anhui and Henan—the two provinces with the largest summer soybean planting areas in the Huang-Huai-Hai region—and is rapidly expanding.

Heilongjiang Province, as China's major soybean-producing region, faces challenges of low and unstable yields in early-maturing and medium-early-maturing varieties. Supported by the "Innovative System of Designer Breeding by Molecular Modules" program, the Liu Baohui and Kong Fanjiang teams from the Northeast Institute of Geography and Agroecology applied the early-maturity module *e1-as* to chassis varieties, successfully breeding the medium-early-maturing, high-oil, high-photosynthetic-efficiency, high-yield variety "Dongsheng 77", the early-maturing, high-oil, high-yield variety "Dongsheng 78", and the high-oil, high-yield variety "Dongsheng 79". "Dongsheng 77" was approved by the Heilongjiang Provincial Crop Variety Approval Committee in May 2015, with an average yield of 3,226.3 kg/ha (7.3% higher than the check variety Suinong 26), and has been demonstrated on 780,000 mu, generating economic benefits of 25.11 million yuan. It is suitable for planting in the second accumulated temperature zone of Heilongjiang. "Dongsheng 78" was approved in January 2017, showing 10.2% higher yield than the check "Hefeng 50" across 25,000 mu of demonstrations, with economic benefits of 937,000 yuan. "Dongsheng 79" was approved in January 2018, with an average oil content of 24.16% from two years of regional and production trials, making it the first variety among 485 varieties bred in Heilongjiang since 1966 to exceed 24% oil content.

Future Prospects for Soybean Molecular Module-based Designer Breeding

Analysis of Soybean Development Shortcomings 1. No breakthrough in soybean yield, significantly lower than other major crops. With advances in breeding technology, the yields of various crops in China have improved to different degrees. According to USDA statistics , since the 1960s, global average yields of wheat, maize, and rice have achieved qualitative improvements: wheat from 40-50 kg/mu to about 350 kg/mu, rice from about 130 kg/mu to about 440 kg/mu, and maize from about 80 kg/mu to about 400 kg/mu. However, soybean yield has increased relatively slowly, with current average yields of only about 120 kg/mu, showing no qualitative breakthrough.

2. Lagging infrastructure development constrains long-term soybean scientific innovation. Several soybean-related databases have been established internationally, integrating different types of basic research results, such as NCBI, Phytozome, SoyBase, SoyKB, Soy-TFKB, and SoyDB. Most importantly, USDA has established a completely free and shared germplasm resource database covering worldwide soybean collections, recombinant inbred lines, single-segment substitution lines, and systematic multi-year, multi-location trait investigations and genetic analysis results. These databases not only facilitate domestic scientific research but also, through data integration, generate comprehensive information that promotes integration of scientific research with production practice while avoiding redundant work. Although China possesses the world's richest soybean germplasm resources and its basic soybean research is gradually catching up with international levels, significant gaps remain in data sharing compared to foreign countries.

3. Soybean R&D funding is lower than for other staple crops. Overall, soybean research lags behind other major crops. Insufficient funding for soybean R&D is a major factor constraining soybean scientific and technological innovation in China. Analysis of funding from the National Natural Science Foundation of China over the past decade for research on four major crops (rice, wheat, maize, and soybean) shows that rice received the most funding at 1.765 billion yuan, significantly higher than other crops; maize and wheat received similar amounts at 923 million and 852 million yuan, respectively; soybean received the least at 461 million yuan, only 26% of rice's funding. Statistics from the 2016-2017 National Key R&D Program's "Agricultural Science and Technology" category show rice received 9 projects totaling 405 million yuan; wheat received 8 projects totaling 285 million yuan; and both maize and soybean received 4 projects each, but soybean received the least funding at only 89 million yuan.

Future Trends in Soybean Production 1. China's soybean demand will continue to increase, with widening gaps. With continued population growth, urbanization, reduction of high-quality arable land, and upgrading of dietary structure, China's rigid demand for food will continue to increase. If breakthrough progress cannot be achieved in domestic soybean production, China's soybean consumption will continue to rely on imports for a considerable future period, with import volumes continuing to grow. According to predictions by consulting firm High Quest Partners , by around 2020, global soybean annual production will need to increase by an additional 100 million tons to meet worldwide demand, with China's consumption accounting for one-third of global production.

2. Enhancing domestic soybean production capacity is the fundamental solution to China's soybean demand. Currently, China's imported soybeans mainly originate from Brazil, the United States, and Argentina. However, soybean seeds in Brazil and Argentina basically come from the American seed industry, meaning that over 90% of China's soybean imports are controlled by the U.S. seed industry, greatly affecting China's soybean industry and even food security. On one hand, high import dependence leads to instability in China's food structure and supply. Imported soybeans are primarily used for oil extraction and meal production. Soybean meal accounts for about 25% of feed production raw materials, and import fluctuations affect over 38 million tons of feed production, subsequently impacting nearly 100 million tons of meat production. Once international situations affect soybean imports, domestic consumer demand for meat, eggs, oil, and milk cannot be satisfied. On the other hand, soybean pricing power is completely controlled by foreign entities. Historical instances of dramatic price fluctuations due to production changes include 2003-2004, 2006-2008, and 2010-2012, with each production decline (or even anticipated decline) causing soybean prices to surge 1-3 fold within short periods.

In summary, China's primary soybean problem lies in the contradiction between insufficient production capacity and total domestic demand. From a long-term development perspective, enhancing soybean production capacity is the fundamental approach to addressing China's soybean demand and ensuring national food security.

Future Prospects for Soybean Science and Technology **1. Develop breakthrough high-yield technologies to achieve a soybean "Green Revolution."** Low yield is the greatest challenge facing China's soybean industry, making yield improvement the primary task for reversing China's passive soybean situation. Over the past decades, yield improvements in rice, wheat, and maize have largely benefited from "Green Revolution" technologies such as semi-dwarf genes and heterosis utilization. For soybean, although breeders have improved certain traits and achieved some yield increases, no breakthrough technology has been formed, and no qualitative yield improvement has been realized. Future efforts should boldly explore innovative concepts, conduct molecular basic and breeding technology research for super-high-yield soybean, and create revolutionary varieties to achieve a soybean "Green Revolution."

2. Conduct research on soybean stress tolerance and adaptability to expand planting areas. Arable land area is the primary factor ensuring food production. In addition to the 1.8 billion mu of red-line farmland, China has 1.17 billion mu of marginal land (saline-alkali, beach, high-cold, drought areas) that could be reclaimed, providing new directions for soybean development. Additionally, developing new overseas soybean markets in Africa and Latin America to diversify import sources is an important approach to solving China's single-channel import problem. These efforts require strengthened research on soybean stress tolerance and adaptability (drought resistance, saline-alkali tolerance, wide adaptability, etc.) to expand soybean cultivation regions and increase production capacity.

3. Develop soybean meal replacement feed to mitigate downstream industrial impacts. Soybean meal feed is China's primary use for soybean. We should intensify research on soybean meal replacement feed to address the impact of soybean gaps on downstream industries. In recent years, China's forage industry has developed rapidly, with potential replacements including alfalfa, sweet sorghum, cottonseed meal, and rapeseed meal. However, these alternatives currently require supplementation with other products and rational formulation to achieve optimal results. Forage soybean has shown good application prospects, but corresponding varieties are scarce and supporting technologies are lacking. Strengthening forage soybean breeding and timely application in animal husbandry production represents another important approach to solving China's soybean gap.

4. Accelerate molecular design breeding innovation system construction to catch up with foreign soybean production. Science and technology constitute primary productive forces. With rapid development in molecular biology, genomics, systems biology, and synthetic biology, along with continuous biotechnology advances, molecular design breeding technology—born from multidisciplinary integration—represents a new revolution in modern breeding. This places China and international competitors on a relatively similar new starting line. Therefore, constructing a molecular design breeding innovation system presents new opportunities for China's breeding technology development. Seizing this opportunity and accelerating system construction will lead soybean breeding to achieve leapfrog development and create opportunities to surpass foreign soybean production.

5. Promote artificial intelligence breeding technology development to lead international soybean breeding innovation. Artificial intelligence provides tremendous opportunities for future breeding technology revolution and represents a new opportunity for China to lead international soybean breeding innovation. Through 3D soybean morphological simulation and phenotypic reconstruction associated with genomics, digital computer simulation of plant phenotypic characteristics under different gene combinations will be realized, bringing new transformations to breeding technology. Achieving AI-based breeding scheme design will greatly promote China's transition from traditional breeding and molecular design-assisted breeding to AI breeding. The efficiency of AI breeding systems can greatly accelerate new variety development. Establishing theoretical and technical systems for AI breeding technology will place China at the forefront of international breeding technology.

6. Strengthen systematic evaluation, mining, utilization, and creation of germplasm resources, and improve sharing mechanisms. Vigorous efforts should be made in germplasm resource research and innovation, including genomic and phenomic analysis of China's unique wild resources, construction of a core soybean breeding resource database, analysis of pedigree characteristics and genetic evolution patterns of superior parents, and in-depth analysis of soybean origin and evolutionary pathways to establish foundational materials for soybean development.

7. Promote autonomous integrated public database construction and improve data sharing mechanisms. Integrate various omics data to establish systematic, integrated public databases that achieve real-time, systematic, efficient, and shared data resources, laying foundations for functional genomics and germplasm innovation.

8. Establish a national soybean innovation laboratory. Oriented by national major demands, integrate advantageous forces from current institutions and improve the R&D layout of the soybean science and technology innovation chain. Through national laboratory construction and talent cultivation, further enhance China's original innovation capability in soybean science and technology to achieve high-quality development of the soybean industry.

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Note: Figure translations are in progress. See original paper for figures.