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Abstract

High-yield and high-quality forage varieties are the key to sustainable development of grass-based livestock husbandry in China. However, the forage breeding was started late in China, and the progress is very slow, and the forage varieties of independent intellectual property rights are seriously lacked. Forages generally have self-incompatibility, natural allogamy, polysomic inheritance, and marked inbreeding effects. Subsequently, it is difficult to characterize agronomically important complex traits, resulting that the breeding technology is still in the 2.0 era of hybrid breeding. The molecular design-based breeding is a fine strategy to speed up the breeding process, however, there is a lack of theoretical and technical system for the molecular design-based forage breeding. Recently, the Chinese Academy of Sciences has launched the strategic priority program "Establishing Scientific and Technological System of Ecological Grass and Animal Husbandry", to dissect complex forage genomes, establish a new molecular design-based forage breeding technologies, and breed high-yield and high-quality forage varieties with independent intellectual property rights.

Keywords

forage; breeding technology; molecular design-based breeding; genome-wide association studies; whole genome selection breeding

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Current Situation and Prospect of Forage Breeding in China

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Abstract: High-yield and high-quality forage varieties are the key to sustainable development of grass-based livestock husbandry in China. However, since the forage breeding started late and developed slowly in China, the forage varieties of independent intellectual property rights are in serious shortage. Forage species generally have self-incompatibility, natural allogamy, polysomic inheritance, and inbreeding effects. Therefore, it is difficult to characterize important complex agronomic traits, which makes the breeding technology still stay in the 2.0 era of hybrid breeding. Molecular design-based breeding is a fine strategy to speed up the breeding process, however, there is a lack of theoretical and technical system for the molecular design-based breeding of forage. Recently, the Chinese Academy of Sciences has launched the strategic priority research program Establishing Scientific and Technological System of Grass-based Livestock Husbandry to decipher complex forage genomes, develop new molecular design-based breeding technologies for forage, and breed high-yield and high-quality forage varieties with independent intellectual property rights. **DOI:** 10.16418/j.issn.1000-3045.20210511003-en

Keywords: forage; breeding technology; molecular design-based breeding; genome-wide association study; genomic selection

1 China needs to strengthen the innovative utilization of forage germplasm resources and breed high-yield and high-quality forage varieties

As the proportion of protein-based food in China's residential dietary pattern keeps increasing, it has become a pressing matter to breed high-quality forage varieties. China's demand for forage, dairy, and beef is on the rise due to the shortage of domestic supply. The forage breeding industry has become one of the obstacles to China's food supply security and rural revitalization.

1.1 China faces intensifying forage supply-demand conflicts

In the new era, China's residential dietary pattern continues to upgrade, which is manifested by the increasing demand for high-quality animal protein. Against this backdrop, the rigid demand for forage is expanding. The annual demand for forage feed in China is expected to reach 10 million tons in the future^①. However, the quality of China's forage products is poor, and in winter more than 75% of the area

lacks forage for livestock. As a consequence, the supply of forage hay has to heavily rely on import. China's total forage hay import increased dramatically from 460 200 tons (including 442 200 tons of alfalfa hay) in 2012^② to 1 626 800 tons (including 1 356 100 tons of alfalfa hay) in 2019^③. Alfalfa is known as the king of forage. China's self-sufficiency rate of high-quality alfalfa is only 64%, and the total import of alfalfa hay in the United States accounts for 93.5%. Given the economic and trade frictions between China and the United States, the international trade of forage faces intensifying risks.

The surging demand and the limited annual production of forage seeds make China import large quantities of forage seeds every year. In recent years, China's annual demand for commercial grass seeds has stayed at 150 000 tons, more than 1/3 of which depend on import. In 2019, China imported a total of 51 300 tons of seeds of ryegrass, sheep fescue, Kentucky bluegrass, alfalfa, and clover, with the imports of 110 million dollars^④. From January to November in 2020, China imported 59 800 tons of grass seeds (102 million dollars), with a year-on-year increase of 18%. In particular, the import of alfalfa seeds amounted to 3 500 tons, with a year-on-year increase of 37%^⑤.

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^①Market demand and trend of forage in China (2020). (2020–08–09). <https://www.chinairn.com/hyzz/20200819/100452768.shtml>.

^②2021 Sees China importing a large amount of alfalfa hay. (2013–03–16). <https://www.ppxmw.com/yangzhi/5393.html>.

^③Trends of major grass products and beef and mutton in China 2019. (2019–12–31). <http://www.forage.org.cn/front/article/1202.html>.

^④Trends of major grass products and beef and mutton in China 2019. (2019–12–31). <http://www.forage.org.cn/front/article/1202.html>.

^⑤Trends of major grass products and beef and mutton in China from January to November in 2020. (2020–12–27). <http://www.forage.org.cn/front/article/1207.html>.

Chinese President Xi Jinping has repeatedly stressed that the Chinese must realize food self-sufficiency. Hence, in terms of forage supply, China must mainly rely on its own, supplemented by imports. China should quicken its step to breed forage varieties with independent intellectual property rights.

1.2 China should strive to conserve and utilize forage germplasm resources

The breeding of new varieties is genetically based on germplasm resources. China is rich in the germplasm resources of forage. The grassland forage plants alone amount to 6 704 species belonging to 1 545 genera of 246 families, which include 1 231 leguminous species and 1 127 graminous species^[1]. To collect, preserve, evaluate, utilize, and innovate forage germplasm resources, China has established one center for grass germplasm resources, two backup centers for grass germplasm resources, one tissue culture center, and 17 grass germplasm resources nurseries, collecting and preserving 30% of forage germplasm resources^[2]. By 2016, China had evaluated the drought resistance, saline tolerance, cold resistance, heat resistance, disease resistance, crude protein content, and pest resistance of more than 16 000 accessions of germplasm resources. China had screened out 157 accessions of high-protein alfalfa as well as 396 accessions of powdery mildew-resistant red clover and brown blotch-resistant alfalfa^[3].

However, some valuable forage germplasm resources in China are on the verge of extinction before they can be fully identified and protected. At present, *ex situ* conservation is the typical pattern for the protection of forage germplasm resources in China, which fails to contain the decrease in the genetic diversity of forage. In addition, urbanization, climate change, environmental pollution, species invasion and other factors are accelerating the loss of rare and endangered species, endemic species, and wild relatives.

Due to the unknown genetic background of germplasm resources, only about two percent of forage resources have been evaluated^[4,5]. Therefore, it is urgent to adopt *in situ* conservation approach to maintain the genetic diversity of forage germplasm resources, establish the technology system for the mining of elite genes of forage, and strengthen the innovative utilization of forage germplasm resources.

1.3 China lacks the forage varieties with independent intellectual property rights

China's forage breeding industry has just started recently and develops slowly. As a result, there are few forage varieties and the traits of forage are not superior. Compared with foreign countries, China is falling far behind in terms of forage quantity and quality. By 2020, China has approved 604 new varieties of forage, only 227 of which have been growing. However, the number of forage varieties registered

by the member states of the Organization for Economic Cooperation and Development (OECD) mainly comprised of the United States and European countries exceeds 5 000^[6,7]. In addition, the quality, productivity, and stress resistance of forage varieties bred in China are inferior to those of the imported varieties, making China rely on import for major plant varieties^[8].

The United States collected and screened alfalfa germplasm resources from Eurasia in 1897–1909 and bred high-yield, high-quality, stress-resistant, and pest-resistant varieties according to the actual demands^[9]. The successful alfalfa breeding in the United States was not accomplished in an action. Instead, it experienced from dependence on import to independence via innovation. In 1920, 49% of alfalfa seeds in the United States were imported. Moreover, American farmers often suffered huge economic losses for they were poorly informed of the characteristics of the imported varieties. In 1925, due to the outbreak of bacterial wilt in the Midwest of the United States, alfalfa seed industry was hit hard. Not until 1940–1943 when Ranger and Buffalo resistant to bacterial wilt disease were bred, did American alfalfa seed industry recover. China began to examine and approve new varieties of forage in 1987^[9]. Now, China's alfalfa seed industry is experiencing what the United States' did earlier.

At present, more than 80% of China's alfalfa seeds are imported. Owing to the differences in climate and soil conditions between countries, some foreign varieties may be not adaptive to the new environment, which may be exposed to the potential risk of huge economic losses. Global climate change, especially frequent extreme weather, limits alfalfa production in China. Therefore, it is urgent to breed high-yield and high-quality forage new varieties with independent intellectual property rights and suitable for different regional production conditions in China.

2 Status quo of China's forage breeding and technological bottleneck

2.1 Status quo of China's forage seed industry and breeding technology

The production of forage seeds in China dates back to the early 1980s. Through years of efforts, great progress has been made. However, in this sphere, China still falls far behind than the countries boasting flourishing animal husbandry. Currently, two of the top 20 multinational seed companies are mainly engaged in forage and turf business. They enjoy large global supply chains and high market coverage, with sales in 2018 reaching 678 million and 304 million dollars, respectively^①. In China, only a listed company called M-Grass deals in forage. The company is dedicated to germplasm resource library building, core variety breeding, scale

^①Cnagri.com. Global top 20 seed companies. (2019–11–11). <https://kuaibao.qq.com/s/20191111A0680U00?refer=spider>.

propagation, and marketing. However, it has a long way to catch up with the two transnational companies mentioned above, with the major problems of primitive production mode, lack of regional production base, backward seed production technology, forage variety shortage, and unsound forage seed breeding system.

Not benefiting from modern biological technology, China's forage breeding remains to be developed. Studies about the fundamental biological law of forage underpin modern forage breeding. Unfortunately, China remains weak in this regard^[10], which is manifested mainly in three respects. First, China's research on forage has just started recently and lags behind the international advanced level. Second, relevant disciplinary accumulation remains inadequate. In terms of research hotspots, China is lagging behind advanced countries. Third, the molecular genetics mechanism of complex traits of forage in China remains to be explored. Relevant basic research remains insufficient.

2.2 Biological characteristics of forage and bottleneck problems of forage breeding

Biological characteristics of forage are one of the major factors affecting the advance of breeding technology. Given allogamy, polysomic inheritance, heterozygosity of forage, it is hard to mine the molecular markers associated with superior traits, which limits the molecular breeding of forage. Therefore, a large majority of forage products have to be bred through conventional breeding methods. Alfalfa and Chinese wildrye are the leguminous and gramineous kings of forage, respectively. Their polysomic inheritance, inbreeding effect, allogamy, and self-incompatibility as well as large genetic variation and phenotype difference between individuals of the same variety all seriously restrict the research on their functional genome and the breeding^[11]. First, since alfalfa and Chinese wildrye are polyploid, it becomes rather difficult to use variants to mine the genes of important agronomical traits. Even if the variants with extreme phenotypes can be obtained, it is difficult to locate the mutant genes because of allogamy and self-incompatibility. Second, two extreme phenotype individuals are often used to construct recombinant inbred lines (RILs) in rice and other crops, so as to obtain the quantitative trait loci (QTLs). As RILs cannot be constructed for alfalfa and Chinese wildrye, it becomes extremely difficult to mine the QTLs^[12]. Third, even if QTLs can be fine mapped, it is rather difficult to introduce superior alleles into the starting varieties. Given the severe inbreeding depression of alfalfa and Chinese wildrye, it is necessary to simultaneously select multiple individuals and starting varieties containing superior alleles for back crossing. The individuals carrying superior alleles can be selected from progeny so as to increase the frequency of such individuals in populations, which is labor-consuming^[11].

Genome-wide association study may be a better approach

to mine superior alleles from alfalfa and Chinese wildrye. Due to the large genetic variation among individuals within the same variety, a single individual cannot represent a variety. Therefore, it is essential to select multiple individuals of one variety for genome-wide association study. However, it is unclear how many individuals should be selected to represent the polymorphism of a variety. In addition, the polysomic inheritance of alfalfa and Chinese wildrye poses great challenge to genome-wide association studies^[13]. If such a problem can be solved, genomic selection can be adopted. In other words, the breeding value of high-density molecular markers covering the whole genome can be estimated, and the individuals with a high breeding value sum of the molecular markers can be selected via recurrent selection from the progeny populations^[14].

3 Policy suggestions on innovation and development of China's forage breeding

So far, science and technology has demonstrated the contribution rate of over 56% for the development of global agriculture. However, the development of China's forage industry is lagging far behind because of the low science and technology level for forage breeding and insufficient governmental investment. The insufficient science and technology support has severely affected the modernization of forage breeding industry. According to statistics, from 1997 when the Ministry of Science and Technology launched the National Key Basic Research Development Program (973 Program) to 2014, China has established more than 60 projects of agriculture, only of four of which are related to forage (even these projects focused on ecological remediation). Although China's forage seed industry is gaining momentum, the low investment, low output, and poor platform make it difficult for China's forage seed industry to rely on science and technology and to further guarantee good security.

Chinese Academy of Sciences (CAS) launched the strategic priority research programs of Molecular Module-based Designer Breeding Systems and Precise Seed Design and Innovation in 2013 and 2019, respectively. With the support of these two programs, a batch of molecular modules with breeding value has been mined, and the theoretical and technological systems of molecular design-based breeding have been built. Compared with that for crops, the molecular design-based breeding for forage is complex and challenging.

It is suggested that the project supporting the molecular design-based breeding of forage should be launched as soon as possible. Technological innovation should be undertaken to make full use of forage resources to develop an efficient molecular breeding system integrating multiple breeding technologies (e.g., smart and precise accelerated breeding of plant factory, high-throughput phenotype acquisition) to expedite the breeding of high-quality and high-yield forage varieties.

3.1 Development and utilization of forage resources

Forage germplasm resources are important national strategic resources. They are the material foundation for agricultural innovation and sustainable development of grass-based livestock husbandry. They matter much to food security, ecological civilization, and agricultural supply-side structural reform and sustainable development. Forage germplasm resources are the basic material and gene pool for screening and breeding superior forage varieties. Thus, it is essential to collect germplasm resources for forage breeding^[15]. On this basis, systematic research on the identification and evaluation of forage germplasm resources is fundamental for mining elite germplasm resources. Establishing a scientific and standardized evaluation system for forage germplasm resources will provide strong support for screening superior forage materials, analyzing the genetic relationship between different forage varieties, and mining elite alleles^[15].

3.2 Creating new forage breeding technology based on the idea of molecular design

Conventional breeding mainly depends on experience, which is inefficient. Molecular design-based breeding, as a transforming technology for breeding super forage varieties, can precisely improve forage varieties. First, based on rich forage germplasm resources, multi-omics approaches, and the big data of genotypes and phenotypes, molecular design-based breeding integrates genome data, omic data, phenotype data, and superior allele data, thus being capable of rapidly extracting and identifying the genes conferring forage traits. Second, based on gene editing and synthetic biological technologies, molecular design-based breeding can create the forage varieties with stress resistance and high yield by modifying gene components and synthesizing gene circuits^① so as to further study the law and the forming basis of the genetic variation of stress-resistance traits, the dissection and regulation of important functional genes. Third, we should make efforts to develop new technologies of early selection, pyramiding breeding, mutagenesis breeding, ploidy breeding, cell engineering breeding, molecular marker-assisted breeding, transgenic breeding, and molecular design-based breeding to build an efficient modern forage breeding system. We should, in line with the phenological-conditions of China's forage production regions, mine the high-yield, stress-resistance, disease-resistance, and high-quality molecular modules to decipher the molecular basis of important traits and further develop high-throughput directed molecular breeding technology so as to breed elite forage varieties.

3.3 Developing technologies for accelerating forage breeding

Based on the intelligent IoT model of plant factory construction, we should develop the plant cultivation mode integrating water and electricity control, temperature and humidity monitoring, water and fertilizer control, and central control and other systems. A fully-enclosed clean production system with controllable temperature, humidity, light, and fertilizer management can be developed for accurate and efficient forage breeding. It is recommended to use high-throughput phenotype acquisition technologies (e.g., *in vivo* imaging, hyperspectrum, CT tomography, magnetic resonance imaging, unmanned aerial vehicle, and remote sensing) to create a complete high-throughput forage breeding technology from test tube to crop and from laboratory to field. Such a loop-closed mode can ensure the accuracy of molecular design-based breeding.

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