Green Revolution Gene SD1

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The green revolution gene sd1 in rice has been used for decades, but was not identified for a long time. The SD1 gene encodes the rice Gibberellin 20 oxidase-2 (GA20ox2). As such, the SD1 gene is instrumental in uncovering the molecular mechanisms underlying gibberellin biosynthesis There are ten different alleles of SD1.

Keywords: rice; green revolution; molecular mechanism; breeding

1. Introduction

Because of its success in producing more agricultural products, green revolution technologies spread worldwide in the 1950s and 1960s, and significantly improved the number of calories per acre of agriculture $^{[\underline{1}][2]}$. A major factor for the success of the green revolution was the introduction of high-yielding semi-dwarf varieties with the successful application of the nitrogen fertilizer. By contrast, the semi-dwarf varieties respond to fertilizer inputs properly with an increased yield because of their lodging resistance even under high nitrogen fertilization. This is the major reason why the green revolution can tremendously increase the yield in semi-dwarf wheat and rice $^{[\underline{3}][\underline{4}]}$.

This green revolution change in rice was caused in large part by introduction of semi-dwarf mutations, which led to a shortened culm with improved lodging resistance and a greater harvest index [4][5]. Strikingly, these short stature changes in the semi-dwarf lines were achieved mostly through mutations in a single gene, Semi-dwarf 1(SD1). This gene encodes an oxidase enzyme, GA20ox2, involved in the final steps of gibberellin synthesis [6][7][8]. Several mutations of SD1 were identified and used in rice breeding for a long time.

2. History of sd1 Utilization in Rice Semi-Dwarf Breeding

There have been many landmark achievements in rice improvement over the past 50 years, especially in theindicasub-species. Dwarf usually refers to the dwarf mutant whose plant height is equal to or less than half of the wild-type plant height at maturity, and semi-dwarf refers to the type of plant height between dwarf and normal height. In China, varieties with plant heights between 70 and 110 cm are generally classified as semi-dwarf, those below 70 cm as dwarf, and those higher than 110 cm as tall $^{[\mathfrak{Q}]}$. A major breakthrough resulted from the independent development of a series of semi-dwarf varieties in China and the International Rice Research Institute (IRRI) in the 1950s and 1960s, leading to the green revolution in rice $^{[10][11][12]}$.

Since then, a large number of semi-dwarf and high-yielding varieties carrying the semi-dwarf genesd1increased rice yield by 20% to 30%, triggering a green revolution in rice breeding [13][14][15]. In the United States, semi-dwarf rice varieties accounted for 80% of the rice acres grown in Louisiana and 55% of the total US rice acreage. Two alleles were present in the US germplasm, one semi-dwarf variety was Calrose76 [16]. The reason why it is called rice green revolution is that almost all the traditional farm rice varieties are of high-stem type, showing low yield and no lodging resistance, while semi-dwarf rice varieties show excellent characteristics such as fertilizer tolerance and lodging resistance, sturdy leaves and more panicles, high harvest index and so on [2].

3. Advantages of Semi-Dwarf Gene sd1 in Rice Breeding

At present, the main dwarf sources ofindicarice used in production are Ai-jiao-nan-te, Dee-geo-woo-gen, Ai-zai-zhan, Hua-long-shui-tian-gu and Ai-zhong-shui-tian-gu, which are all controlled bysd1^{[17][18]}.SD1can be widely used in rice breeding, especially inindicarice breeding, it has many advantages: (1)sd1promotes the moderate dwarfing of rice plants and enhanced the lodging resistance. In addition, many cloned dwarfing mutants lead to extreme dwarfing of rice plants, which are not conducive to mechanical harvesting and affects other agronomic characters. The agronomic characters, such as

heading date, plant height, effective panicles, panicle length, grain type and 1000-grain weight The results shows thatsd1only inhibits the growth of plant stem nodes, not affecting grain type, panicle type and other yield traits, but promotes the improvement of effective panicle number, seed setting rate and harvest index [19].

From the late 1950s to the mid-1970s, the mainsd1type dwarf and semi-dwarf varieties were used to replace farm high-stem varieties, and through continuous renewal, the rice yield increased from 1.892 t·hm-2in 1949 to 3.619 t·hm-2in 1977, the total yield increased from 48.65 million t to 128.57 million t [20]. With the rise of hybrid rice from the mid-1970s to the mid-1980s, excellent semi-dwarf varieties are the basis of male sterile lines and restorer lines. Most male sterile lines and restorer lines in China contain semi-dwarf genesd1. The semi-dwarf genesd1combined with heterosis have made an important contribution to the improvement of rice yield.

In order to achieve another breakthrough in yield on the basis of dwarfing breeding and hybrid rice breeding, China launched a super rice research project in the 1990s, which requires the breeding of new varieties with high yield, high quality, multi-resistance and wide adaptability. The combination of conventional technology and biotechnology was adopted in breeding. The ideal plant type of rice should have three basic conditions: strong lodging resistance, high optimum leaf area index and large number of filled grains per unit area. Through the use of markers to quickly identify the combination ofsd1and other excellent genes to achieve the purpose of molecular-assisted breeding, so as to quickly obtain super rice varieties with ideal plant type [21][22].

The yield of super rice is about 15.0% higher than that of conventional varieties $^{[20]}$. The diversity of natural variation alleles enablessd1to be widely selected and used in rice breeding. Inindicarice breeding, there are seven natural alleles ofsd1,which are the most widely selected and used $^{[21]}$. Based on the genetic analysis ofindicarice varieties popularized in China from 1950 to 1985, there are four main dwarf sources ofindicarice widely used in China, namely Ai-jiao-nan-te, Deegeo-woo-gen, Ai-zai-zhan and Guang-chang-ai—all plant heights of which were controlled bysd1 $^{[18]}$.

The derived varieties account for 83.3% of the total number of bred varieties. so on [9]. By 2012, the statistical analysis of 3656 conventional rice varieties showed that there were 19 most important core backbone parents of conventionalindicarice in China, of which seven had the largest extension area and more than 100 derived varieties, of which six contained different alleles of the semi-dwarf genesd1^[20]. In sum, the wide application ofsd1inindicarice breeding is not only related to its own gene function, but also to its widespread polymorphism in nature.

4. Prospects of Utilization of sd1 in Rice Breeding

In the past half-century, the use ofsd1has greatly increased rice yield and set off the wave of a green revolution in rice breeding. Many alleles of sd1 have been used for decades in rice breeding across many different countries. Even now,sd1is still widely introduced into elite rice varieties, demonstrating the utility and importance ofsd1in rice breeding. Therefore, the control of GA is important in cereal breeding for improved plant architecture.

With the arrival of the era of molecular design breeding, breeding objectives ranges from a single increase in yield to high quality, disease resistance and green health. Therefore, how to tap the new application value ofsd1is a new challenge for breeders. The yield output potential of the varieties bred bysd1tends to be stable, and the response to the increasing nitrogen fertilizer input is weakened. Through the further study of the functions ofsd1in nutrient element absorption, biotic stress, abiotic stress and so on, the combination of traditional breeding methods and modern molecular techniques to develop high-quality and multi-resistant semi-dwarf varieties is the direction of breeding in the future.

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