Genetic Analysis of Semidwarfness and Grain Shattering of Chinese Rice Variety “Ai-Jio-Nan-Te”

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In order to clarify the inheritance of the semidwarfness of a Chinese variety Ai-Jio-Nan-Te (AJNT), two semidwarf near-isogenic lines of a variety Norin 29, SC-AJNT and SC-TN1, were developed through recurrent backcrosses. SC-AJNT exhibited the semidwarfness and shattering habit derived from the donor parent AJNT, while SC-TN1 exhibited the semidwarfness of a variety Taichung (Native) 1, which was proved to be controlled by the semidwarfing gene *sd-1*. SC-TN1, as well as Norin 29, showed non-shattering habit. The genetic analysis of culm length in the cross of SC-AJNT/Norin 29 demonstrated clearly that the semidwarfness of AJNT is controlled by a single recessive gene. Allelism test between the semidwarfing genes of SC-AJNT and that of SC-TN1 revealed that AJNT has a semidwarfing gene at the same locus as that of *sd-1*. The shattering habit of SC-AJNT was found to be controlled by a single recessive gene. The existence of a linkage relationship between the semidwarfing gene and recessive shattering gene was observed in the F₂ of the cross SC-AJNT/Norin 29 and BC₁ of the cross SC-AJNT/Norin 29//SC-AJNT. The recombination value was estimated 13.7±4.6%.

KEY WORDS: *Oryza sativa*, Chinese semidwarf variety, semidwarfing gene, grain shattering gene, linkage, near-isogenic line.

Introduction

Semidwarfing genes have contributed significantly to the development of high-yielding varieties of rice with lodging resistance and favorable plant type. Recently, the semidwarfing gene *sd-1* has attracted the attention of a large number of rice researchers because it has become apparent that the semidwarfing genes carried by the semidwarf varieties of economic importance are present at the same locus as Dee-Geo-Woo-Gen (DGWG) gene, *sd-1*, in spite of their different origin (AQUINO and JENNINGS 1966, FOSTER and RUTGER 1978, HARGROVE *et al.* 1980, RUTGER 1983, KIKUCHI *et al.* 1985, CHANG *et al.* 1985, HU 1986).

Some studies have identified other semidwarfing genes differing from *sd-1*, but most of these genes showed unfavorable pleiotropic effects with a decrease of grain yield due to the reduction of, for example, panicle length and grain size (MACKILL and RUTGER 1979, OKUNO and KAWAI 1977, CHANG *et al.* 1984). These facts indicate that the semidwarfing genes useful for practical breeding are rather limited in number. Such a narrow genetic base of semidwarfness may reduce genetic diversity and bring about genetic vulnerability (HARGROVE *et al.* 1980, KIKUCHI *et al.* 1985). Therefore the allelism tests between semidwarfing genes of source are necessary to find out new useful semidwarfing genes.

In China, the semidwarf varieties which were released during the 1960's covered an estimated 90% of the total rice-growing area by 1974 (DALRYMPLE 1986). Many *indica* semidwarf varieties of this country were derived from the Chinese semidwarf variety Ai-Jio-Nan-Te

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(AJNT). AJNT, as well as DGWG and Ai-Zai-Zhan, is one of the representative semidwarfing gene sources in China (SHEN 1980). CHANG *et al.* (1984) suggested that the semidwarfing gene of AJNT is *sd-1*. But clear experimental evidence has not yet been presented.

In the current study, we examined the allelic relation between the semidwarfing gene of AJNT and *sd-1* by using semidwarf near-isogenic lines, as well as the linkage relation between the culm length and grain shattering habit. KIKUCHI *et al.* (1985) reported that the recessive shattering gene was linked with *sd-1*, whereas KOBAYASHI (1973) and YOKOO and SAITO (1986) started that the dominant shattering gene was associated with semidwarfness. This paper enabled to demonstrate that the semidwarfing gene of AJNT is *sd-1*, and that a single recessive shattering gene is closely linked with *sd-1*.

Materials and Methods

By transferring the semidwarfness from AJNT into the Japanese tall and non-shattering variety Norin 29 through five backcrosses, a near-isogenic line SC-AJNT was developed. SC-AJNT also exhibited grain shattering habit similar to that of AJNT. The recurrent parent Norin 29 did not have grain shattering habit.

The semidwarf near-isogenic line SC-TN1 was used as a tester of the semidwarfing gene *sd-1*. This line was developed by transferring the semidwarfness of Taichung (Native) 1 into Norin 29 genetic background through seven recurrent backcrosses and did not have grain shattering habit. KIKUCHI *et al.* (1985) reported that SC-TN1 carry the DGWG's semidwarfing gene, *sd-1*.

To investigate the inheritance of semidwarfness in the near-isogenic line SC-AJNT, the line was crossed with Norin 29 and SC-TN1 in 1985. In the following year, F₂ seeds were obtained by self fertilization of F₁ plants, and BC₁ seeds were obtained by backcrossing the F₁ to their parents. The F₁, F₂ and BC₁ plants as well as their parents were grown in the paddy field of the Agricultural and Forestry Research Center of the Univ. of Tsukuba. Materials were sown in nursery beds on April 18 and transplanted with one seedling per hill at spacings of 24cm between rows and 20cm within rows on March 27, 1987. Material populations were sized to approximately 144 plants for each parent, 48 for each F₁, 450 for each F₂ and 90 for each BC₁.

Heading date, culm length and grain shattering habit were recorded from all plants. The culm length was defined as the distance from the ground level to the panicle base of the tallest tiller, and the shattering habit was evaluated by the number of grains shed when one panicle of a primary tiller was gripped tightly by the hand at about 50 days after heading. Most of the plants with the shattering habit shed more than 10 grains, while those without the shattering habit shed very few grains.

Results

Heading times of Norin 29, SC-TN1 and SC-AJNT, which have almost the same genetic background except for the loci of the semidwarfing genes, ranged from 28 Aug. to 31 Aug., while the heading time of AJNT were 14 Aug.. Heading times of the hybrids were also similar to those of the parents (Table 1).

Table 1. Characteristics of semidwarf variety Ai-Jio-Nan-Te, tall variety Norin 29, two near-isogenic lines, SC-AJNT and SC-TN1, of Norin 29 and their F₁s

Line and F ₁	Source of Semidwarfing genes	Heading time	Culm length	panicle length
			cm	cm
Ai-Jio-Nan-Te	(Donor parent)	Aug. 14	54.2	23.9
Norin 29	(Recurrent parent)	Aug. 29	75.4	21.6
SC-AJNT	Ai-Jio-Nan-Te	Aug. 29	55.2	19.6
SC-TN1	Taichung (Native) 1	Aug. 31	55.8	20.7
SC-AJNT/Norin 29 F ₁		Aug. 28	70.6	21.4
SC-AJNT/SC-TN1 F ₁		Aug. 29	56.9	19.7

Culm length of Norin 29 averaged 75.4cm, while those of semidwarf variety and lines, AJNT, SC-TN1 and SC-AJNT averaged 54.2cm, 55.2cm and 55.8cm, respectively (Table 1). Accordingly, the differences between Norin 29 and SC-TN1 indicated that the *sd-1* reduced the culm length of Norin 29 by about 20cm. Culm length of the F₁ plants of SC-AJNT/Norin 29 which averaged 70.6cm was higher than that of the mid-parent and close to that of the higher parent. On the other hand, the F₁ plants of SC-AJNT/SC-TN1 were semidwarf and their culm lengths averaged 56.9cm.

Culm length in F₂ of SC-AJNT/Norin 29 ranged widely from 44cm to 92cm and exhibited a bimodal distribution (Fig. 1). By taking the valley of distribution as the dividing point, the F₂ population was separated into two height classes with 345 tall and 107 short plants, which fitted to the 3:1 segregation ratio expected for one gene segregation model (Table 2). Furthermore, in the BC₁ of SC-AJNT/Norin 29//SC-AJNT, culm length ranged from 50cm to 88cm and exhibited a bimodal distribution segregating 54 tall and 42 short plants. This segregation pattern fitted to the 1:1 segregation ratio expected for the one gene segregation model in the backcrossed generation. Culm length of the BC₁ of SC-AJNT/Norin 29//Norin 29 ranged from 66cm to 88cm, and was distributed in the range of Norin 29. These results obtained in the three hybrid populations suggest that a single recessive gene controls the semidwarfness of SC-AJNT and AJNT.

In order to test the allelism between a single recessive gene of AJNT and *sd-1*, we investigated the variations for culm length in the hybrids between SC-AJNT and SC-TN1. In the F₂, almost all the plants were distributed in the ranges of two parental values. Also the culm lengths in two BC₁s of SC-AJNT/SC-TN1//SC-AJNT and SC-AJNT/SC-TN1//SC-TN1 were distributed within the range of the parents and all the plants exhibited a short stature (Fig. 2). These results indicated that SC-AJNT and SC-TN1 have the semidwarfing recessive gene *sd-1* in common.

SC-AJNT and AJNT exhibited grain shattering habit, while Norin 29 and SC-TN1 exhibited non-shattering habit. Therefore, we investigated the mode of inheritance of shattering habit by using the hybrid populations of SC-AJNT/Norin 29 and SC-AJNT/SC-TN1. It was shown that the F₁s of SC-AJNT/Norin 29 and SC-AJNT/SC-TN1 exhibited non-shattering habit. In the F₂ of SC-AJNT/Norin 29, the BC₁ of SC-AJNT/Norin 29//SC-AJNT, the F₂ of SC-

Fig. 1. Frequency distribution of culm length and relationship between culm length and grain shattering in the F₂ and BC₁ populations between SC-AJNT and Norin 29 (N29).

Black histogram indicates frequency of plants with shattering habit.

Fig. 2. Frequency distribution of culm length and relationship between culm length and grain shattering in the F₂ and BC₁ populations between SC-AJNT and SC-TN1.

Black histogram indicates frequency of plants with shattering habit.

AJNT/SC-TN1 and the BC₁ of the SC-AJNT/SC-TN1//SC-AJNT, plants with and without the shattering habit appeared (Fig. 1 and Fig. 2). The F₂ population of SC-AJNT/Norin 29 was separated into 328 plants without the shattering habit and 124 plants with the shattering habit, while the F₂ of SC-AJNT/SC-TN1 was separated into 336 plants without the shatter-

Table 2. Segregation of plant height and shattering habit in two F₂ and two BC₁ populations derived from the crosses among SC-AJNT, Norin 29 and SC-TN1

Population	Number of plants					Combination of two characters	Tall: Semidwarf	NS:SH
	Tall		Semidwarf		Total			
	NS	SH	NS	SH				
						χ^2	χ^2	χ^2
SC-AJNT/Norin 29 F ₂	306	39	22	85	452	195.69 (9:3:3:1) P<0.001	0.42 (3:1) 0.75>P>0.50	1.43 (3:1) 0.25>P>0.10
SC-AJNT/Norin 29 //SC-AJNT BC ₁	53	1	2	40	96	87.92 (1:1:1:1) P<0.001	1.50 (1:1) 0.25>P>0.10	2.04 (1:1) 0.25>P>0.10
SC-AJNT/SC-TN1 F ₂	0	0	336	114	450	————	————	0.03 (3:1) 0.90>P>0.75
SC-AJNT/SC-TN1 //SC-AJNT BC ₁	0	0	41	43	84	————	————	0.05 (1:1) 0.90>P>0.75

NS; plants without shattering habit SH; plants with shattering habit

ing habit and 114 plants with the shattering habit. These segregation patterns fitted to the 3:1 segregation ratio (Table 2). Also the BC₁ of SC-AJNT/Norin 29//SC-AJNT was separated into 55 plants without the shattering habit and 41 plants with the shattering habit, and the BC₁ of SC-AJNT/SC-TN1//SC-AJNT was separated into 41 plants without the shattering habit and 43 plants with the shattering habit. These segregation ratio fitted to 1:1 expected for the one gene segregation model in the backcrossed generation. These results suggest that a recessive shattering gene controls the shattering habit of SC-AJNT.

Thus, in the F₂ of SC-AJNT/Norin 29 and the BC₁ of SC-AJNT/Norin 29//SC-AJNT, it was obvious that shattering habit was associated with culm length (Fig. 1). This association implied the existence of a linkage relation between shattering habit and semidwarfness. In the F₂ of SC-AJNT/Norin 29, most of the tall plants exhibited the non-shattering habit while most of the semidwarf plants exhibited the shattering habit, though tall plants with shattering habit and short plants with non-shattering habit, which were considered as recombinants, were also found. The recombination value between the shattering gene and semidwarfing gene *sd-1* which was calculated by the productive ratio method (FISHER and BALMUKAND 1928) on the basis of F₂ data was $13.7 \pm 4.6\%$.

Discussion

The use of the semidwarfing gene has contributed to the development of high-yielding semidwarf rice varieties in recent years. However, excellent semidwarfing gene sources, such as a native variety DGWG in China and Jikkoku in Japan as well as a semidwarf mutant variety Reimei in Japan and Calrose 76 in USA, that have played the significant role in the breeding of rice, were found to carry the same semidwarfing gene *sd-1* on the 3rd linkage group (AQUINO and JENNINGS 1966, HEU *et al.* 1968, HU 1973, SUH and HEU 1978, RUTGER 1983, KIKUCHI *et al.* 1985.)

The Chinese semidwarf variety AJNT was developed by pure line selection from Nan-Te 16 (SHEN 1980) which was derived from the cross between Nan-Tei-Hao and Sheng-Li-Xian. After AJNT was released in South China in 1957, many semidwarf varieties such as Ai-Nan-zao, Nan-Lu-Ai, Tie-Gu-Ai and Qiu-Ai were derived from AJNT. In this study, we could clarify that AJNT carry the semidwarfing gene *sd-1*. Therefore, it was inferred that a large number of the Chinese semidwarf varieties derived from AJNT carry the semidwarfing gene *sd-1*, just as most of the semidwarf varieties in other countries.

In practical crossbreeding, the use of semidwarf varieties carrying *sd-1* as parents increases the chance of finding desirable plants with a short stature and other favorable traits, because the segregating plants are likely to exhibit semidwarfness and therefore the probability of the appearance of superior semidwarf plants may increase.

However, though the use of most of the semidwarf varieties which have the semidwarfing gene *sd-1* is convenient for semidwarfness breeding as described above, it is anticipated that genetic vulnerability may occur through the reduction of genetic diversity (HARGROVE *et al.* 1980, KIKUCHI *et al.* 1985). Since it is assumed that many semidwarf varieties in China also carry *sd-1* from the results of this study, it is important to detect other useful semidwarfing genes in order to expand the genetic diversity of semidwarfness.

In addition, this study revealed that the semidwarf near-isogenic line SC-AJNT derived from AJNT carried a single recessive shattering gene linked with *sd-1*. It was suggested that this shattering gene was incorporated into SC-AJNT together with *sd-1*, as chromosome block of AJNT. This assumption is based on the fact that Norin 29 which is the recurrent parent of SC-AJNT exhibited the non-shattering habit while AJNT, the donor parent, exhibited the grain shattering habit. KIKUCHI *et al.* (1985) reported the presence of a linkage between *sd-1* and a recessive shattering gene, based on the genetic analysis of semidwarf near-isogenic lines derived from DGWG and Jikkoku, respectively. Also, in Shirasenbon which is the native variety in Central Japan, OBA *et al.* (1988) observed that one recessive shattering gene was linked with *sd-1*. Therefore, it is suggested that like *sd-1*, the recessive shattering gene in this report may be present in many other shattering varieties worldwide.

Though a large number of studies on the inheritance of the shattering habit have been published (RAMIAH and HANUMANTHA 1936, KADAM 1937, NAGAO and TAKAHASHI 1963, KOBAYASHI 1973, SHASTRY and SEETHARAMAN 1978, JIN *et al.* 1982, ISHKUMAR and SHARMA 1982, GOTO and BALUCH 1984, YOKOO and SAITO 1986), the *sh* gene on the 8th linkage group (KINOSHITA 1984) is the only shattering gene in which the locus was identified. The shattering gene observed in this study differs from *sh*, in being linked with the semidwarfing gene *sd-1* on the 3rd linkage group. KOBAYASHI (1973) demonstrated the presence of a dominant shattering habit associated with semidwarfness in the genetic analysis of the cross between the semidwarf *indica* variety IR8 with the shattering habit and two tall *japonica* varieties without the shattering habit, Todorokiwase and Fujiminori. Also, YOKOO and SAITO (1986) reported similar findings in the crosses between Milyang 23, a semidwarf Korean variety with the shattering habit, and some tall *japonica* varieties without the shattering habit. JIN *et al.* (1982) reported that two dominant genes control the shattering habit of Yushin, a Korean variety. One of these dominant genes controls the formation of an abscission layer at the longitudi-

nal section of the pedicel and the other controls the crack of parenchymatous cells in the abscission layer. According to the pedigree records of IR8, Milyang 23 and Yushin, these varieties which are derived from DGWG carry the recessive shattering gene together with the semidwarfing gene *sd-1* which was presumably inherited from DGWG. Therefore it is assumed that the other shattering gene modify the expression of the recessive shattering gene linked with *sd-1*. However, to confirm this hypothesis further studies are required.

The existence of a linkage relation between the recessive shattering gene and the semidwarfing gene *sd-1* has an important implication in the selection of semidwarf plants in hybrid populations. In using a semidwarf variety with the shattering habit as parent for cross-breeding, if the breeder pays attention only to the selection of semidwarfness, the selected plants will most probably exhibited shattering. Furthermore, even by selecting plants without the shattering habit, there is a high probability that these plants may be heterozygotes at the shattering gene locus, and the progeny of the selected heterozygous plants without the shattering habit would result in the segregation of plants with the shattering habit. Therefore, the breeders must pay attention to the linkage relationship between semidwarfness and the grain shattering habit in the process of selection for desirable genotypes.

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中国のイネ品種矮脚南特の半矮性と脱粒性の遺伝子分析

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中国のイネ品種矮脚南特が示す半矮性と脱粒易に関する遺伝子分析を行った。実験には、わが国の水稻品種農林29号と、その遺伝的背景に矮脚南特および台中在来1号の半矮性遺伝子をそれぞれ導入した半矮性準同質遺伝子系統SC-AJNTおよびSC-TN1を用いた。SC-AJNTは脱粒易を示したが、農林29号とSC-TN1はともに脱粒難であった。また、SC-TN1は低脚烏尖の半矮性遺伝子*sd-1*を持つことが明らかにされている系統である。

SC-AJNTと農林29号を交雑した結果、矮脚南特の示す半矮性は単一劣性の半矮性遺伝子に支配されることがわかった。次に、SC-AJNTと半矮性遺伝子*sd-1*を持つSC-TN1とを交雑したところ、その雑種はすべて半矮性を示し、矮脚南特は半矮性遺伝子*sd-1*を持つことが明らかになった。脱粒性に関しては、SC-AJNTと農林29号、SC-AJNTとSC-TN1の雑種から、SC-AJNTの脱粒易は矮脚南特に由来する単一劣性の脱粒性遺伝子に支配されることが明らかになった。また、SC-AJNTと農林29号の雑種F₂、BC₁集団における脱粒性と稈長の分離比から、矮脚南特に由来する脱粒性遺伝子は半矮性遺伝子*sd-1*と13.7±4.6%の組換え価で連鎖することがわかった。