

Historical Review of Semidwarf Rices and Breeding of a New Plant Type for Sustainable Agriculture¹

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ABSTRACT

The evolution of rice was not under the pressure of fertilization and its relationship to insects and parasites until recent years. DGWG semidwarf (sd_1) is a major gene mutation which has pleiotropic effects causing dark erect leaves and compact assembly stems that respond to N application, making the plant look like a bush. High density of planting with intensive fertilization maximizes the productivity and the use of space. However, it also provides an excellent environment for insect and parasite reproduction. The occurrence of pest epidemics has resulted in a disaster for rice history.

This paper analyzes plant morphologies in relationship to high yield and presents a new semidwarf plant type (sd_6) secured from an induced mutation. The reduced tillering compensated by more spikelets per panicle and the open-stemmed morphology provide better ventilation within the plant and direct sunlight to the bottom of the plant, an unfavorable environment for insect and fungus growth which is a primary concern in the agro-ecosystem. This will reduce pesticide use, water pollution and soil damage. The new plant type provides for a natural self-protection system.

Studies on increasing genetic diversity of cultivars, the sd_6 semidwarf of Indica long-grain has been crossed with sd_1 semidwarf of Japonica short-grain sweet rice. The F_1 plants showed high fertility (85%) and the F_2 seed-set segregated into a 9 (>70): 3(60-69%): 3(40-59%):1(<40%) ratio. The variation of brown rice size (L/W ratio) of F_3 seeds fell into the normal distribution range between two parents. This variation was exemplified by the sample of rice seeds excavated from Homudo, China, which is estimated to be about 7000 years old. The results suggest that the Japonica Indica cross can be traced to the original genetic diversity of the rice species, *Oryza sativa* L.

Selection on conventional semidwarf vs. open-stemmed semidwarf plant type with various grain size, glutinous vs. non-glutinous, different maturity, etc. were done. The high fertility F_2 segregants were found bred true at advanced generations. Yielding tests on conventional and new cultural method will be carried out. The results of breeding primarily obtained are encouragement.

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Key words: rice, semidwarf, intensive culture, pest-management, ecosystem, genetic diversity, Indica-Japonica breeding.

Introduction

The modernization of agriculture is characterized by monoculture with uniform genotype which covers a large area⁽⁵¹⁾. Intensive field management includes high density of plants (or livestock), heavy fertilization, chemicals for growth regulation, and spraying herbicides and insecticides, *etc.* Often other organisms which are associated with the cropping are ignored. The current production system is not always appropriate. Like a spider's network for the ecosystem, Darwin's concept of natural selection was largely dismissed by later scientific approaches. Agricultural research has often been poorly informed and sometimes misguided. Therefore, the whole picture of the agro-ecosystem deserves more attention. We are facing the changing environment with polluted air, water, soil and food contamination resulting from industrialization. For human survival, these problems cannot be solved merely by plant breeders. Plant scientists should firstly increase the genetic diversity of cultivars in the breeding programs; secondly reorganize the cultural practices, and thirdly lessen the soil damage by using the appropriate organic fertilizers⁽²⁷⁾. This paper aims to review the development of rice production resulting from an unexpected disaster when a semidwarf plant type provides an excellent host plant for insects and parasites. A breeding program for genetic diversity with alternative semidwarf plant type is also presented.

Historical Review of Semidwarf Rice Origin and Use for High Yield Varieties (HYV's) Breeding

The so-called "Green-Revolution" in rice started in the late 1960's when semidwarf cultivars carrying the DGWG (sd_1) gene were developed by hybridization. Today most of the HYV's share this sd_1 locus. Why does sd_1 contribute to high yield? Why do we need an alternative? How to increase the genetic diversity and maintain plant type in semidwarf? First of all, let us trace back to the origin of semidwarf rice.

Semidwarf rice was first listed in an official report of the Japanese colonial government (1906) who took over Taiwan and surveyed the rice cultivation. Among 375 rice cultivars listed, as many as 8 to 9 had a "short-leg" or dwarf on the name. For instance, Woo-Gen (WG) was a leading cultivar spreading over the west coast of Taiwan at that time. Dee-Gee-Woo-Gen (DGWG) was found in Hsinchu which was known to be a strongly windy area. Dee-Gee means short-leg and DGWG probable arose from spontaneous mutation⁽²²⁾. Two Chinese books: Taiwan Fu-Shi (Government note) and Tanshui Tein-Shi (County note) published in 1717 and 1871, respectively, described the rice cultivars and methods of cultivation, but none of them were named short-leg^(31,32). Therefore, semidwarf rice must have appeared in Taiwan during the late 19th century⁽²⁷⁾.

Semidwarf rice can be artificially induced by radiation. Thermal neutrons and chemicals were also used to successfully develop the semidwarf mutants in Taiwan^(22,42,43). But due to the similarity of the plant type, induced mutation for rice improvement was ignored in Taiwan⁽³⁰⁾ until admitted by Reimei in Japan and Calrose 76 in USA^(15,47,54,58).

Mainland China is thought probably to have the earliest semidwarf rice which then spread into Taiwan about two to three hundred years ago^(14,40). According to two authorized books on rice, recently published in 1986 and 1991 in China^(2,44), breeding of reducing plant height was not accomplished until Ai-Jiao-Nan-Teh (AJNT) was found in 1959. The short plant AJNT was discovered after an incident of typhoon passing which knocked down all the tall rice. DGWG has no other origin but Taiwan. IR8 introduced to China from the International Rice Research Institute (IRRI), Philippines of 1967. Apart from the IRRI, at least four or more semidwarf rices were introduced from southeast Asia during the 1950 to 1960's or earlier. Among them, Ai-Zai-Zhan was originated from Indonesia domesticated in Guangsi⁽⁴⁴⁾. It was the most widely used as semidwarf donor parent for cross-breeding as well as involving in hybrid rice. Incredibly, with over 30 million hectares of rice grown in China⁽¹⁴⁾, all semidwarf germplasms, either local or imported, carried at the same locus of DGWG⁽⁴⁴⁾.

Rice Evolution in Response to Nitrogen (N) Application

Generally speaking, rice was not affected from the pressure of fertilization until early in this century. Since the 1920's, applying chemical fertilizer, especially nitrogen, was the way to increase crop production per unit area. Before the semidwarf was widely grown, rice cultivation in the Asian tropics depended on tall or long stem rice as the only possible survivor from weeds and flooding. As a matter of fact, rice yield in tropical Asia has depended with organic manure. Table 1 shows that before HYV's were available, only a little N was used in south and southeast Asia.

Table 1. Nitrogen use per hectare of crop area in Asia from 1961/62 to 1969/70
(Source: FAO Production Year Books). (from R. Barker 1972)

	Nitrogen applied (kg/ha)		
	1961/62	1965/66	1969/70
South Asia (a)	2	4	8
Southeast Asia (b)	3	4	9
East Asia (c)	115	122	155

a. Ceylon, India, Nepal, Pakistan (E & W).

b. Burma, Indonesia, Malaysia, Philippines, Thailand, S. Vietnam.

c. Japan, Taiwan, Korea.

From the data taken in Taiwan, averaging six years of the first decade of 20th century shows that Indica rice at N: 7.5 kg/ha yielded 2.79 t/ha brown rice in comparison to Japonica rice at N:10.4 kg/ha with yields of 2.86 t/ha⁽³⁴⁾. This indicates that the two ecotype rice cultivars were a little different. However, as an example, during 1905 to 1962, Hokkaido rice in Japan had gradually increased its N application to 120 kg/ha for production. New cultivars development were since carried out under such condition. By gradually reducing the plant height and increasing tillers, yields were doubled from 3 tons to 6 tons per hectare^(48,49). Cross-breeding in Taiwan was started in the late 1920's by using the Japanese varieties. A group of Japonica cultivars adapted to sub-tropical environment known as "Horai" (or Ponlai in Chinese) was developed in 1930's. These cultivars were also reducing plant height with N application from 90 to 130 kg/ha⁽³⁴⁾.

Taiwan native rice, Indica, was also hybridized in 1920's but no cultivar has been released. Indica rice was found producing straw weight more than grain weight. As to efficiency of N for grain yields, Japanese rice was twice that of the first crop of Taiwan native rice, and the second crop of native rice had only half the yielded of the first crop⁽³⁵⁾. Because of lodging of Indica rice increasing the N rate of application has not brought positive effect on grain yields.

After World War II in Taiwan Mr. Hong Chiu-Tseng, at the Taichung District Agricultural Improvement Station (DAIS), used a lodging resistant short-stature DGWG to cross with drought resistant tall rice Tsai-yuan-chung for a breakthrough to develop a lodging resistant Indica rice, TN1, with high yielding capacity. The N application to improve the Indica semidwarf rice in Taiwan was carefully increased up to 80 kg/ha level^(30,42,43). The productivity of TN1, IR8 or DGWG derivatives was later found to be basically similar to Japonica. Presently N application to Indica semidwarf rices is recommended to 150-180 kg/ha for the 1st crop and 125-160 for the 2nd crop, about 25% more than for Japonica cultivars in Taiwan⁽⁴⁴⁾.

Farmers in South Korea used chemical fertilizers in excess of the government recommendation of N:200 kg/ha dosage. Thus, the "Successful Green Revolution" by the shift from Japonica rice to Indica semidwarf cultivars was depressed by the outbreak of rice blast disease mainly due to blast fungus adaptation by accelerated of the excess N application^(13,14,27).

Rice culture in California began with introduction of Japonica cultivar from Japan in 1912. It started with grain yield at 3 t/ha which was gradually raised to 6 t/ha in the early 1970's mainly by improvement of field management. The plant type remained the tall and late maturing until improved by induced mutation^(27,54). Calrose 76 was the first semidwarf rice cultivar in California⁽⁵³⁾. It carried a similar DGWG semidwarfing gene (sd_1) which was able to elevate productivity to 9 t/ha⁽¹⁴⁾ without much change in its genotype and field management. Calrose 76 was further improved by integration of desirable Indica genes and developed Calpearl⁽²⁴⁾ raising productivity 10% more with early maturing and yield stability. The super productive genotype of Calpearl was then crossed to Japanese glutinous rice and developed NFD 109⁽²⁵⁾. It was the first time for California sweet rice to reach 10 t/ha in commercial production and to provide superior quality rice for mochi-cake making. Rice growers in California generally apply 160 to 220 kg/ha of N chemicals. The excess N application does not increase yields significantly⁽¹⁹⁾. The fewer rice disease and insect found in California primarily because of low humidity and isolated from other rice growing area⁽²⁷⁾.

The Mechanism of High Yielding by Means of Semidwarf

The high yield in relation to semidwarf plant type can be considered in several ways. Firstly, the plant morphology analyses of semidwarf plants in comparison with tall lodging cultivars were completed⁽²²⁾. To eliminate the effects of other genes on lodging and yields, the writer used induced semidwarf mutants to compare to their tall parents, DGWG and WG, and TN1 and IR8 were used as checks. All materials were grown side by side under the same field managements. Rice plant at maturity generally has five elongated internodes. All semidwarf rices had a sd_1 gene and showed the same pattern of

internode elongation which reduced the length in all internodes, especially in the 4th and 5th that were responsible for lodging resistance. The same pattern of shortening was also found in Reimei, an induced mutation cultivar developed in Japan⁽¹⁵⁾.

The semidwarf mutants had little effect on the panicle length, number of spikelets and the size of kernel⁽²²⁾. High yields found in induced semidwarf mutants and their derivatives revealed that the parent materials used for this breeding were a good genotype in grain yield components except for their long stem. In other words, induced mutation of semidwarf has removed the genetic barrier and manipulated the real productivity of the genotype without any loss by lodging. Therefore, to use the semidwarf genotype as a donor for cross breeding genes other than semidwarf should be considered. DGWG or TN1 and IR8, as well as AJNT in China, usually are associated with poor rice quality and disease such as susceptibility to bacterial leaf blight⁽²²⁾.

Semidwarf can be caused by a different pattern of internode elongation. The first internode length can be changed by gene *eui* mutation⁽⁵⁵⁾, or by genes of *Shp* which are responsible for the incomplete panicle exertion⁽⁴⁵⁾. Genes that change the panicle characters sometimes affect the plant height. A non-shattering short-stature mutant was found to lack the abscission layer. An erect mutant, with shorter plant height, changes in structure of the culm enlarged diameter of cross-section, and increased number of vascular bundles, was found to have reduced elasticity and to break easily with the passing of strong wind⁽²³⁾. Chromosomal aberration and changes in the number of chromosomes associated with short-stature and sterility⁽²¹⁾ were not desirable for developing of cultivars. Semidwarfs other than DGWG locus were found to be poor in productivity and agronomic characteristics⁽¹¹⁾. However, an exceptional semidwarf mutant which had an open-stemmed normal agronomic characteristic may be useful as an alternative plant type^(25,26), as will be discussed later in this paper.

Secondly, the *sd₁* gene expressed a compact stem and pleiotropic effect on the characteristics of leaves. Leaves changed to dark green with erect and thick blade that were considered to be better for light interception. Consequently, the semidwarf plant increased the efficiency of photosynthesis^(46,49,64).

Thirdly, The vegetative characteristics of Indica rice are maintained in the semidwarf plant. The number of tillers is increased, providing additional heads per plant. Shorter internodes and leaves also significantly reduced the proportion of straw weight and resulted in high harvest index⁽²⁷⁾. The most critical time for spikelet development is at the elongation of internodes. Reducing the length of internodes results in increased translocation of hydrocarbon to the panicle and in high harvest index of semidwarf rice (comm. with Prof. J. S. Weng of NCHU).

From the plant physiological aspects, Yoshida⁽⁸⁾ has stated that erect thick leaf, short stiff stem, assembly stems, high fertility of spikelets, and high harvest index are five important morphologies for HYV's⁽⁴⁶⁾. The semidwarf plant type of IR8 as a model for Indica rice breeding⁽³⁶⁾ has provided a guide line for about 30 years. The canopy formation and maintenance of Japonica short-stature rice proposed by Tsunoda⁽⁶⁴⁾ emphasized similar morphological traits and was cited by Japanese textbooks of

breeding^(46,48,49). However, semidwarfing gene sd_1 is a gene which controls the length of stem but is not involved directly in yielding components⁽²⁷⁾. It is a very important gene as a building block of HYV⁽⁵⁵⁾.

Fourthly, perhaps the most important factor related to high yielding, is the planting density. Traditional planting of tropical single cropping rice is around 10 plants (hills) per 1 m. Intensive field management recommended additional hills with high dose of N application, resulting in more panicles per unit area and maximizing the use of a given space. For a long time, rice production in India averaged about 1 t/ha^(8,52). When the old tall cultivars were replaced by a new semidwarf in a high density with intensive management irrigated field, IR8 was able to produce as many as 7-11 t/ha⁽⁵⁹⁾.

The above review has shown that the yielding capacity of rice, either Japonica or Indica, grown in temperate or tropical areas, has raised to 10 t/ha level during the 20th century. Genetically speaking, a Mendelian gene DGWG (sd_1) mutated in Indica rice has brought productivity equivalent to that of the short-statured Japonica produced by selection of polygenes during a half century in Japan. California rice (Japonica) has not under the pressure on selection of short-stature until 1969. By induced mutation and followed cross breeding, in less than 20 years have completely changed rice cultivars into semidwarf, caused by the same locus of DGWG (sd_1)^(27,55).

The Relationship between Pest Epidemic and sd_1 Plant Type

To meet with the crisis of increasing population in Asia after the second world war, a semidwarf genotype with high N fertilization and high density planting which was considered to be a scientific high production in food supply. Basically, this is not a bad idea but unfortunately the rice field with intensive and widely grown a same type of cultivars are changing environment which provided a good condition and host plants for insects and disease fungi reproduction. Virus disease was not known in rice before IR8 grown in the Philippines in 1960's, and bacterial leaf blight and brown planthopper (BPH) were only minor problems before semidwarf cultivars widely spreaded in tropical Asian rice growing countries in 1970's^(27,38,39).

In 1973, the writer tested three sets of semidwarf cross to their tall mother lines in National Chung-Hsing University (NCHU), Taichung. The F_2 populations were grown as a second crop for genetic studies. Unpredictably, rice populations were subjected to a heavy incidence of naturally occurring BPH. Data of the damaged plants were collected from the individual plants during the heading to ripening.

Fig. 1 shows the distribution of plant height and segregants subjected to BPH in F_2 population of DGWG X WG. Plant height segregation was in good fitness of 3 tall:1 semidwarf ($P=0.90\sim 0.95$). The proportion damaged by BPH was calculated to be a ratio of 1 tall:7 semidwarf. The other two F_2 populations (IKB 4-2 X IKB and KT20-74 X KT) appeared to show the same characteristics and are omitted here⁽²⁷⁾.

As mentioned above, the semidwarf plant has pleiotropic effects in the compact assembly stems and dark green erect leaves which make poor ventilation within the plant. The foliage canopy produces higher humidity than for tall plants with open stems and light green leaves. The writer has seen a lot of BPH getting to the stems of semidwarf plants while the tall plants experienced none or few. When the

semidwarf stems were exposed, BPH reacted to the light and quickly moved to the back side of stems. The tall and semidwarf segregants of F_2 population were randomly transplanted at one plant per hill (25 X 25 cm). The damaged plants revealed that BPH selectively chose the semidwarf plants as its host.

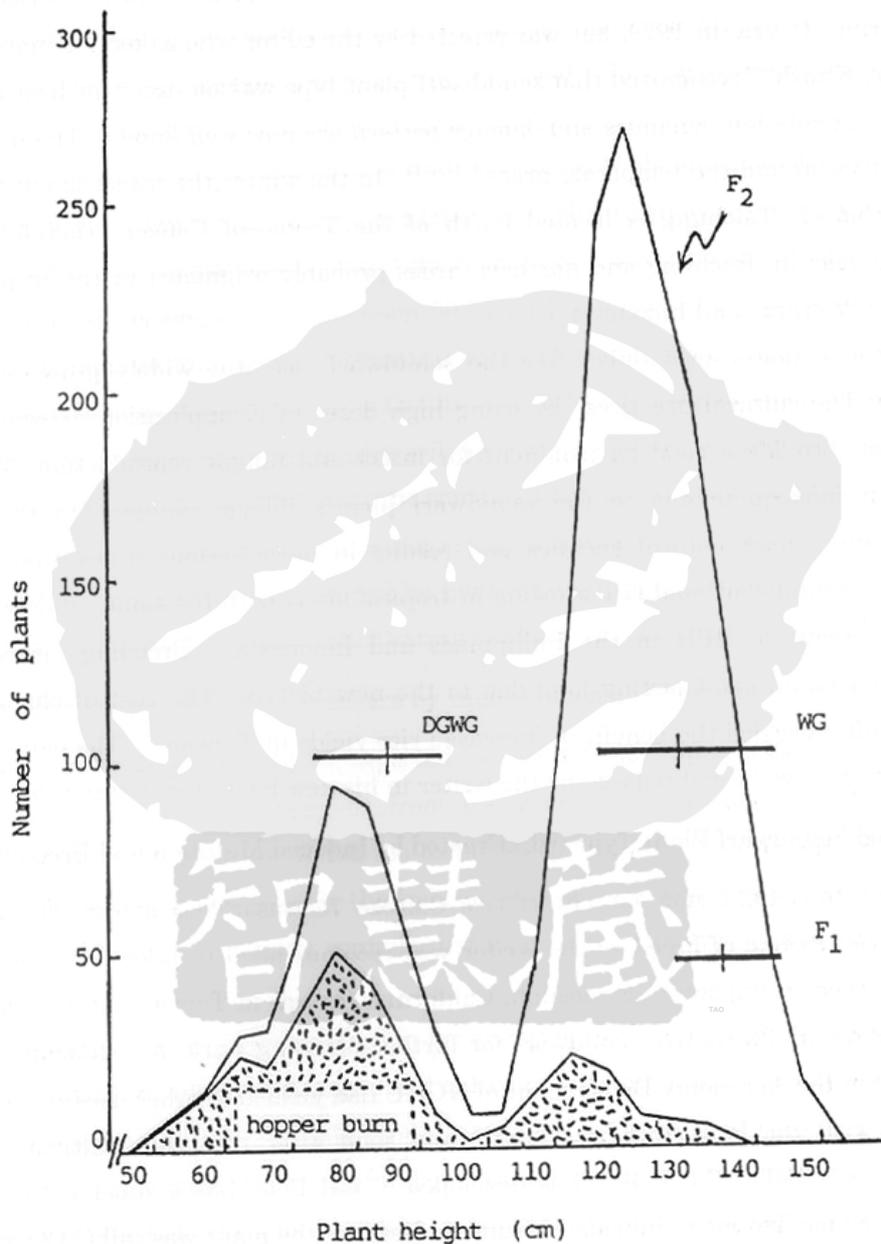


Fig. 1. Distribution of plant height and brown planthopper damaged plants in F_2 population of DGWG x WG.

Since the tall and semidwarf segregants differed within allele but other genes of the studied F_2 populations were identical, there should be no resistant or susceptible segregation occurring. To verify this point of view, the writer sent seedlings of semidwarf mutants and of their tall mother varieties to the Dept. of Entomology of NCHU and to the Taiwan Agricultural Research Institute in Chiayi for cage feeding tests. Both locations came up with the same results: that semidwarf and tall were equally susceptible.

During the early 1970's we did not have enough information about the habitat of BPH in rice. However, while as a life member of Rice Technique Workers Association in India, the writer had learned that India suffered from BPH damage. He had sent short notes of the observations to the association journal "Oryza" in 1979, but was rejected by the editor who asked for more observations. Five years later, Khush⁽³⁸⁾ recognized that semidwarf plant type was an excellent host plant for BPH. BPH's behavior, population dynamics and damage pattern are now well known. The life cycle of BPH is different in tropical and the temperate areas^(57,59,63,66). In the winter, the insect is not found north of the Tropic of Cancer. Taichung is located north of the Tropic of Cancer, therefore, infestation developed every year in Taichung and northern areas probably originates in the tropics and comes from Philippines, Vietnam and Indonesia.

BPH became a major pest only after the semidwarf rice was widely grown to replace the traditional tall. The cultural practices, by using high doses of N application associated with high density of plants, provide a good environment for insect and fungus reproduction. The insecticide sprays are often inadequate due to the semidwarf plant's foliage canopy. On the other hand, insecticide also kills those natural enemies and results in more serious infestation the following year⁽³³⁾. The year around continual rice growing in tropical areas with the same semidwarf plant type has brought outbreaks of BPH in the Philippines and Indonesia⁽⁹⁾. Breeding for resistant BPH cultivars has been found can't lasting long due to the new biotype. The cost of chemicals for pest control has already exceeded the benefit of increased rice yields in Taiwan⁽²⁷⁾. The gains and losses of the green revolution have been discussed by the writer in his new book, *Rice Cytogenetics and Breeding*.

An Open-stemmed Semidwarf Plant Type (sd₆) Created by Induced Mutation and Breeding Program

In 1976, the first California semidwarf rice Calrose 76 was released from the University of California at Davis, as one of breeders the writer was recommended to take over the rice breeding program at N. F. Davis Company in Firebaugh, California. He was in Taiwan but was thinking of the possibility of finding an alternative semidwarf for further breeding work in California, because 90% of the rice facility in the Agronomy Department of NCHU had yielded to other uses.

He started with the long-grain rice cross, and soon after that first cultivar of California long-grain, California Belle (Cal Belle) was developed⁽²⁴⁾. Cal Belle has a super eating quality and opened a brand new market for California consumers. Because the plant was tall (113 cm height) and subject to lodging if over-fertilized, the next step was to improve its lodging resistance by induced mutation. The seeds were treated with Co⁶⁰ in 1981 and a number of elite plants were secured at M₂. Among them, R-31 (109 cm height with strong culms), R-16 (92cm height) and R-34 (85 cm height) were taken into the genetic studies. R-16 had a locus similar to sd₁. Crosses between R-16 and R-34 showed a 9 (>95 cm):6:(65-94 cm):1(>63 cm) ratio in F₂ which revealed that R-34 is a new semidwarfing gene and was assigned as sd₆^(25,26). The characteristics of sd₆ are that it is slightly shorter than sd₁, with stiff open-stem and increased number of spikelets per panicle but slightly smaller in grain size. To remedy this short-coming, a large seed size with good fertile Brazilian long-grain segregating line L. S. 79-1 was used for

cross-breeding. The line was purified and maintained in the laboratory by the writer. A vigorous growing open-stemmed semidwarf line NFD 148 was selected and its sib NFD151 (R-16/R-31), and check varieties (L-202, sd_1) etc. were taken into various tests. To find out the differences between sd_1 and sd_6 in grain productivity, reaction to N application, and/or organic fertilization, tests were done at N. F. Davis rice experimental farm in Firebaugh and different rice growing areas of California. The performance of sd_1 , sd_6 and their derivatives had about the same productivity, except sd_1 showed a slightly higher yield. This was probably due to the field management not designed for the new sd_6 plant type^(28,29).

It is interesting to point out that R-34 mutant reacted to N chemical fertilizer slower than other lines or check cultivars, but its derivative, NFD148, was able to show the same yielding capacity as sd_1 varieties. When the winter cover crop (green manure) was plowed into the rice field before planting, however, all tested rices at minimum 50 kg/ha N chemical block were found to yield equal or higher than maximum 200 kg/ha N chemical block (without green manure) from the previous year. This reveals the importance of organic fertilizer, with less N chemicals, for higher yield⁽²⁸⁾.

As indicated previously, sd_1 worked primarily as a building block with desirable yield component genes through cross-breeding for HYV's. In the same manner, sd_6 can also be a building block because both sd_1 and sd_6 are major Mendelian genes. An aromatic long-grain rice with Cal Belle genotype and sd_6 semidwarf plant type has been developed by hybridization, in California having the same level of productivity but earlier maturing and better eating quality than the check cultivar A-301⁽²⁹⁾.

Increasing Genetic Diversity of Rice Cultivars by Indica-Japonica Cross and Breeding

Increased genetic diversity can be expected to result from interspecific hybridization, from *in vitro* cell fusion of unrelated genera, or from the genetic engineering transfer of exotic genes; however with only one exception, these bio-technological studies have not proved useful for rice cultivar development. This exception is the hybridization of the wild species, *Oryza nevara*, with the closely related cultivated rice *O. sativa*, contributing its gene for virus resistance through conventional cross breeding⁽¹²⁾.

Oryza sativa has enough genetic variation for adapting to widely varying environments. Rice has been cultivated for several thousand years, and cultivars have differentiated into two major ecotypes, Japonica vs. Indica, and an intermediate group sometimes referred to as Javanica. The conventional cross-breeding of Indica-Japonica is still fundamental for increasing the diversity of cultivars today. The only problem is hybrid-sterility for which a break-through recently was shown when using the intermediate group rice (better referred to as undifferentiated rice) as bridge parent. Taikeng No. 9, recently released from Taichung DAIS, Taiwan, has demonstrated successful selection by combining Japonica Koshihikari's eating quality, Indica TN1 semidwarf with TKM-6 disease resistant (IR -747B2-6) through K-71 (originated from the Pamirs) (IR-5470) crosses.

Another possibility is by using the modified Japonica-Indica cultivars cross which shows less F_1 sterility (mean 84%) than the direct Japonica/Indica (mean 21%)⁽⁶⁹⁾. Both intermediate and modified rices have a genetic mechanism to control the spikelet fertility. Two theories proposed by geneticists are: (1) a two-gene (duplicated fertility) model theory (referred to as gamete development (GD) lethal genes by

Oka^(50,52), and (2) a one-locus model theory with wide-compatibility genes differentiated within locus^(4,16). Both wide-compatibility gene(s) and GD one of lethal genes are known to link with anthocyanin activator and glutinous gene *wx*.

One of the writer's breeding studies used Indica new semidwarfing *sd₆* to cross with traditional semidwarf (*sd₁*) Japonica sweet rice. This study, along with some of the interesting un-published data is included here. NFD148 is an improved open-stemmed long-grain semidwarf breeding line which showed good response to green manure with less chemical N, but it also had over 10 t/ha yielding capacity⁽²⁸⁾. The partner, NFD109E, is an early maturing strain of a pearl type glutinous rice, known as "Hakubai sweet" in the California market. The super quality sweet rice is being exported to Japan and is recognized as a first class rice⁽²⁷⁾. Both NFD148 and NFD109E (later patented as NFD108) are similar in the growth period (heading at 90 days from seeding) and considerably heavy kernel weight, but they are different in semidwarfing genes. NFD109E has waxy endosperm with hairy glumes and red color in apicule, while NFD148 is a translucent long-grain rice with smooth glumes and no anthocyanin coloration in any part of the plant. Fig. 2 shows the variation of brown rice size (ratio of length/width) of the two parents, F₂'s seeds and F₃'s population.

The F₁ plants had a normal plant height with high seed fertility (85%) in both winter green house and crop season in California. The seed-set in F₂ population segregated into a 9(>70%):3(60-69%):3(40-59%): 1(<40%) ratio of four peaks curve. The seed size of F₃ fell into the normal distribution from the ratio of 1.6 to 3.8 which surprisingly was comparable to the rice sample excavated from Homudo, China, as shown on the bottom portion of Fig. 2.

The rice sample excavated from the Homudo site (about 200 km south of Shanghai) in 1973 is the oldest known rice, estimated to be about 7000 years old. Rice seeds buried as much as 40-50 cm in depth were well preserved and unearthed with the nearby wooden house which suggests that these seeds were in storage from the harvested crop. While visiting the Homudo museum, the writer noticed the variation of hulled rice, long and short, and also that some of them with long awns without broken. From a photograph found in the book of "*Origin of China*" published in Taiwan in 1991 it was possible to measure seed size without difficulty except for one seed. A total of 45 seeds were measured showing a continuous variation from ratio of 1.8 to 3.8. According to the standards of the U. S. Dept. of Agriculture, seed size (ratio of L/W) with hull smaller than 2.2 (for brown rice is 2.0) and greater than 3.4 (for brown rice is 3.1) belongs to the short grain and long grain, respectively. Comparison between F₃ seed population of NFD149E/NFD148 and Homudo rice sample reveals that grain size differentiated into Japonica and Indica during the passing several thousand years resulted in "disruptive selection". Cultivated rice can be traced back to their original variation by hybridization. The both had a similar pattern of variation with mean value of only 0.3 ratio difference.

As to segregation of plant height of *sd₁* and *sd₆*, it is not difficult to identify the differences of the two semidwarf plant types. Selection of high seed fertility with different plant height of F₂ plants and F₃ lines appear to include a great range of recombination in agronomic characteristics. Some of the them

resemble semi-wild rice in coloration, open-stemmed, long-awned, various grain size with different number of spikelets per panicle, except that grains do not shatter due to both parents providing good genes shattering-resistance.

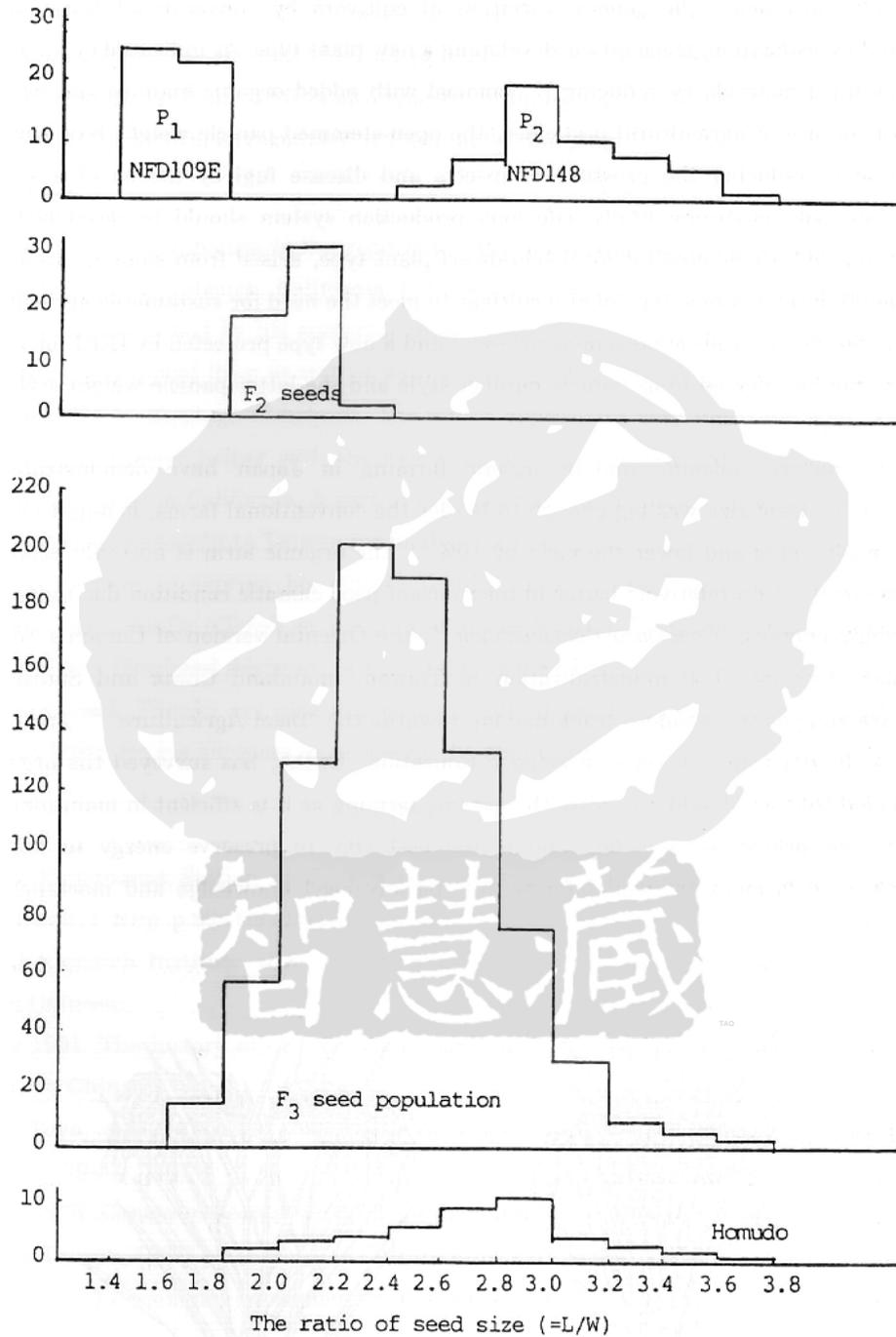


Fig. 2. The seed size (brown rice) of Japonica (NFD109E) and Indica (NFD148) Parents, F₂ and F₃ population in comparison with Homudo hulled rice.

This discovery of abundant variation from this Japonica and Indica cross has been discussed and with confirmed with Dr. M. Nakagahra, Director of the Genetic Resources I of National Institute of Agrobiological Resources, Japan (personal comm.) at a scientific meeting in Taiwan (1993).

After all, increasing the genetic variation of cultivars by conventional breeding, induced mutation and hybridization, is useful for developing a new plant type. As indicated by the writer^(25,26,28,29), applying cultural methods by reducing N chemical with added organic manure and by reasonable reduction of the use of agricultural pesticides, the open-stemmed panicle weight type rice should be circumstances in reducing the pressure of insects and disease fungi by means of a self-protectin system. A low-cost, environmentally safe food production system should be developed. IRRI has recently announced a new goal for ideal semidwarf plant type, arised from same conception. In any case, we should develop a new type of rice cultivar to meet the need for sustainable agriculture. Fig. 3 shows the difference in traditional semidwarf (sd_1) and a new type projected by IRRI for comparison. The former may be referred to as panicle number style and the latter panicle weight style, probably carryin sd_6 .

Finally, natural farming and/or organic farming in Japan have demonstrated average production. If the farm size was big enough to border the conventional farms, it might be influenced by insects and diseases and lower the yield by 10%⁽¹⁷⁾. The organic farm is not only producing high quality food but the crop relatively better in tolerance of poor climatic condition due to its healthy. A book describing chemical *Compound Contamination*⁽⁵⁾, the Oriental version of Carson's *Silent Spring*, arise popular attention. The industrialization in Taiwan, mainland China and Southeast Asian countries, are stepped in Japanese track moving towards the "Dead Agriculture"⁽⁶⁵⁾. In USA a team led by Dr. A. R. Bertrand, Director of Science Education, USDA, has surveyed the organic farms. They concluded that we should recognize the organic farming as it is efficient in maintaining the soil productivity and preventing erosion, and is the best way to preserve energy to minimize the pollution. Organic farmers are well informed of the advanced knowledge and machinery and are using less agricultural chemicals. Further more, the



Fig. 3. Left: The traditional semidwarf plant type (sd_1).
Right: IRRI new goal -- Ideotype ($sd_6?$).
(Source: IRRN cover page and IR reporter 1991).

writer wishes to indicate here that cultivars for organic farms should be developed for their adaptability to those conditions. Sustainable agriculture should have a breeding program. This is also true for ordinary farming which also needs a new type of cultivar because the natural environment is continually changing.

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The hybridization of Japonica-Indica reported in this paper was started in 1990 by the writer in Davis Custom Farming, Firebaugh, California, USA. The hybrid selection of this cross was remained in the company but discarded by his successor after the writer's retirement in 1992. For studies of seed size, fertility of selected lines as well as eating quality, often the writer could not complete the laboratory work due to shortage of helpers. The writer appreciates very much his wife, Yu-Hsiang, who has been my volunteer helper with the rice work at home. Several cultivars of NFD patented rice were then developed in California. A part of the materials were studied in home after retirement consequently saved and brought to Taiwan for further testing.

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水稻短稈品種歷史的回顧暨永續性農業新株型育種¹

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中文摘要

水稻栽培品種之演變，迄本世紀初葉，未受過肥料及關連病蟲害之壓力。氮肥對秈稻有增加莖葉生長量，促進成熟前倒伏，因而提升稻穀產量有困難。低腳烏尖是一孟德爾式遺傳基因(sd₁)之短稈突變品種，最初記錄於台灣(1906)。在50年代本場選用作雜交親本育成台中在來1號，是對水稻改良建立一新典範，建立後來所謂「綠色革命」之高產品種時代。

低腳烏尖的短稈基因在遺傳上附帶有多面作用，除使秈稻各節間成熟時短縮稻株不倒伏，稻穗得以正常結實外，葉片亦減短直立而色濃，葉莖集結株型在加施氮肥下形成多蘖叢狀。集約栽培鼓勵多肥密植，充分利用空間增加穗數而達到提高單位面積的產量。不幸的短稈多蘖株型密植卻也是提供病蟲害菌繁殖的溫床，在東南亞大面積的推廣短稈品種地方發生稻作歷史上從未有過之大災害。

著者早年中興大學從事水稻誘變短稈品種之遺傳研究，發現褐飛蟲對高矮稈分離植株之侵蝕有選擇性，具有低腳烏尖的半矮基因的植株多受害枯死，而高稈植株因稈分開葉色較淡，則多逃避未死(見圖一)。因而創想育出短稈開散莖品種或可以減少蟲害，維持抗倒伏豐產特性。後在美國加州得用誘變方法找到一株型與低腳烏尖有異的新半矮基因(sd₆)，並研究其對產量之作用，發現稻田冬作綠肥加半量氮肥便可提高25%產量。又短稈基因(sd₁)通常不影響穗部性狀或改變構成產量的遺傳成分，其可貴處在獨立自由與其他孟式基因組合，產生豐產優良遺傳型品種。而日本經過半世紀上所育成較矮稈型水稻則屬微效基因累積，較難從秈稈稻交配有半不稈性後代中選出短稈與優良基因之組合。新半矮基因(sd₆)亦是孟氏主效基因，具有穗大粒多可補償較少分蘖，散開株型特性可讓日光直接照射稻株基部空氣流通，理論上可以減少蟲病菌寄生繁殖，隨而減少殺蟲菌農藥之使用，避免土壤用水之污染，從農業生態觀點這是一種利用植物本身自然防禦體系的育種，一新株型育種體系於是成型(見圖三)。

現代農業的特徵是單一遺傳型品種之大面積密集多肥栽培方式，一旦發病或蟲生因無其他遺傳型品種之緩衝有潛在性危險。預防措施噴佈農藥，不但增加生產成本造成土壤惡化用水及生產品之污染，而天敵因施藥而被殺害使翌年蟲病更猖獗。抗蟲育種例如對褐飛蟲之新品種育成效果不能持久，因昆蟲有了新型之適應遺傳。因此，增加栽培品種之遺傳歧異性是首急之務。

¹ 台中區農業改良場研究報告第 0315 號。

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著者為要從秈稻長粒米品種找出的新半矮型基因(sd_6)轉移到稉稻內而與傳統的短稈(sd_1)圓粒糯米品種雜交，發現 F_1 結實有高達85%以上的組合，其 F_2 稈實率分離為9 (> 70%) : 3 (60~69%) : 3 (40~59%) : 1 (<40%)從高稈實個體中選取各種有利性狀的組合植株，其 F_3 系統稈實性多不再分離，種子(糙米)之大小變異連續於兩親之間，形成常態分佈與近年在浙江省餘姚河姆渡出土之稻穀之大小變異相仿(圖二)。這一事實的發現啓示栽培水稻品種，例如穀粒之長短分化秈稉稻為中裂選擇(disruptive selection)，可用不具雜種不稈性之組合予以回復應有之變異。按河姆渡出土之稻穀估計已7000年之久，可代表未經人為淘汰原始稻種的遺傳變異。依此，傳統的突變基因誘發及秈稉稻雜交仍是最實用找尋水稻遺傳變異的育種方法，本場最近良質米台稉9號之育成可作佐證。又因，不同的遺傳型對環境的要求亦異，為避免株型及密植招致蟲病滋生，選出的品系分別以傳統及新栽培方法在本場內種植比較，將作進一步試驗證實台灣在工業發展下水稻新株型之育種效果及可行性。

關鍵字：水稻、短稈、集約栽培、病蟲害管理、生態體系、遺傳歧異性、稉秈稻育種。

