## INHERITANCE OF GRAIN DORMANCY IN FOUR RICE CROSSES

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#### Introduction

Grain dormancy is a valuable trait in the monsoon crop of rice (Oryza sativa L.) in tropical areas, where prolonged rains frequently fall during harvest time. Mature grains of non-dormant varieties, especially those of lodged plants, would germinate on the panicle under such conditions. The lack of seed dormancy in many japonica varieties developed in Taiwan has partly handicapped their commercial usefulness in the monsoon crop of the tropics. On the other hand, grain dormancy of a long duration would be a limiting factor when the varieties concerned are grown continuously in a multiple cropping system. While dormancy in freshly harvested seeds can be effectively broken by dry heat treatment or an appropriate chemical, such seed treatments would not be feasible on certain farms. Therefore, seed dormancy of moderate intensity and short duration would be a desirable trait where rice is grown more than once a year.

Available genetic information on grain dormancy in rice is limited to brief mentions in a few abstracts. For the further development of varieties which will possess short stature coupled with high yielding ability, early maturity, grain dormancy, and other characters desired in the tropical areas, additional genetic information on grain dormancy is needed.

## Materials and Methods

Peta (from Indonesia) was used as a parent to represent dormant varieties of the tropics. A selection from Century Patna 231 × SLO-17 (IRRI Accession 6993, from U.S.A.) and PI 215936 (Tainan Yu 487, from Taiwan) were weakly dormant types. Taichung Native 1 (from Taiwan), I-geo-tze (from Taiwan), and Dawn (from U.S.A.) were the non-dormant parents in the crosses. Four crosses were included in the study: (1) Peta × I-geo-tze, (2) Acc. 6993 ×

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Taichung Native 1, (3) Acc.  $6993 \times PI$  215936, and (4) Acc.  $6993 \times Dawn$ . The sample size was from 20 to 50 plants each for the parents, 120 to 200  $F_2$  plants for each  $F_2$  population, and about 100  $F_3$  lines of 10 plants each taken at random from the  $F_2$  populations. The parents and  $F_2$  populations were grown in the 1965 wet season, the parents and  $F_3$  progenies in the 1966 wet season.

Plants of parents,  $F_2$ , and  $F_3$  progenies were tagged when the first panicles flowered on the plants. Five to six earlier maturing panicles from each plant were harvested at from 32 to 34 days following flowering, placed in a paper bag, and air-dried in the air-conditioned laboratory (about 25°C) for 4 days. One panicle was taken at random from each  $F_2$  plant for germination tests on the 5th, 21st, 50th, and 80th day followed harvest, respectively. For the 5-day-old panicle samples, the rag-doll method was used for germination test. The other three samples were made in Petri dishes on threshed grains incubated at 25-30°C for 7 days.

Grain samples of F<sub>3</sub> lines were tested for germination on the 5th and 21st day following harvest. The rag-doll method was used.

Control tests were made on 5-day-old triplicate samples of hulled and dehulled grains of parent varieties harvested in the 1967 dry season. The dehulling process was made on a manually operated dehuller made of rubber rollers. The dehulled caryopses were examined by placing the brown rice above an illuminated glass pane. Broken or damaged kernels were excluded from the germination tests.

#### Results

Cross of dormant × non-dormant varieties: Dehulling increased the germinability of 5-day-old Peta grains from a mean of less than 1% to about 65%. In I-geo-tze, the percentage of germination was raised from 73% to 93%. These differences are significant at the 1% level. These findings also indicate that the hulls (maternal tissues) play a significant role in conferring dormancy to freshly harvested grains.

The distribution of Peta  $\times$  I-geo-tze  $F_8$  grain samples (from  $F_2$  plants) with respect to germinability at four time intervals is shown in Fig. 1. The frequency of dormant progenies exceeded those of moderately dormant and non-dormant progenies at 5 days after harvest. The distribution indicates a complex mode of inheritance which is suggestive of a multiplicative type of gene action. With time, the frequency of dormant samples became much lower in the 21-day samples. The hybrid population also showed a wider range of variability. In 50-day samples, most of the  $F_8$  grains behaved like the non-dormant parent, I-geo-tze. At 80 days, dormancy was no longer detected in the  $F_8$  and Peta samples.

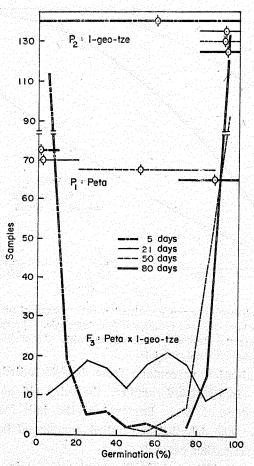


Fig. 1. Distribution of parents and F<sub>3</sub> grain samples by germination percentage in the cross of Peta × I-geo-tze at 5, 21, 50, and 80 days after harvest. Horizontal lines show the range of parents about the means (dotted circles).

The changes in mean germinability of the parents and  $F_2$  progenies over time were traced by second-degree polynomials. The Y-intercepts are 56.28 for I-geo-tze, -7.56 for Peta, and -6.28 for the mean of  $F_2$  plants ( $F_3$  grain samples). Figure 2 indicates that the mean germination percentage of the  $F_3$  grain samples initially followed that of the strongly dormant Peta parent, then the mean germination percentage gradually shifted to that of the non-dormant I-geo-tze parent, involving a reduction in the number of dormant samples. An estimate of heritability of grain dormancy based on the linear regression coefficient between grains of  $F_2$  plants and of  $F_3$  progenies was 37% for the 5-day samples and 44% for 21-day samples, respectively.

Cross between weakly dormant varieties: The 48 samples of Accession 6993 gave a mean germination of 29% in the 5-day test. The removal of hulls

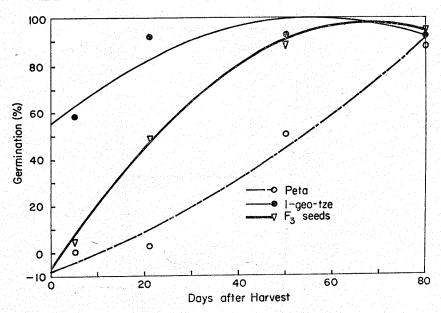


Fig. 2. The change in mean germination percentages of parents and  $F_8$  of Peta×I-geo-tze seed samples at four intervals. The symbols  $(\bigcirc \bullet \nabla)$  indicate the observed mean values, while the curves represent the second-degree polynomials.

increased the germination percentage from 14% in hulled samples of 60% in dehulled samples. In PI 215936 samples, the 5-day old samples gave a mean germination percentage of 38%. Removal of the hull increased germination from 51% to 90%. The dehulled and hulled samples of both parents differed significantly in germination percentages.

The mean germinability of 204 F<sub>3</sub> samples (27%) in the 5-day test was similar to that of the parents, but the distribution was wider in range than those of the parents with dormant and weakly dormant samples constituting the majority (Fig. 3). The distribution again suggests the dominant nature of weak dormancy and a multiplicative type of gene action. In the 21-day test, the distribution became multimodal. Only a few weakly-dormant samples were found in the 50- and 80-day tests.

The Y-intercepts of the second-degree polynomials for Accession 6993, PI 215936, and  $F_3$  seed samples are 18.77, 34.21, and 18.78, respectively. The trend in the loss of dormancy with time was similar among the two parents and the  $F_3$  mean. The heritability estimates based on 144 seed samples in 5-day and 21-day tests were 16% and 19%, respectively. The low heritability values suggest that the expression of grain dormancy in this cross was highly variable and greatly influenced by environment.

Crosses between weakly dormant and non-dormant varieties: Taichung Native 1 is a non-dormant variety and its 42 samples gave a mean germinability of

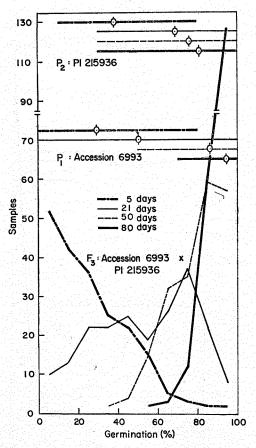


Fig. 3. Distribution of parents and F<sub>3</sub> grain samples by germination percentage in the cross of Accession 6993 × PI 215936 at 5, 21, 50, and 80 days after harvest. Horizontal lines show the range of parents about the means (dotted circles).

66.5% at 5 days after harvest. Hulled samples gave 59.0% germination and dehulled samples gave 96.3% germination in another test.

Dawn is another non-dormant variety, producing 62% germinable grains at 5 days after harvest. Dehulling did not markedly increased germinability in this variety since the hulled and dehulled samples gave 52% and 50% germination respectively.

The crosses of Acc.  $6993 \times \text{Taichung Native 1}$  and Acc.  $6993 \times \text{Dawn showed}$  similar distributions in the  $F_3$  grain samples. Moderately dormant progenies constituted the majority in 5-day tests of the  $F_3$  samples, indicating the dominant nature of weak dormancy. Most of the  $F_3$  samples gave germination readings similar to that of the common, weakly-dormant parent in the crosses of Acc. 6993. However, in the 21-day tests, most of the  $F_3$  samples behaved like the non-dormant parents, showing a rapid loss in dormancy with lapse in

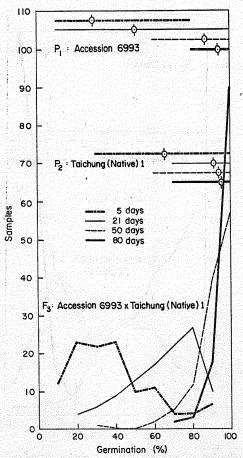


Fig. 4. Distribution of parents and F<sub>3</sub> grain samples by germination percentage in the cross of Accession 6993 × Taichung (Native) 1 at 5, 21, 50, and 80 days after harvest. Horizontal lines show the range of parents about the means (dotted circles).

time (Fig. 4). In the 50- and 80-day tests, only a small number of progenies showed indications of weak dormancy. The mean trend in loss of dormancy among  $F_3$  grain samples was similar to that of Acc. 6993. The 97  $F_4$  grain samples of Acc. 6993 × Dawn gave heritability estimates of 12% and 19% in the 5- and 21-day tests, respectively.

Association between maturity and dormancy readings: Peta and I-geo-tze differed by approximately 25 days in maturity when grown in the wet season at Los Baños. In the  $F_2$  population of this cross, the simple correlation coefficient between the number of days to harvest and germination percentage of  $F_3$  seed samples in 5-day test was computed at +0.08. The r value indicated that there was no association between these two readings.

Acc. 6993, Taichung Native 1, PI 215936, and Dawn differed less in time to

maturity, ranging from 5 to 15 days. The correlation coefficients estimated from 5-day germination percentages and days to harvest were 0.12 for Acc.  $6993 \times PI$  215936, 0.54 for Acc.  $6993 \times Taichung$  Native 1, and 0.43 for Acc.  $6993 \times Dawn$ . The last two estimates were significant at the 1% level, but the variation in maturity among  $F_2$  plants was less than 20 days in total range.

#### Discussion

The complex nature of physiologic mechanisms controlling grain dormacy in rice varieties is indicated in this study by the differential effects of dehulling upon germinability in five-day post-harvest samples of six varieties. Dehulling was partially effective in breaking dormancy. Our findings on hulled and dehulled samples support the postulate of Roberts (1961), Nair and Sahadevan (1962), and Takahashi (1963, 1968) that in addition to the hulls, other tissues in the caryopses, such as the embryo, pericarp, and tegmen, are also involved in the expression of dormancy.

Our data also suggest the complex nature of genetic control. In 5-day samples, the dominance of dormancy over non-dormancy was expressed in F<sub>2</sub> progenies of all four crosses. The distribution of F<sub>2</sub> plants in 5- and 21-day samples also indicates multigenic control, probably of a multiplicative type of gene action. The multigenic type of inheritance has been suggested by Samad (1961), Shanmughasundaram and Ramaswamy (1961), Nair et al. (1964), and Namboodiri and Ponnaiya (1964). With lapse in time the distributions were modified, probably resulting from a differential change in the effectiveness of various genmination-inhibitors.

The rather low heritability estimates obtained from  $F_3$  and  $F_4$  grain samples of three crosses indicate the influence of environmental condition on the expression of grain dormancy. Germination tests at The International Rice Research Institute of samples of a number of rice varieties in different seasons led to the observation that the expression of strong dormancy was frequently associated with raining weather at the time of flowering and grain development.

In a separate study at the Institute by Z. Harahap (unpublished, 1967) in which different dormant parents of tropical origin were used, the  $F_2$  grains from  $F_1$  hybrids in ten dormant  $\times$  non-dormant crosses showed that in three cross the mean germination counts of  $F_2$  seeds in the 7-day tests were similar to those of the dormant parents, while in the other seven crosses the  $F_1$  hybrids showed relatively higher germination readings than the dormant parents. The  $F_3$  grain samples representing  $F_2$  genotypes showed wide ranges of distribution in all crosses. The  $F_3$  data also suggested a complex mode of inheritance. The breeding behavior of dormancy readings in the  $F_3$  and  $F_4$  seed samples varied among crosses involving different parents. However, the data indicated

that it was feasible to select from  $F_2$  populations a number of dormant plants that would breed true for this trait in the  $F_3$ . Heritability estimates based on  $F_4/F_3$  grain samples averaged 40% in two dorment × non-dormant crosses. Selection in  $F_3$  lines also showed that in dormant × non-dormant crosses where the dormant parent was photoperiod-sensitive, it was possible to obtain dormant lines that are early maturing and non-sensitive (cf. International Rice Research Institute, 1968).

The two series of experiments conducted at the Institute indicated three common features on grain dormancy: (1) a complex mode of inheritance, (2) the effect of variations in environmental factors on the expression of dormancy, and (3) the relative ease in identifying moderately dormant genotypes by conducting germination tests at 2 to 3 weeks following grain maturation. The above postulates are supported by a number of lines which were isolated from the breeding nurseries at the Institute and which have short-term, moderate levels of dormancy, and which also have short stature, insensitivity to photoperiod, early maturity, and medium to long grains (International Rice Research Institute, 1967).

#### Summary

Post-harvest germinability of rice appears to be a complex trait in which hulls play a significant part in conferring dormancy to freshly harvested grain samples. Data obtained from  $F_3$  seed samples representing  $F_2$  genotypes in crosses between dormant  $\times$  non-dormant, weakly-dormant  $\times$  weakly-dormant, and weakly-dormant  $\times$  non-dormant varieties suggest that grain dormancy has a complex mode of inheritance which probably involves a multiplicative type of gene action. With grain dormancy gradually diminishing with time, changes are noted in the distribution of dormant and non-dormant plants among  $F_2$  progenies in the hybrid populations.

The changes in mean germination percentages of  $F_3$  seed samples by time intervals in crosses of weakly-dormant  $\times$  non-dormant varieties and of weakly-dormant  $\times$  weakly-dormant parents were similar to that of the weakly-dormant parents, but in a dormant  $\times$  non-dormant cross the  $F_3$  mean gradually shifted with time lapse from one approximating the dormant parent.

No evidence of genetic association was detected between late maturity and grain dormancy in the late-dormant × early-non-dormant cross.

The heritability estimates of grain dormancy based on  $F_4/F_3$  regression indicate that grain dormancy is a complex and variable trait and is appreciably influenced by environmental conditions prevailing during the grain ripening period.

# 四水稻雜交組合內種子休眠性之遺傳

## 張德慈嚴威添

水稻種子收穫後之發芽能力,爲一極複雜之性狀。在新收穫種子之休眠性內,谷殼甚有影響。

由强休眠性×無休眠性;弱休眠性×弱休眠性;和弱休眠性×無休眠性品種雜交 F<sub>2</sub> 植株上取得之 F<sub>3</sub> 種子樣品試驗所得結果,顯示出種子休眠性屬于複雜之遺傳模式,其中似包括 Multiplicative 型之因子作用。同時休眠性是隨時間之逝去而消失。在强休眠性和無休眠品種之雜交 F<sub>2</sub> 植株中,休眠和無休眠植株分佈形態隨時間而改變。在弱休眠品種間和弱休眠品種與無休眠品種之雜交組合中,其 F<sub>3</sub> 種子平均發芽率隨時間之變化情形和弱休眠親本之變化情形相似。但在强休眠品種和無休眠品種雜交組合中,其 F<sub>3</sub> 種子發芽率平均值之變化,隨時間之變化由接近休眠親本型介入與無休眠親本相似之型值。

在晚熟休眠與早熟無休眠品種之雜交組合中,並未發現有成熟期與種子休眠性間有遺傳相關之現象。

利用 F<sub>4</sub>/F<sub>3</sub> 廻歸係數所估計得之種子休眠性遺傳率介於12~44%, 顯示種子休眠性是一複雜並變異甚大之性狀,亦易受環境條件,尤其是成熟期之環境因子所影響。

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