# STUDIES ON SOYBEAN BREEDING IN TAIWAN

## 2. Breeding Experiments with Successive Hybrid Generations Grown in Different Seasons

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Soybean varieties introduced from overseas were, as mentioned in our previous paper (Lu *et al.* 1967), either adaptive to one of the two crop seasons found in Taiwan, or inadaptive to any season. Generally, their yield was fluctuating and unstable. As the history of development of the Ponlai rice varieties indicates, it seemed that hybridization should be conducted in Taiwan for obtaining really adaptive genotypes.

Though no introduced varieties seemed to be adapted to spring as well as summer season, we have adopted a selection plan generally used in Taiwan for rice breeding, that is growing segregating generations successively in two crop seasons and repeating selection, advancing by two generations every year. The results showed that a part of the progeny lines thus selected were adapted to both seasons and their yield was relatively stable in different years, as is reported in this paper.

### Materials and Methods

Varieties of various origins shown in Table 1 were used as cross-parents. Cross combinations were chosen so that a strain selected from a Taiwanese green-manure variety was mated with introduced varieties having different photoperiod and temperature responses. Of 12 crosses so far made, seven from which promising lines were obtained and one used for estimating genetic parameters are listed in Table 2.

As already mentioned, the hybrid populations were raised successively in spring and summer crop-seasons. The $F_2$ to $F_4$ or $F_5$ populations were grown in bulk and a weak mass selection was made eliminating a few inadaptive plants. The size of a bulk population was 2000 to 3000. A number of plants

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**Table 1.** *Parental varieties used for hybridization.*

| Acc. no. | Local name | Origin | Type** | I | II | III | IV |
|---|---|---|---|---|---|---|---|
| 2 | Hsingying-tatou | North China | Inadapt. | 44 | 64 | 9 | 4.5 |
| 5 | Nungyuan-1 | Taiwan* | Spring | 47 | 57 | 5 | 6.0 |
| 6 | Pingtong-chingpitou | Taiwan | Summer | 64 | 81 | 15 | 5.4 |
| 9 | Utou | Taiwan | Spring | 57 | 57 | 8 | 7.6 |
| 127 | Jikkoku | Japan | Spring | 45 | 59 | 11 | 5.8 |
| 142 | Tamana-zairai | Japan | Inadapt. | 44 | 46 | 24 | 5.2 |
| 144 | Sangoku | Japan | Summer | 53 | 72 | 21 | 4.5 |
| 145 | Yonegake | Japan | Summer | 51 | 70 | 27 | 2.4 |
| 173 | Wakajima | Japan | Summer | 51 | 70 | 7 | 4.4 |
| 203 | Palmetto | U. S. A. | Summer | 54 | 72 | 8 | 5.5 |
| 227 | Avoyelles | U. S. A. | Summer | 52 | 70 | 32 | 2.4 |

*: Pure-lines selected from green-manure varieties native to Taiwan.
**: Adaptive to spring or summer crop-season, or inadaptive in any season (Lu *et al.* 1967).
I: Average number of days to flowering of plants seeded at different dates.
II: Average number of days from flowering to maturity.
III: Day-length sensitivity in T. D. M. degree.
IV: Index of temperature response (shortening of the days to flowering due to 1°C rise, in %).

**Table 2.** *Cross combinations and number of progeny lines tested.*

| Symbol | Combination | Crop-season of $F_2$ | No. of lines tested | | | | No. of lines selected |
|---|---|---|---|---|---|---|---|
| | | | $F_5$ | $F_6$ | $F_7$ | $F_8$ | |
| A | 5× 2 | Spring 1956 | 100 | 50, 123 | 63 | 12 | 3 |
| B | 5×127 | Summer 1956 | 80 | 20, 50 | 30 | 3 | 2 |
| C | 5×144 | Summer 1956 | 109 | 20, 200 | 42 | 6 | 2 |
| D | 5×227 | Summer 1956 | | 253 | 50 | 3 | 1 |
| E | 5×145 | Summer 1956 | 240 | 53, 200 | 102 | 45 | 19 |
| F | 5×142 | Summer 1956 | 44 | 8, 196 | 62 | 38 | 4 |
| G | 127× 9 | Summer 1956 | 715 | 84, 726 | 150 | | |
| N | 203×127 | Summer 1959 | 200 | 200 | 12 | 5 | 5 |

were selected from $F_4$ or $F_5$ populations and pedigree lines were raised, as shown in Table 2. Line and plant selections were continued until $F_8$. The materials were space-planted according to the scheme mentioned in our previous paper. Yield trials of short strains (50 cm or less in plant height) were made at a high planting density, 45 cm (row interval)×15 cm (between-plant space), instead of 50 cm×20 cm.

## Results

1. *Genetic variations in hybrid populations.*

Examples of the variances of plant weight obtained from $F_2$ to $F_4$ hybrid and parental populations are given in Table 3. The data in the table show that the hybrid populations grown in the spring season tended to have larger variances than those grown in the summer season. It is also found that in Cross E the $F_4$ population in spring had a markedly smaller variance than the $F_2$ had in the same season. This is indicative of the effect of natural selection. C and other crosses also showed the same tendency. They produced more promising strains than those not showing this tendency.

**Table 3.** *Variances of plant weight in parental strains and hybrid populations (Unit: $gm^2$).*

| Cross $P_1 \times P_2$ | Generation | Date seeded | $V_{P_1}$ | $V_{P_2}$ | $V_{Hybrid}$ | $h^2$ (%) |
|---|---|---|---|---|---|---|
| (B) 5×227 | $F_2$ | Mar. 2 | 33 | 33 | 123 | 73 |
| | $F_3$ | July 25 | 36 | 63 | 76 | 36 |
| | $F_4$ | Feb. 24 | 50 | 140 | 200 | 53 |
| (E) 5×145 | $F_2$ | Mar. 2 | 33 | * | 489 | — |
| | $F_3$ | July 10 | 37 | 206 | 158 | — |
| | $F_4$ | Feb. 14 | 50 | * | 87 | — |
| (G) 127×9 | $F_2$ | Mar. 2 | 10 | 40 | 238 | 89 |
| | $F_3$ | Aug. 2 | 22 | 50 | 46 | 22 |
| | $F_4$ | Feb. 24 | 49 | 187 | 267 | 56 |

* Not reaching maturity

$$h^2 = \frac{V_{Hybrid} - \frac{1}{2}(V_{P_1} + V_{P_2})}{V_{Hybrid}} \times 100$$

Heritability values were estimated by subtracting the mean parental variance from the phenotypic variance of hybrid populations. Those obtained from the data for two $F_2$ populations seeded at different dates are given in Table 4. The table shows that populations grown in spring generally had higher heritability than those grown in summer. It also shows that a 20-day difference in seeding date in the spring season gave rise to considerable differences in heritability value, suggesting that the hybrid genotypes are quite sensitive to environmental conditions.

Heritability values basing on parent-offspring regressions were estimated in $F_5$ and later generations. The results are in Table 5, together with parent-offspring correlation coefficients. The data in the table show that in plant weight as well as in bean yield, the regression or correlation is positive when estimated from plants grown in the same season, but when plants grown

**Table 4.** *Heritability values estimated from $F_2$ plants seeded at different dates (in %).*

| Character | Seeded on Feb. 1 | Feb. 21 | July 15 |
|---|---|---|---|
| Days to flowering | 81 | 34 | 39 |
| Plant height | 76 | 84 | 81 |
| Plant weight | 64 | 89 | 37 |
| Bean no./plant | 67 | 74 | 41 |
| Bean yield | 73 | 83 | 43 |

Average figures for E1×173 and E32×173 are shown.
E1 and E132 are strains selected from cross E.

**Table 5.** *Parent-offspring regressions and correlations for plant weight and other characters.*

| Cross | Growing season: Parent | Offspring | No. of lines | $V_P$ | $V_O$ | $W_{PO}$ | *b* or *r* (%) |
|---|---|---|---|---|---|---|---|
| Plant weight (gm): | | | | | | | (*b*) |
| (E) 5×145 | $F_5$ (Summer) | $F_6$ (Spring) | 130 | 39.6 | 39.3 | −4.0 | −10.1 |
| (E) 5×145 | $F_6$ (Spring) | $F_7$ (Summer) | 60 | 35.3* | 14.0 | −3.2 | −9.1 |
| (E) 5×145 | $F_5$ (Summer) | $F_7$ (Summer) | 60 | 28.8 | 14.0 | 4.8 | 16.7 |
| (A) 5×2 | $F_6$ (Summer) | $F_7$ (Spring) | 178 | 44.6 | 18.0 | −1.7 | −3.8 |
| (C) 5×144 | $F_5$ (Summer) | $F_6$ (Spring) | 128 | 46.7 | 11.0 | −0.3 | −0.7 |
| | | | | | | | (*r*) |
| (G) 127×9 | $F_5$ (Summer) | $F_6$ (Spring) | 485 | 21.0* | 12.1 | −0.8 | −5.2 |
| (G) 127×9 | $F_6$ (Spring) | $F_7$ (Summer) | 29 | 28.4* | 18.3 | −0.1 | −0.2 |
| (G) 127×9 | $F_6$ (Spring) | $F_6$ (Summer) | 29 | 28.4* | 14.0 | −5 2 | −25.8 |
| (G) 127×9 | $F_6$ (Summer) | $F_7$ (Summer) | 29 | 14.0* | 18.3 | 13.0 | 81.6 |
| Plant height (cm): | | | | | | | (*r*) |
| (G) 127×9 | $F_6$ (Spring) | $F_7$ (Summer) | 29 | 151.0* | 23.9 | 26.1 | 43.4 |
| (G) 127×9 | $F_6$ (Summer) | $F_7$ (Summer) | 29 | 22.7* | 23.9 | 20.3 | 87.3 |
| Bean yield (gm): | | | | | | | (*r*) |
| (G) 127×9 | $F_6$ (Spring) | $F_7$ (Summer) | 29 | 5.94* | 4.08 | −0.33 | −6.7 |
| (G) 127×9 | $F_6$ (Summer) | $F_7$ (Summer) | 29 | 3.70* | 4.08 | 3.16 | 81.2 |

$V_P$: Variance of individual plants used parents.
*: Variance of line means is shown.
$V_O$: Variance of offspring line means.

in different seasons are compared, the values tend to be negative. This indicates that plants adapted to spring season are inadaptive in summer season, and *vice versa*, in the same manner as was found among introduced varieties.

Genetic correlations were estimated from genetic variances and covariances obtained by subtracting individual variances or covariances of parental varieties from those of hybrid populations. The averaged values of correlation coefficients obtained from two $F_2$ populations are given in Table 6, as the two populations had quite similar patterns. As shown in the table, the number of days to flowering was in the spring season positively, and in the summer season negatively genetically correlated with bean yield and other characters which were generally positively inter-correlated.

**Table 6.** *Genetic correlations of characters among $F_2$ plants seeded at different dates and corresponding environmental correlations.*

| Character | Date seeded | Days to flowering | Plant height | Plant weight | Bean no. p. plant | Bean yield |
|---|---|---|---|---|---|---|
| Days to flowering | Feb. 1 | (Genet.) | .40 | .34 | .45 | .07 |
| | Feb. 21 | | .66 | .73 | .37 | .12 |
| | July 15 | (Env.) | −.31 | −.60 | −.67 | −.40 |
| Plant height | Feb. 1 | .13 | | .80 | .82 | .72 |
| | Feb. 21 | −.02 | | .63 | .61 | .56 |
| | July 15 | −.23* | | .53 | .62 | .57 |
| Plant weight | Feb. 1 | −.01 | .39** | | .77 | .98 |
| | Feb. 21 | −.58** | .30** | | .92 | .98 |
| | July 15 | −.13 | .35** | | .99 | .99 |
| Bean no. p. plant | Feb. 1 | .14 | .63** | .93** | | .87 |
| | Feb. 21 | .08 | .29** | .51** | | .87 |
| | July 15 | −.04 | .29** | .83** | | .96 |
| Bean yield | Feb. 1 | .10 | .48** | .92** | .87** | |
| | Feb. 21 | −.01 | −.04 | .59** | .60** | |
| | July 15 | −.11 | .24* | .85** | .91** | |

Averaged figures for E1 × 173 and E32 × 173 are shown in the same manner as in Table 4. Above the diagonal: genetic correlations, below the diagonal: environmental correlations. ** Significant at 1% level, * at 5% level.

These genetic correlations may be compared with the within-varietal seasonal correlations in which some reversed situation was found between maturity and vegetative characters, namely, the number of days to flowering was negatively correlated with vegetative characters in varieties of spring type, and uncorrelated in varieties of summer type (our previous paper). It seems that in spring late flowering genotypes tend to have large values for vegetative characters, which increase in a flowering-accelerating condition. In summer, early maturing genotypes may have large values for those characters, but they are not increased by flowering acceleration.

The so-called environmental correlations (due to minor environments) were low between the days to flowering and other characters, which were mutually positively correlated in both spring and summer seasons.

2. *Yield and seasonal adaptability of selected strains.*

Fixed strains, 36 in total number, were selected from the $F_8$ and later generations of the hybrids under observation. Cross E (5×145) produced a larger number of promising strains than others. It was interesting to find that among these selected strains, bean yields of spring and summer crops were positively correlated, the coefficient being 0.288, making a contrast with the negative correlation found in earlier generations. This indicates that the selected strains tend to have equal productivity in both spring and summer seasons.

The selected strains were tested in spring and in summer crop for three years, using Jikkoku (from Japan) and Palmatto (from U. S. A.) as the control. The data for some of the strains are in Table 7. The table shows that a part of the strains, *e. g.*, E32 and A92, produced similarly high yield in spring as well as in summer crop. The results of variance analysis of the yield data are in Table 8. Comparing the data in the table with those for introduced varieties (Lu *et al.* 1967, Table 4), we find that our selected strains had apparently smaller variances due to strain×season, year and to strain×year than the introduced varieties. It may be suggested that repeated selections in two different seasons bring about a general adaptability to both and a stability of yield in different years.

**Table 7.** *Bean yield and other characters of selected strains, shown as examples (Average for 1959, 1960 and 1961).*

| Strain | Yield (kg/10a) | | Days to maturity | | Plant height (cm) | | Pod number p. plant | | 100 bean weight (gm) | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Spr. | Sum. | Spr. | Sum. | Spr. | Sum. | Spr. | Sum. | Spr. | Sum. |
| A92 | 204 | 199 | 106 | 87 | 36 | 49 | 45 | 82 | 13.8 | 10.8 |
| B11 | 121 | 238 | 95 | 85 | 30 | 39 | 40 | 91 | 18.1 | 12.3 |
| C15 | 173 | 238 | 113 | 92 | 33 | 39 | 58 | 94 | 14.7 | 10.7 |
| E27 | 150 | 235 | 98 | 86 | 23 | 42 | 27 | 98 | 21.1 | 12.7 |
| E31 | 185 | 293 | 105 | 95 | 24 | 39 | 31 | 142 | 18.4 | 10.4 |
| E32 | 237 | 260 | 104 | 94 | 27 | 51 | 50 | 111 | 16.3 | 10.3 |
| E64 | 236 | 203 | 98 | 89 | 60 | 54 | 84 | 97 | 13.4 | 10.8 |
| F15 | 209 | 227 | 107 | 88 | 31 | 55 | 44 | 104 | 16.0 | 11.4 |
| F19 | 188 | 220 | 107 | 94 | 30 | 49 | 55 | 96 | 17.7 | 13.1 |
| Palmetto | 117 | 235 | 129 | 100 | 74 | 93 | 109 | 145 | 9.9 | 10.9 |
| Jikkoku | 100 | 130 | 97 | 82 | 28 | 33 | 26 | 66 | 21.6 | 13.4 |

As shown in Table 7, the selected strains had a growth period (seeding to maturity) of 95 to 110 days in spring, and 85 to 95 days in summer. They were generally short (plant height ranging from 25 to 35 cm in spring and 40

**Table 8.** *Variance analysis of yield data for 36 selected strains (Unit: kg/a).*

| Variation due to | d. f. | M. S. | Expectation (season fixed) |
|---|---|---|---|
| Year | 1 | 434.000** | $2\sigma^2_{vy}+72\sigma^2_y$ |
| Season | 1 | 1,857.20** | $\sigma^2_e+2\sigma^2_{vs}+36\sigma^2_{ys}+72\sigma^2_s$ |
| Year × Season | 1 | 8.44 | $\sigma^2_e+36\sigma^2_{ys}$ |
| Strain | 35 | 16.60** | $2\sigma^2_{vy}+4\sigma^2_v$ |
| Strain × Year | 35 | 8.30 | $2\sigma^2_{vy}$ |
| Strain × Season | 35 | 8.29 | $\sigma^2_e+2\sigma^2_{vs}$ |
| Error | 35 | 5.81 | $\sigma^2_e$ |

| Variance component | | Selected strains | Introduced[(1)] varieties |
|---|---|---|---|
| Error (Strain × Year × Season) | $\sigma^2_e$ | 5.81 | 9.93 |
| Strain × Year | $\sigma^2_{vy}$ | 4.15 | 16.21 |
| Strain × Season | $\sigma^2_{vs}$ | 1.24 | 18.32 |
| Strain | $\sigma^2_v$ | 2.08 | 0.69 |
| Year × Season | $\sigma^2_{ys}$ | 0.07 | 8.12 |
| Year | $\sigma^2_y$ | 5.91 | 8.14 |
| Season | $\sigma^2_s$ | 25.64 | 14.71[(2)] |

Experiments in 1960 and 1961, with 3 replications.
** Significant at 1% level.
(1) From Lu *et al.* (1966), Table 4. Recomputed according to the season-fixed model.
(2) This value is smaller than 25.64 for selected strains, because both spring and summer types are present in the varieties used. In selected strains, summer yields were generally higher than spring yields.

to 55 cm in summer), and their beans were of medium size. Regarding growth habit, all were found to be of *determinate* type. They were tested in a growing-season experiment, repeating seedings throughout the year at one-month interval. From the results, their day-length sensitivity (requirement for a certain short-day, in "T. D. M. degree") and index for temperature response (shortening of the days to flowering due to 1°C rice, in %) were computed, by the method described in our previous paper. As shown in Table 9, the strains were found to have a low day-length sensitivity and a high temperature response. In these respects, they may be considered to be varieties of spring type.

## Discussion

Heritability values of bean yield and other agronomic characters in soybean hybrids have been estimated by a number of workers (Bartley and Weber

**Table 9.** *Variations in indices for photoperiodic sensitivity and temperature response of selected strains, as compared with those of introduced varieties.*

| Strain group | Photoperiod sensitivity in T. D. M. | | | | | | | | No. of strains |
|---|---|---|---|---|---|---|---|---|---|
| | 0° | 5° | 10° | 15° | 20° | 25° | 30° | 35° | |
| Selected strains | | 16 | 11 | 1 | | | | | 28 |
| Introduced varieties, Spring type | 1 | 15 | 11 | 1 | 3 | 1 | 1 | | 33 |
| Summer type | | 2 | 3 | 3 | 10 | 3 | | 2 | 23 |
| | Index of temperature response in % | | | | | | | | |
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | |
| Selected strains | | | | 2 | 1 | 8 | 18 | 6 | 35 |
| Introduced varieties, Spring type | | | | | 8 | 20 | 4 | 2 | 34 |
| Summer type | 1 | 2 | 4 | 4 | 4 | 10 | 5 | 1 | 31 |

1952, Johnson *et al.* 1955a, b, Hanson and Weber 1962, Anand and Torrie 1963, Horie *et al.* 1965, etc.). As reviewed by Johnson and Bernard (1962), it is known that bean yield has a quite low heritability, though other characters show varying degrees of heritability according to the involved genotype-environment interaction. This indicates that individual selection in early hybrid generations cannot be very effective, and that the bulk method may be preferable.

The efficiency of selection by bulk and by pedigree methods was compared by Raeber and Weber (1953), who concluded that selections from space-planted plots by both methods were similarly effective. On the other hand, natural selection experiments made by Mumaw and Weber (1957) indicated that in populations composed of different varieties, branching types increased against non-branching ones, with no bearing on the yield in pure stand. In view of these informations, we have adopted the bulk method, growing hybrid populations in bulk up to $F_4$ or $F_5$. A number of plants were then visually selected and pedigree selection followed.

Both the bulk and the pedigree populations were raised successively in spring and summer seasons. We found that the bulk populations grown in spring generally had larger genetic variances and higher heritabilities than those grown in summer. This was also pointed out by Yü *et al.* (1965). It may be that in spring, plants with different degrees of photoperiod sensitivity react with different growth patterns, weakly sensitive plants being naturally selected. In summer, photoperiodically sensitive plants may have an advantage. As different genotypes are advantageous in the two seasons, the parent-offspring regression in yield and other characters will, as we have found, tend to be negative. It may then be inferred that when hybrid populations are successively grown in the two different seasons, natural selection works in opposite directions. This may be considered as a disruptive selection.

It is known that disruptive selection favors an increase in heterozygotes resulting in polymorphism, as theoretically pointed out by Haldane and Jayakar (1963). In autogamous populations, further, it may result in selection of genotypes with a wide adaptability to various conditions, the so-called "general-purpose genotypes" (Baker 1965). The positive correlation found between spring and summer yields of our selected strains, as well as their reduced variances due to strain×season and to strain×year, suggest the selection of such genotypes.

The selected strains generally had a low photoperiod sensitivity. It seems that a low photoperiod sensitivity is selected in spring, and in summer, a particular temperature response may be selected. Though the selected strains showed a high index of temperature response, this was due only to an overall estimate of seasonal changes in growth period. Actually, temperature responses at different stages of development would be interrelated constituting a complex. Yield depends upon the interrelation of many component characters, which are modified in response to outer conditions at different stages. Therefore, the effects of natural and artificial selections in different seasons cannot be easily resolved into a few distinict factors. We may conclude that our "disruptive seasonal selection" has brought about a wide seasonal adaptability.

The similarly high yields in both spring and summer seasons of some of our strains indicates that the results of our soybean breeding are comparable with the results of rice breeding so far achieved in Taiwan. The Ponlai varieties of rice have been obtained after repeated "disruptive seasonal selections" in the first and second crop seasons. They are insensitive to photoperiod and produce high yield in both crop seasons. In our previous paper, we have pointed out that within one year two adaptive seasons occur in rice as well as in soybean, though the underlying physiological factors remain almost unknown. Our soybean strains, adaptive to both spring and summer seasons, may be considered as having such a seasonal adaptability as the Ponlai rice varieties have.

Regarding rice as well as soybean breeding in Taiwan, it is a subject of discussion which is more profitable, selection of strains specifically adapted to the one or the other season, or generally adapted to both. The season-limited adaptabilities of introduced soybean varieties as well as of some of our selected strains suggest the advantage of selecting strains specifically adapted to a season. Our breeding experiments however indicate that "disruptive seasonal selection" may bring about a wide adaptability and a stability of yield. The successful extension of the Ponlai rice varieties also indicates the advantage of growing successive generations in different seasons.


### Summary

Hybridization was made in 12 cross-combinations of various soybean varieties. The $F_2$ to $F_4$ or $F_5$ populations were propagated in bulk, and then pedigree selection was made. The bulk as well as pedigree populations were successively grown in spring and in summer crop seasons, progressing by two generations each year. Comparing the same population grown in the two seasons, the spring crop was found to give larger genetic variances of characters and higher heritability values than the summer crop. It was also found that the parent-offspring regression and correlation were negative when two generations in different seasons were compared. Among the finally selected 36 strains, however, a positive correlation was found between spring and summer yields. Some of them produced a high yield in both crop seasons, and appeared to be relatively stable in different years. The selected strains were *determinate* types, generally short, and showed a low photoperiodic sensitivity. It was pointed out that "disruptive seasonal selection" may bring about a wide seasonal adaptability, and in this respect our soybean strains may be compared with Ponlai rice varieties.


## 臺灣之大豆育種的研究

### 2. 栽培於不同季節之雜交雜種的育種

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大豆不同品種間雜交12組合，採混合育種法，春作與夏作反覆進行集團繁殖至 $F_4$ 或 $F_5$ 世代，任其自然淘汰後選拔單株育成系統，系統選拔亦仿照集團繁殖採一年兩世代法。雜種集團春作之遺傳變量較夏作爲大，親裔系統播種於不同季節時，回歸或相關爲負，惟栽培於同一季節，此等數值却爲正。選拔之優良系統多係有限型 (determinate type)，植株矮生，弱感光性，春作與夏作間產量適成正相關，其中有部份系統在春夏兩作之產量相當高，並不同年度間產量亦相當隱定，可與蓬萊種稻媲美。由上述結果可指出「分裂季節的選拔」(disruptive seasonal selection) 能產生較大的季節適應性。

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