STUDIES ON SOYBEAN BREEDING IN TAIWAN

3. Yield Stability of Strains Obtained from Disruptive Seasonal Selection of Hybrid Populations

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In our previous papers (Lu *et al.* 1967), we concluded that 1) varieties introduced from overseas were adapted either to the spring (February to March planting) or to the summer (June to July planting) crop season, or poorly adapted to any season, but 2) some of the strains selected from hybrid populations planted successively in the two different seasons (from "disruptive seasonal selection") were adapted to both. It was suggested further that the yield of such season-insensitive strains could remain stable in different years. Their adaptability to various locations and stability of performance are discussed in this paper.

Materials and Methods

A number of hybrid-derived strains selected at Taichung (*cf.* Tables 1 and 2 of the second paper of this series) and introductions from the U. S. A. and Japan were used. Palmetto, Jikkoku and some other introduced strains, recognized to be well adapted, were used as controls. These varieties were tested at the Chung-Hsing University, Taichung, and at Agricultural Improvement Stations located in various districts of Taiwan. They were also tested by farmers in Hsinchu district (north-western part).

Standard cultural practices were described in the first paper of this series. Dense planting (15 cm × 45 cm) was made for short-stature strains whose height was about 50 cm or less (most of our hybrid-derived strains and a part of introduced varieties), while standard spacing (20 cm × 50 cm) was used for taller strains.

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Results

1. Regression analysis of yield variation due to location.

In the spring and summer crops of 1961, seven hybrid-derived and twelve introduced varieties were tested at the Agricultural Improvement Stations located at Taipei (north), Lotung (north-east), Taichung (central-west), Tainan (south-west), Pingtung (south), Hualien (central-east), and Taitung (south-east), respectively. The data showed a wide variation in yield according to variety, season and location. The summer crop at Taipei and the spring crop at Hualien were failures on account of heavy rainfall and insect pests, giving low yields for all tested varieties. The yield data were discarded. The spring-Taipei and summer-Tainan crops also gave low yield records, but they were included in the computations as they appeared to show certain varietal differences. A part of the data taken as examples and the mean yield at each location in each season (location means) are in Table 1.

Table 1. *Examples of yield records at different locations and location means.*
(kg/10a, in 1961)

Season	Location	Hybrid-derived		Introduced		Mean yield of 19 varieties (Location mean)
		E27	F19	Chichibu-syakukin-nashi	Dortchsoy	
Spring	Taipei	19	32	11	17	22
	Lotung	169	40	23	183	85
	Taichung	135	130	108	95	102
	Tainan	111	95	126	110	93
	Taitung	160	214	117	219	148
	Pingtung	158	186	125	127	153
Summer	Lotung	93	92	68	73	64
	Taichung	143	138	123	83	126
	Tainan	66	75	29	15	33
	Hualien	157	106	215	95	121
	Taitung	127	141	105	109	122
	Pingtung	160	116	83	75	118

For a comparison of yield variability between hybrid-derived and introduced varieties, variance analysis was made of the data for both groups, respectively, excluding those from Taipei and Hualien. Before computation, the data were transformed into common logarithms, as will be explained later. The results are in Table 2. The table shows that the hybrid-derived varieties generally had small variance components due to variety × location and to other interactions, as compared with the introduced ones. They also had a smaller component due to location than the latter. It seems that in response to locations, the hybrid-derived varieties showed a more stabilized performance than the introduced ones.

Table 2. *Variance analysis of yield data for 7 hybrid-derived and 12 introduced varieties* (*in log.*).

Variance due to	Hybrid-derived		Introduced		Expectation (season fixed)
	D. F.	M. S.	D. F.	M. S.	
Season (S)	1	0.0857	1	0.7084	$\sigma_e^2+5\sigma_{VS}^2+k\sigma_{SL}^2+5k\sigma_S^2$
Location (L)	4	0.3307	4	0.9332	$2\sigma_{VL}^2+2k\sigma_L^2$
Variety (V)	6	0.0222	11	0.0609	$2\sigma_{VL}^2+10\sigma_V^2$
S×L	4	0.0402	4	0.5503	$\sigma_e^2+k\sigma_{SL}^2$
V×S	6	0.0209	11	0.0574	$\sigma_e^2+5\sigma_{VS}^2$
V×L	24	0.0168	44	0.0349	$2\sigma_{VL}^2$
V×S×L	24	0.0103	44	0.0272	σ_e^2

(Spring and summer seasons; 5 locations in each season; *k* varieties)

Comparison of variance components

		Hybrid-derived	Introduced
V×S×L	σ_e^2	0.0103	0.0272
V×L	σ_{VL}^2	0.0084	0.0175
V×S	σ_{VS}^2	0.0021	0.0060
S×L	σ_{SL}^2	0.0043	0.0436
Variety	σ_V^2	0.0005	0.0026
Location	σ_L^2	0.0224	0.0374
Season	σ_S^2	0.0010	0.0021

As Finlay and Wilkinson (1963) have asserted, the environmental value of a location may presumably be represented by the mean yield of many varieties tested at that location (location mean). Then, the variety-location interactional variance may be divided into one portion due to the regression of varietal yields on location means and the other portion due to deviation from the regression. This compuation was made of the yield data for spring and summer crops and of the pooled data (with the sums of mean squares and of mean products from spring and summer data), respectively, after transformation of the original data into logarithms. The results are in Table 3.

Table 3 shows that the hybrid-derived varieties, producing higher mean yield than the introduced ones, generally had smaller standard deviations due to location and smaller regression coefficients than the latter. They seem to have given stable performance at different locations. The difference in the

Table 3. *Regression analysis of yield variation due to location for individual varieties.*

Variety	Mean yield (ton/ha)	Sea-$^{(1)}$ sonal difference (%)	σ due$^{(2)}$ to location (log)	Regression coef.$^{(3)}$ on location mean			Deviation from$^{(3)}$ regression (in σ)		
				Spring	Summer	Pooled	Spring	Summer	Pooled
Hybrid-derived:									
E27	1.25	0.4	0.280	1.05*	0.5 7*	0.87**	0.170	0.052	0.136
E31	1.22	−14.4	0.223	0.77**	0.68*	0.73**	0.036	0.068	0.055
E32	1.28	5.6	0.256	0.84**	0.83**	0.84**	0.115	0.088	0.096
E44	1.13	−10.2	0.248	0.51*	1.02*	0.71**	0.136	0.145	0.152
E49	1.19	6.4	0.308	1.07**	0.73*	0.94**	0.172	0.151	0.156
F14	1.10	−5.1	0.288	0.79*	1.00	0.87**	0.124	0.239	0.149
F19	1.14	2.2	0.253	0.94*	0.38**	0.72**	0.190	0.045	0.154
Introduced (from Japan):									
Kanto-11	0.89	9.4	0.299	0.97**	1.02**	0.99**	0.063	0.055	0.054
Takidani-1	0.87	2.5	0.417	0.86	0.96**	0.90	0.514	0.084	0.334
Norin-3	0.70	−3.4	0.417	1.22*	1.42**	1.30**	0.224	0.106	0.165
Chichibu-s	0.94	−10.0	0.387	1.30*	0.99*	1.18**	0.238	0.166	0.198
Aso-1	0.98	−4.2	0.283	0.38	0.91**	0.59	0.324	0.110	0.240
Kimusume	0.80	2.1	0.405	1.05	1.29**	1.15**	0.264	0.073	0.233
Tsurunoko	0.76	15.2	0.398	1.18**	1.48**	1.31**	0.063	0.105	0.093
Introduced (from U. S. A.):									
Roanoke	0.92	12.7	0.356	1.17*	1.07*	1.13**	0.160	0.108	0.128
Jackson	0.57	22.0	0.355	0.83	1.10*	0.94*	0.321	0.141	0.233
Perry	0.96	16.8	0.371	1.23*	1.16**	1.20**	0.153	0.063	0.108
Lee	0.73	14.7	0.422	1.40**	1.30**	1.36**	0.106	0.169	0.133
Dortchsoy	1.00	25.1	0.362	1.13*	1.15**	1.14**	0.212	0.140	0.170

(1) Seasonal difference $=\dfrac{\bar{X}_{\text{spring}}-\bar{X}_{\text{summer}}}{\bar{X}_{\text{spring}}+\bar{X}_{\text{summer}}}$ (in %)

(2) Standard deviation computed from the mean square due to location on a logarithmic scale.

(3) Significance of the mean square due to regression is shown.
** Significant at 1% level, * at 5% level.

(4) Standard deviation computed from the mean square due to deviation from regression, on a logarithmic scale.

mean yield between spring and summer crops of each variety (in per cent of the sum of spring and summer yields) is also shown in Table 3. Most hybrid-derived varieties (excepting E31 and E44) showed small seasonal differences than the introduced ones. As mentioned in our previous paper, they are adaptive to both seasons; introduced ones might be adaptive only to the spring or only to the summer season, but a few of them appeared to be "two-season types".

Co-variations of the regression coefficients on location means with standard deviations for the variation due to location, varietal mean yields, and with seasonal yield differences are in Figures 1 to 4, respectively. Fig. 1 shows that the regression coefficient was strongly correlated with the standard deviation for location variation, excepting three varieties with a large deviation from regression. On the whole, a 77.3%-portion of the sum of squares of varietal yields due to location was found to be attributable to regression. Thus, in

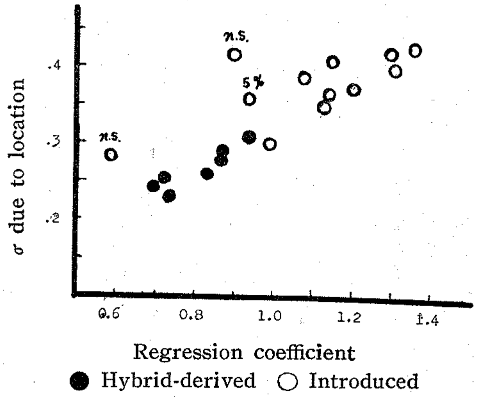

Fig. 1. Scatter diagram showing the relation between regression coefficients of varietal yields on location means (abscissa) and standard deviations for the variation due to location (ordinate).
n. s.: Regression being non-significant.
5%: Significant at 5% level.
Others with no mark were significant at 1% level.
(The same applies to the following figures.)

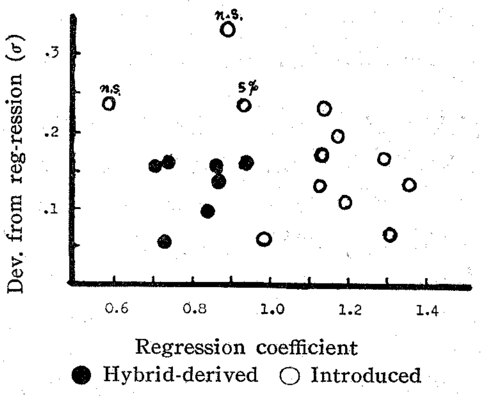

Fig. 2. Scatter diagram showing the distributions of regression coefficient of varietal yields on location means (abscissa) and standard deviation from regression (ordinate).

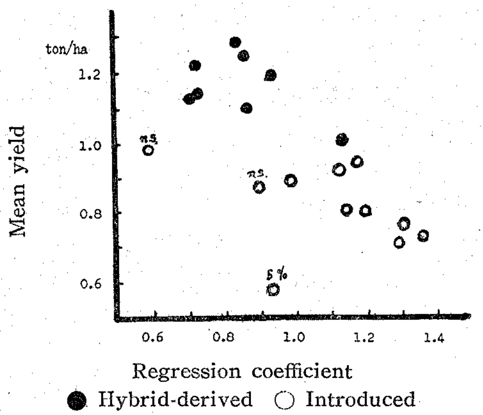

Fig. 3. Hybrid-derived and introduced varieties scattered according to the regression coefficent of yields on location means (abscissa) and mean yield (ordinate).

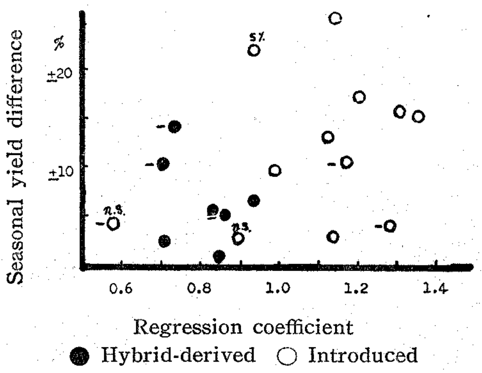

Fig. 4. Hybrid-derived and introduced varieties scattered according to the regression coefficient of yields on location means (abscissa) and seasonal yield difference (ordinate).

Seasonal yield difference $= \frac{\bar{X}_{\text{spring}} - \bar{X}_{\text{summer}}}{\bar{X}_{\text{spring}} + \bar{X}_{\text{summer}}}$ (in %)

Minus sign shows that $\bar{X}_{\text{spring}} < \bar{X}_{\text{summer}}$.

most varieties, the yield variation due to location could be largely represented by the regression on location means. Fig. 2 shows that the deviation from regression was slightly negatively correlated with the regression coefficient, and that the hybrid-derived varieties generally had smaller deviations from regression than the introduced ones.

Fig. 3 shows that the regression coefficient was negatively correlated with mean yield. In other words, varieties with high performance generally had a wide regional adaptability. This relation is found not only between hybrid-derived and introduced variety-groups, but also among introduced varieties. Fig. 4 shows that the hybrid-derived varieties tended to have smaller seasonal difference than the introduced ones, suggesting a weak correlation between seasonal and regional adaptabilities.

These computations are, as mentioned, based on the data transformed into logarithms. When the original data were directly used, the above intervarietal correlations were almost nullified. It was also found that the use of a logarithmic scale gave a higher linearity of regression than the use of actual figures. As reported by Finlay and Wilkinson (1963), yield variation may be better estimated in terms of ratios than from differences.

2. *Comparison of location variations in Hsinchu district.*

To estimate varietal yield variations due to experimental sites with relatively similar environmental conditions, a Taichung selection (E27) having a high yield stability and three introduced varieties known to be adaptive were tested in eight villages in Hsinchu district. The results are in Table 4. The data show that E27 produced almost the same yield in spring and summer crop at different sites. After transformation into logarithms, variance analysis of the data was made for each variety. The results in Table 4 indicate that E27 had a smaller season×location mean square than the other three varieties. It may be inferred that at least some of our hybrid-derived strains, obtained after selections in different seasons, are stable in yield at different locations.

Table 4. *Yields and variences of four varieties tested at eight locations in Hsinchu district.*

(kg/10a, in 1961)

Location	E27		Dortchsoy		Jikkoku		Kochi-akidaizu	
	Spring	Summer	Spring	Summer	Spring	Summer	Spring	Summer
Tahsi	154	165	149	145	112	140	128	140
Hsinwu	149	151	151	117	118	124	126	167
Chupei	147	153	167	125	126	130	135	178
Peipu	177	170	173	107	134	143	128	183
Nanchuan	153	169	144	101	101	140	98	179
Chunan	145	145	158	111	110	131	128	180
Houlung	163	144	176	101	128	133	137	187
Tunghsiao	179	163	177	150	115	138	137	188
Mean	158	158	162	120	118	135	127	175
	(D. F.)			(Mean square,in log.)				
Season	1	0.000,01		0.073,17		0.014,52		0.079,81
Location	7	0.001,54		0.003,03		0.000,98		0.002,09
S×L	7	0.000,55		0.002,70		0.001,12		0.001,86

3. *Variations due to micro-environments.*

The above experiments indicate the stability in performance of our hybrid-derived strains. With the view to estimating how their yields fluctuate in response to minor environments, a series of experiments was conducted. First, the yields of five varieties seeded at three different dates in the spring season were compared. As shown in Table 5, planting on February 21 generally gave the highest yield. However, E27 was found to have produced similarly high yields throughout three planting dates ranging from February 1 to March 13. This variety is known to be stable at different locations, as already mentioned. This suggests that in certain genotypes seasonal and regional adaptabilities are correlated.

Table 5. *Yield variation due to seeding time.*

(kg/10a, 1962, Taichung)

Variety	Yield of plants seeded on			C. V. (%)	C. V. for individual variation (%)		
	Feb. 1	Feb. 21	Mar. 13		plant height	plant weight	pod number p. plant
A92	227	281	244	11.1	10.4	21.9	17.8
E27	286	281	276	1.8	10.3	22.8	19.3
E31	263	235	213	10.8	12.5	24.2	25.7
Jikkoku	139	185	159	14.2	10.6	23.7	25.8
Palmetto	257	283	185	20.9	17.4	21.0	20.6

Table 5 also shows that the variations of individual plants within plots did not differ much among varieties. Further, four hybrid-derived and four introduced varieties were repeatedly seeded every day starting from July 21 to August 2 (summer crop), and the yield data were recorded. The variations due to seeding date and to individual plants within plots, in terms of variability coefficient, are given in Table 6. The table shows that the varieties tested did not differ much in the variability due to minor environments.

These experimental results suggest that hybrid-derived strains, having wide seasonal as well as regional adaptabilities, do not necessarily show stability in the growth of individual plants, and that regional and seasonal yield stability is not correlated with insensitivity to minor environments.

Discussion

It has long been recognized by plant breeders that certain crop varieties perform well over a wide range of environments and that this ability is genotypically conditioned. As the environment varies from location to location, and from year, a wide adaptability to changing environments is usually a desired character of crop plants. For evaluating varietal performance in

Table 6. *Coefficients of variabiltty for variations due to seeding time and to individual plants within plots.*

(Seeding was made everyday from July 21 to August 1, 1965, at Taichung.)

Variety	C. V. due to seeding time (%)				C. V. for individual variation (%)			
	Yield	Bean no.	Pod no.	Height	Yield	Bean no.	Pod no.	Height
A92	24.1	20.7	24.5	14.9	53.8	11.5	42.7	14.4
B11	26.8	25.2	24.1	10.0	40.3	31.5	23.5	11.5
E27	18.7	36.2	29.9	14.8	48.2	45.4	26.2	12.7
E32	27.2	21.8	24.9	17.8	35.2	30.1	26.7	10.3
Jikkoku	18.4	17.0	15.7	9.1	41.5	35.3	28.0	10.7
Wakajima	26.7	20.3	24.7	19.8	34.2	29.3	28.4	12.2
Palmettto	27.2	26.6	24.1	13.9	29.8	30.9	27.8	12.7
Improved pelican	15.6	13.7	15.7	15.9	44.9	36.7	31.8	12.0

different environments, methods of variance analysis have been developed, which allow a general picture of interactional variations involved in a population. Some workers consider that interactional variances camouflage real genotypic values, while others, from the viewpoint that genotypes determine reaction norms, consider them to be an integral feature of genetic variations.

For estimating the responses to predictable environments of given genotypes, various indices have been used according to practical needs. Regional environment is, however, a complex of climatological and edaphic factors that cannot be easily divided into components. Yield is also a complex determined by various characters each responding to environmental factors in a different way. Dealing with the performance of many varieties in a number of environments, Finlay and Wilkinson (1963) have contended that the response of a variety to regional as well as seasonal environments could be represented by the linear regression of its yield on the mean yield of all varieties at each site in each season (location means). This regression analysis is based on the assumption that the mean yield represents the environmental value of the given site in the given season. By this method, a variety with a regression coefficient of 1.0 is regarded as having average stability over all the environments. From data for many barley varieties tested at different locations in Australia, they showed that varieties with high mean yield tended to have regression coefficients below 1.0, while those with low mean yield varied in a wide range of regression coefficients.

Konishi *et al.* (1965) used this method for analysing yield variation of barley varieties in Japan, and pointed out that two-rowed varieties, seemingly adapted to low soil fertility, showed higher stability of yield than six-rowed ones selected from fertile soils. We also have employed this method of regression analysis for estimating yield variations due to location of our soybean varieties.

For estimating yield stability of crop varieties, Wricke (1962) proposed to use as a measure the within-varietal variance due to deviation from expected values (location means corrected by the difference between varietal mean and grand mean), which he called "Ökovalenz". By this method, varieties with a higher and a lower location-response than the average may have the same value; varietal variations in yield stability may not be correctly evaluated by this method. Eberhart and Russel (1966) consider that varietal yield stability can be estimated by both the regression on location means and deviation from the regression. The deviation from the regression of a variety is due to its different response to the environmental series and to experimental error. But, in many cases, genotype-environment interactional variation may be largely represented by the regressions, and the linearity may depend upon the scale used. We experienced that, as was pointed out by Finlay and Wilkinson (l. c.), a logarithmic scale could better illustrate yield variations than the natural scale.

By employing the Finlay and Wilkinson's method, we found that mean yield was correlated with yield stability among varieties, or that varieties with high mean yield generally performed well over a wide range of environments. Most previous workers investigating this relation seem to have failed to find such a correlation between performance and stability (*e. g.*, Allard 1961, Pfahler 1964, Wricke 1964, Eberhart and Russel 1966, etc.). In general, it may be that stability and performance are independent. It is possible that soybean is, as compared with other grain crops, strongly sensitive to environments, and accordingly relatively insensitive genotypes producing high yields under unfavorable conditions can have a high mean yield.

Our hybrid-derived strains had not only a high average performance but also a high yield stability in different localities and seasons. Among the strains tested, seasonal stability was not strongly correlated with regional stability, but some of them, *e. g.*, E27 and F19, were highly adaptive to different crop-seasons as well as to different locations. As mentioned in our previous paper, their yield seems to be stable in different years. They may be considered as having a general adaptability. In contrast, introduced varieties tended to be low in performance and in stability, though they were studied because they have been considered adaptive by Agricultural Improvement Stations.

It may be noted that genotypes showing general adaptability were obtained from hybrid populations repeatedly selected in different seasons, following the "two-generation-a-year" breeding plan. As mentioned in our previous paper, genotypes adapted to one season were generally inadaptive to the other season.

Accordingly, the breeding scheme brings about a selection pressure working in a disruptive manner regarding the seasonal effects. It may be attributed to such a "disruptive seasonal selection" that the selected strains are generally adapted to changing environments, though this must be confirmed by a comparative breeding experiment of "two-generation-a-year" with a "one-generation-per-year" plan grown in either the spring or summer season. It may be worthy of notice that breeding for wide adaptability can be achieved by repeating selections in different environments.

The adaptability or stability of our soybean strains may be, according to Allard and Bradshaw's (1964) terminology, attributed to "individual buffering", as the strains are nearly homozygous. It may be that in response to changing environments, a population may become polymorphic attaining "populational buffering", while its component genotypes may be selected toward wide adaptability due to individual buffering. Bradshaw (1965) considers that disruptive selection leads to plasticity of character development. Our yield stability is not necessarily due to stability of yield-component characters. The characters may be plastic, but yield may be stable if environmental changes in component characters are inter-correlated so as to result in a buffering mechanism. This is a problem to be investigated in the future. Our experimental results seem to furnish an example of homozygous genotypes acquiring an individual-buffering ability, obtained after repeated "disruptive seasonal selections".

Our experimental results indicated that seasonal as well as regional stabilities of yield were not correlated with phenotypic stability of individual plants. This suggests that the developmental stability of individual plants in a community and that of plant communities in varying environments are due to different buffering systems. According to Sakai and Shimamoto (1965), the stability in size of plant organs is a genotypically controlled character. The interrelation between adaptability to changing environments and developmental homeostasis requires further investigation.

Summary

A number of soybean strains selected from hybrid populations successively grown in spring and summer crop-seasons, and certain introduced ones, which were known to be locally adapted, were tested at seven locations (Agricultural Improvement Stations) in Taiwan. The yield data, transformed into logarithms, were analysed by the regression method as used by Finlay and Wilkinson (1963). The hybrid-derived strains, adaptive to both seasons, generally had a high mean yield and showed stability of yield at different locations. The deviation from regression was minor in most varieties. A similar experiment

made at eight different sites in Hsinchu district also proved that a hybrid-derived strain, E27, had a high yield stability. As suggested in our previous paper, "disruptive selection" of hybrid populations seems to bring about a wide-range adaptability of selected genotypes. Breeding for wide adaptability and yield stability may be achieved by repeating selections in different environments. The phenotypic stability of individual plants within plots did not seem to be correlated with seasonal and regional stabilities.

臺灣之大豆育種的研究

3. 大豆由季節分裂淘汰選拔育成的品系之產量穩定性

蔡國海 盧英權 岡彥一

大豆雜種集團在春作與夏作不同環境條件下經反覆選拔育成的後裔在全省性區域試驗之產量數值轉換對數尺度後，應用 Finlay 與 Wilkinson 兩氏 (1963) 之回歸方法分析結果，發現育成品系不但春，夏兩作產量高，而在不同地域間之產量穩定性亦甚高，尤以E 27品系在新竹地區所顯示產量之穩定性相當高。由此可知經不同環境條件實施反覆選拔所育成的品系顯示具有廣範之適應性，認爲此法係選拔適應性高遺傳型之一種適當的育種方法。

此外，表現型植株間與季節或地域等之穩定性間並未發現有相關關係。

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