Phenotypic stability of double cross cultivar "Wase-homare" (*Zea mays* L.), and its parental sets of single crosses and inbred lines

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Summary

Double cross cultivar "Wase-homare" is widely adapted in Hokkaido. To obtain the information of phenotypic stability, the response of "Wase-homare" to different environments such as a combination of two locations and several seeding dates was compared with that of its parental sets of two single crosses and four inbred lines. In addition, phenotypic stability of the parental sets was also investigated by measuring the magnitude of variation among plants grown under the same environment.

"Wase-homare" and single crosses were more stable than inbred lines in different environments for all characters examined. But no difference in response to different environments was found between "Wase-homare" and single crosses in any character. There were significant differences in response among inbred lines, but the rank in inbred lines changed with characters. While the magnitude of interplant variations varied with genotypes in most characters, inbred lines did not have larger interplant variations on an average when compared with single crosses. It was shown that the response to different environments and the magnitude of interplant variation within an environment are not to be necessarily maintained under common genetical control.

Introduction

One of the most important objectives in plant breeding is the selection of genotypes that are consistently high yielding over the range of environments. When genotypes are compared in a wide range of environments, relative rank in genotypes for an agronomic character frequently changes with environments owing to genotype-environment interaction. The genotype-environment interaction results from the variation in the genetical ability which controls phenotypic stability to different environments. For the adaptability of crop plants, phenotypic stability of each genotype decisively plays an important role.

Double cross maize cultivar "Wase-homare" is widely adapted in Hokkaido[8], and has

contributed to the increase of acreage for silage production in recent years. Therefore, it may be meaningful to obtain genetical information on stability of this cultivar in relation to its parental sets of single crosses and inbred lines.

For the uniformity of agronomic characters in maize, the magnitude of interplant variations under the same environment is also one of the important characteristics in breeding programs, because it can have significant effects on the mechanization of tillage practices and quality of products, and even on grain yield[5]. According to Gotoh[6], the interplant variation of maize inbred lines can be separated into three components, i. e., 1) experimental error, 2) environmental fluctuation itself, and 3) self-regulating ability of plants themselves to micro-environmental fluctuation and to developmental error. Then, he pointed out that self-regulating ability should depend on each inbred line. Shank and Adams[13] compared interplant variations between inbred lines and their single crosses of maize, and concluded that this kind of phenotypic stability is the feature of heterozygosity and at the same time it varies even in homozygotes.

Following the above reports, there are two ways for measuring phenotypic stability of genotypes. One is the response to different environments and the other is the magnitude of interplant variation in non-segregating populations.

The present study was conducted 1) to compare the phenotypic stability to different environments over double cross cultivar "Wase-homare", and its parental sets of two single crosses and four inbred lines, and 2) to clarify the relationship of two kinds of phenotypic stability, response to different environments and the magnitude of interplant variation, over single crosses and inbred lines.

Materials and Methods

Materials examined here consisted of double cross cultivar "Wase-homare", and its parental sets of two single crosses, CM37×CMV3 (dent) and N 19×To 15 (flint), and four inbred lines, CM 37, CMV 3, N 19 and To 15. The experiments were carried out in 1984 at two locations in Hokkaido, the experimental farms of Obihiro University, Obihiro, and Hokkaido University, Sapporo. Materials were grown in seven different environments consisting of four seeding dates at Obihiro and three seeding dates at Sapporo (Table 1) using randomized block design with two replications. Four seeds per hill were planted with a spacing of 75 cm×20 cm. After emergence, seedlings were thinned to one plant per hill. Population density was 6,667 plants/10 a. Fertilizer was applied at the rate of 12 : 18 : 10 kg/10 a of N : P_2O_5 : K_2O as a basal dressing. Other crop management practices were as usual in each location.

Measurements of culm length, ear height, ear weight, the number of kernels per ear, ear length and ear diameter were taken from fifty plants of "Wase-homare" and from fifteen plants of others in each plot. The phenotypic

Table 1. Environmental conditions by combinations of locations and seeding dates in 1984

	Locations	
	Obihiro[a]	Sapporo[b]
Seeding dates	May 11 (Ob 1)	
	May 18 (Ob 2)	May 18 (Sa 1)
	May 28 (Ob 3)	May 28 (Sa 2)
	June 7 (Ob 4)	June 7 (Sa 3)

a : Experimental Farm of Obihiro University of Agriculture and Veterinary Medicine.
b : Experimental Farm, Faculty of Agriculture, Hokkaido University.

value of each character was evaluated by mean value among plants within a plot, and then transformed into the logarithmic scale for statistical analysis to induce a reasonable degree of homogeneity of experimental errors. Interplant variations of ear height, ear weight and ear diameter were estimated from square roots of the standard deviation within a plot. For the other three characters, it was estimated from logarithms of the standard deviation. These scales of interplant variations were suitable to appraise the normality in distribution of the experimental errors and the independence with the experimental errors in phenotypic values[10].

Regression techniques, originally proposed by YATES and COCHRAN[15], were applied to analyze the genotype-environment interactions in phenotypic values. The data Y_{ijk} of the i-th genotype in the k-th replicate of the j-th environment may be expressed as

$$Y_{ijk} = \mu + \alpha_i + \varepsilon_j + \beta_i x_j + \delta_{ij} + e_{ijk}$$

μ =grand mean;

α_i =effect of the i-th genotype;

ε_j =effect of the j-th environment;

β_i =linear regression coefficient from the regression of Y_{ij}. on the environmental index, x_j, for the i-th genotype;

δ_{ij} =deviation from the i-th regression line in the j-th environment.

e_{ijk} =experimental error contribution of the i-th genotype in the k-th replicate of the j-th environment.

For the comparison of relative response to different environments in heterozygous and heterogeneous hybrids to homozygous parental inbred lines and for independence of any information from "Wase-homare" and single crosses, the environmental index, x_j, was estimated from the average of four parental inbred lines in the j-th environment.

Results

1. Phenotypic values

There were significant genotypic and environmental effects in all of six characters (Table 2). The genotypic effects were partitioned into three parts of variations, 1) difference between hybrids ("Wase-homare" and its parental single crosses) and inbred lines, 2) difference among hybrids and 3) difference among inbred lines.

The relative difference between hybrids and inbred lines was detected in all cases; this was caused by the effect of heterosis. But there was no difference between "Wase-homare" and its parental single crosses for ear height, ear weight and the number of kernels per ear. Culm length of "Wase-homare" was higher than those of single crosses at Sapporo, but not at Obihiro (Table 3). Ear length and ear diameter of "Wase-homare" were intermediate in the single crosses. CM 37 × CMV 3 showed larger ear diameter and shorter ear length than N 19 × To 15. Difference among inbred lines was also found except for culm length.

Most of the environmental effects on phenotypic values were explained by the differences between locations in all cases. While culm length increased at Obihiro, the other five characters increased at Sapporo. Culm length and ear height increased with later but not the latest seeding date at both locations.

2. Genotype-environment interactions

There were significant genotype-environment interactions in all characters (Table 2). A sum of square of genotype-environment interaction was partitioned into two parts; 1) difference among regression lines, and 2) deviation from the regression.

For all characters, mean squares due to regression lines were significant, but mean squares of deviation from the regression were

Table 2. Joint regression analyses of variance for phenotypic values of six characters (on a log scale)

Source of variations	df	Mean squares					
		Culm length	Ear height	Ear weight	The number of kernels per ear	Ear length	Ear diameter
Environments (E)	6	0.0300**	0.1248**	0.4325**	0.3033**	0.1010**	0.00105**
Between locations	1	0.0384**	0.1714**	2.4157**	1.7036**	0.5917**	0.04578**
Within locaions	5	0.0282**	0.1155**	0.0358	0.0232	0.0028	0.00344
Genotypes (G)	6	0.8473**	1.6174**	4.1381**	1.6970**	1.1480**	0.17805**
Hybrids vs. Inbreds	1	4.9152**	8.0448**	21.8836**	9.2403**	3.2536**	0.53189**
Hybrids	2	0.0473*	0.0182	0.0134	0.0158	0.5234**	0.07294**
Inbreds	3	0.0246	0.5411**	0.9727**	0.3033**	0.8626**	0.13017**
G × E interactions	36	0.0105**	0.0332**	0.0532**	0.0285**	0.0097**	0.04994**
Regressions	6	0.0155**	0.0929**	0.2212**	0.1140**	0.0368**	0.02005**
Hybrids vs. Inbreds	1	0.0152*	0.3673**	0.6650**	0.4530**	0.0696**	0.09372**
Hybrids	2	0.0014	0.0161	0.0196	0.0063	0.0076	0.00295
Inbreds	3	0.0250**	0.0526*	0.2122**	0.0728**	0.0453**	0.00688**
Deviations	30	0.0095**	0.0213	0.0196	0.0114	0.0042	0.00198
Errors	49	0.0029	0.0149	0.0160	0.0091	0.0027	0.00150

Note: Hybrids include "Wase-homare" and its two parental single crosses.

*, **: Significant at the 5% and 1% levels of probability, respectively.

Table 3. Phenotypic values in each environment and estimates of stability parameter to different environments

	Ob 1[a)]	Ob 2	Ob 3	Ob 4	Sa 1	Sa 2	Sa 3	$Y_{i..}$	β_i
				— Culm length (cm) —					
MC 37	108a[b)]	118a	124a	120a	122b	122b	124ab	119	0.471
CMV 3	124b	117a	122a	121a	126b	120b	121ab	122	0.110
N 19	118ab	114a	127a	110a	97a	98a	116a	112	1.163
To 15	109a	99a	130a	99a	115b	120b	133b	115	2.256
CM 37×CMV 3	169c	167b	193b	187b	162c	158c	172c	173	0.676
N 19×To 15	194d	203c	210c	192b	162c	162c	177c	186	0.396
Wase-homare	198d	202c	202c	194b	175c	187d	194d	193	0.237
$Y_{.i.}$	146	146	158	146	137	138	148		
	Ob 1	Ob 2	Ob 3	Ob 4	Sa 1	Sa 2	Sa 3	$Y_{i..}$	β_i
				— Ear height (cm) —					
CM 37	35.1b	44.9b	51.4b	51.6b	56.4bc	51.8b	53.0b	49.2	0.867
CMV 3	36.9b	32.3a	39.9a	44.6b	49.3b	47.7b	40.2a	41.5	0.786
N 19	31.9ab	27.8a	35.3a	37.1ab	31.5a	38.1a	40.0a	34.5	0.685
To 15	24.5a	21.2a	43.6ab	27.6a	34.7a	35.4a	40.6a	32.5	1.662
CM 37×CMV 3	63.2c	58.9c	73.3c	71.2c	67.7d	61.8c	68.3cd	66.3	0.329
N 19×To 15	62.8c	76.7d	84.2d	67.5c	58.4c	62.3cd	65.0c	68.1	−0.163
Wase-homare	68.6c	69.7d	74.2c	70.6c	69.6d	70.6d	74.3d	71.1	0.127
$Y_{.i.}$	46.1	47.4	57.4	52.9	52.5	52.5	54.5		
	Ob 1	Ob 2	Ob 3	Ob 4	Sa 1	Sa 2	Sa 3	$Y_{i..}$	β_i
				— Ear weight (g) —					
CM 37	59.2a	68.0b	72.7a	74.4c	96.4b	98.2b.	95.5b	80.6	0.717
CMV 3	41.4a	22.4a	35.2a	31.0a	70.1ab	62.5a	65.4a	46.6	1.637
N 19	45.2a	46.0ab	52.3a	56.4b	59.2a	61.7a	62.5a	54.7	0.447
To 15	57.0a	47.9ab	71.9a	41.3ab	80.3ab	97.8b	89.3b	69.3	1.199
CM 37×CMV 3	140.7b	126.5c	150.3b	134.6d	163.9c	158.4c	167.4c	148.8	0.397
N 19×To 15	143.5b	159.9c	146.3b	156.4e	166.7c	161.6c	167.6c	157.4	0.147
Wase-homare	157.8b	148.2c	144.0b	132.9d	169.1c	173.9c	169.0c	156.4	0.321
$Y_{.i.}$	92.1	88.4	96.1	89.5	115.1	116.3	116.4		

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Continued

	Ob 1	Ob 2	Ob 3	Ob 4	Sa 1	Sa 2	Sa 3	$Y_{i..}$	β_i
				The number of kernels per ear					
CM 37	182b	201b	211a	177a	261b	259ab	254b	220	0.745
CMV 3	242c	148ab	191a	169a	313c	298b	280c	234	1.300
N 19	129a	148ab	160a	152a	181a	198a	187a	165	0.621
To 15	166ab	137a	163a	152a	234b	271b	255b	196	1.335
CM 37×CMV 3	362d	350c	386c	308b	415d	406c	401e	375	0.419
N 19×To 15	338d	349c	328b	339b	377d	370c	374d	353	0.226
Wase-homare	375d	372c	365b	331b	384d	405c	392de	375	0.237
$Y_{.j.}$	256	244	258	232	309	315	306		

	Ob 1	Ob 2	Ob 3	Ob 4	Sa 1	Sa 2	Sa 3	$Y_{i..}$	β_i
				Ear length (cm)					
CM 37	11.1a	11.0b	11.1b	10.9b	13.0b	12.6a	12.7a	11.7	0.689
CMV 3	10.1a	7.1a	8.5a	8.6a	12.4b	11.6a	12.0a	10.0	1.831
N 19	10.1a	10.5b	10.3ab	10.9b	11.4a	12.4a	12.1a	11.1	0.627
To 15	15.8c	15.8d	17.0c	16.2d	18.3d	19.7c	19.7d	17.5	0.853
CM 37×CMV 3	13.7b	13.2c	14.9c	13.2c	16.2c	16.0b	15.6b	14.7	0.726
N 19×To 15	20.5d	21.5e	20.1d	20.8e	22.5e	22.4d	23.1e	21.5	0.395
Wase-homare	16.9c	17.6d	17.1c	16.2d	18.2d	18.5c	17.6c	17.4	0.281
$Y_{.j.}$	14.0	13.8	14.1	13.8	16.0	16.1	16.1		

	Ob 1	Ob 2	Ob 3	Ob 4	Sa 1	Sa 2	Sa 3	$Y_{i..}$	β_i
				Ear diameter (mm)					
CM 37	40.0b	41.0c	42.0b	41.0c	44.0cd	44.5c	44.0d	42.4	0.669
CMV 3	37.0ab	30.5a	35.5a	34.0b	40.5bc	39.5b	38.5b	36.5	1.603
N 19	35.5ab	35.5b	36.5a	36.0b	38.5b	39.5b	38.5b	37.1	0.727
To 15	33.5a	33.0ab	34.5a	29.0a	35.0a	35.0a	35.5a	33.6	1.000
CM 37×CMV 3	47.0c	45.5d	46.5c	46.0d	46.5d	46.5c	46.5e	46.4	0.104
N 19×To 15	40.0b	40.5c	40.5b	42.5cd	39.0b	40.0b	38.5b	40.1	-0.443
Wase-homare	45.0c	44.0d	44.0bc	43.0cd	43.0c	42.0bc	42.0c	43.3	-0.275
$Y_{.j.}$	39.7	38.6	39.9	38.8	40.9	41.0	40.5		

a: Environmental conditions, refer to Table 1.
b: Means within each column followed by the same letter do not differ significantly at the 5% level of probability.

Table 4. Analyses of variance for interplant variations in single crosses and inbred lines, measured in terms of standard deviations, of six characters

Source of variations	df	Mean squares					
		Culm length [b]	Ear height [a]	Ear weight [a]	The number of kernels per ear [b]	Ear length [b]	Ear diameter [a]
Environments (E)	6	0.6122**	1.5607**	2.070**	0.5432**	0.4619**	0.0495**
Between locations	1	1.9939**	8.2940**	9.014**	2.2359**	1.6368**	0.2772**
Within locations	5	0.3359**	0.2141	0.682	0.2047	0.2269*	0.0039
Genotypes (G)	5	0.2496**	0.4934	8.716**	0.9323**	0.2405*	0.0141
Single crosses vs. Inbreds	1	0.0179	0.0009	31.356**	0.1682	0.3503*	0.0219
Single crosses	1	0.0404	0.4188	1.132	1.7955**	0.1418	0.0060
Inbreds	3	0.3965**	0.6825*	3.697*	0.8993**	0.2367*	0.0142
G × E interactions	30	0.0653	0.2192*	0.528	0.1164	0.0914	0.0105**
Errors	42	0.0514	0.1028	0.549	0.1018	0.0793	0.0034

a:, b: Transformed to square root and logarithm, respectively, because of the normality in distribution of the experimental errors.

*, ** : Significant at the 5% and 1% levels of probability, respectively.

significant only for culm length. From these results, the significance of genotype-environment interaction mean square could be attributed to difference among regression lines. Thus the response of each genotype to different environments was evaluated by the regression coefficient.

Difference in response between hybrids and parental inbred lines was highly significant in all cases. It was due to relatively higher stability of hybrids than that of the inbred lines (Table 3). It was thus found that heterozygous single crosses and heterogeneous "Wase-homare" are more stable for the environmental changes than homozygous inbred lines. But there was no difference in the response between "Wase-homare" and single crosses in all cases. On the other hand, difference in response among inbred lines was significant for all characters. On the ear characters, CM 37 and N 19 were stable, but CMV 3 was unstable.

3. Interplant variations

In addition to a regression coefficient of the phenotypic value, the magnitude of interplant variations in inbred lines and single crosses

was measured as another parameter of phenotypic stability. The analysis of variance for interplant variations was carried out (Table 4).

There were significant genotypic effects on the interplant variations of culm length, ear weight, the number of kernels per ear and ear length. Single crosses had larger interplant variations than the inbred lines for ear weight and ear length, but in other characters the interplant variations of single crosses and inbred lines had no difference (Table 5). Difference of the interplant variations among inbred lines was observed on the above four characters, but relative rank in inbred lines changed with the characters.

With respect to interplant variations of ear height and ear diameter, there were interactions of genotypes with environments. These genotype-environment interactions of interplant variations also implied the difference in response of each genotype to different environments.

Discussion

In this study, the phenotypic stability of maize genotypes was analyzed by two ways.

Table 5. Mean interplant variations of inbred lines and single crosses over environments in the four characters which had significant genotypic effects

	Culm length	Ear weight	The number of kernels per ear	Ear length
Inbred lines				
CM 37	2.434bc[a]	4.448bc	3.780a	0.504ab
CMV 3	2.596c	3.418a	4.217b	0.397a
N 19	2.585c	3.960ab	3.649a	0.623bc
To 15	2.470bc	4.532c	4.027b	0.691bc
Single crosses				
CM 37×CMV 3	2.470bc	5.184d	4.077b	0.620bc
N 19×To 15	2.394ab	5.584d	3.570a	0.792c

Note: The scales of interplant variations were the same as in Table 4.
a: Means within each column followed by the same letter do not differ significantly at the 5% level of probability.

One was the response of phenotypic values to different environments and the other was the magnitude of interplant variation within plot, excluding heritable variations caused by segregation.

There were genotype-environment interactions in phenotypic values of all charecters, indicating genetical control of the response to different environments. As shown in Tables 2 and 3, "Wase-homare" and single crosses were more stable to the environmental changes than inbred lines. It thus appeared that with respect to the stability in different environments, "Wase-homore" and single crosses are superior to inbred lines. But the response of "Wase-homare" to different environments was not different from that of parental single crosses in any character.

According to ALLARD and BRADSHAW[1], there are two ways to achieve the phenotypic stability for adapting to different environments. These ways are defined as individual buffering and population buffering. Individual buffering is the ability of plants with the same genotype where the individual members are well adapted to a wide range of environments; population buffering is the ability of the population consisting of a number of genotypes each adapted to a somewhat different range of environments. Thus a homozygous or heterozygous genotype such as an inbred line or a single cross possess individual buffering and a heterogeneous population such as a three-way, a double cross and an outbreeding cultivar possess population buffering. SPRAGUE and FEDERER[14] reported that cultivar×location and cultivar × year interactions were smaller in double crosses than in single crosses. JONES[7] stated that the higher stability of double crosses to different environments can be attributed to the buffering ability of heterogeneity. However, it was also reported that there are no relationships between the response

to different environments and the level of heterozygosity[4, 9, 11].

As mentioned above, some points of disagreement are still remaining in regard to the relationship of heretozygosity to phenotypic stability. Therefore, further investigations using other double crosses and their parental sets are necessary. In addition, a considerable difference among inbred lines was found with respect to response to different environments when estimated by β values. This implies that some inbred lines have a superior stability to the environmental changes. So it is of interest to carry out selection experiments in homozygotes to verify genetic behavior of response to different environments.

The mean interplant variations over environments were varied with genotypes in culm length, ear weight, the number of kernels per ear and ear length (Tables 4 and 5). For these four characters, relationships between β_i of phenotypic values and the mean interplant variation are presented in Fig. 1. Simple correlations over single crosses and inbred lines were positive in the number of kernels per ear and negative in the other three characters, but they were non-significant.

The response of each genotype to different environments is attributable to phenotypic plasticity[3]. On the other hand, the interplant variation is known to be due to developmental instability which is assumed to be attributable to accidents in the developmental processes[2, 12], though it might involve effects of undiscernible environmental influences. The low correlations between β_i and the magnitude of interplant variation shown in Fig. 1 suggest that phenotypic plasticity and developmental instability are not to be necessarily maintained under common genetical control.
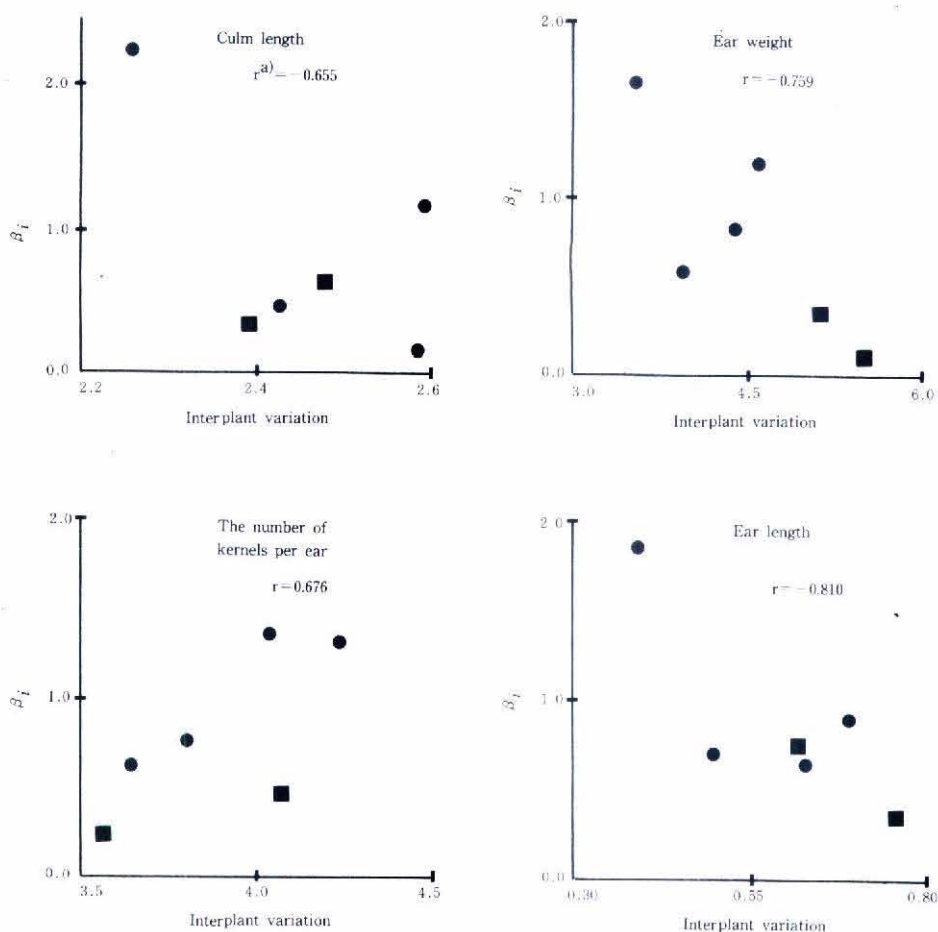
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Fig. 1. Relationships between response to different environments measured by regression coefficient and mean interplant variation over environments.
  a : Correlation coefficient over single crosses and inbred lines.
  ● : Inbred lines. ■ : Single crosses.

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トウモロコシの複交雑品種
「ワセホマレ」とその親
の単交雑および自殖系
統の表現型安定性

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要　　約

　サイレージ用品種「ワセホマレ」は，北海道で高い適応性をもっている。本研究は，「ワセホマレ」と親の単交雑ならびに自殖系統を対象とし，表現型の安定性に関する基礎的資料を得る目的で，地域と播種日を異にしたときの反応性を検討した。また，同一環境内での個体間の表現型安定性の尺度として，単交雑と自殖系統における個体間変異の大きさを検討した。

　調査した6形質いずれでも，遺伝子型と環境との相互作用が認められた。「ワセホマレ」と単交雑は，概して自殖系統よりも環境間での表現型の安定性が高かったが，「ワセホマレ」と単交雑の間には安定性に差異がなかった。環境間での表現型安定性は自殖系統の間でも差異があったが，それらの相対的な順位は形質によって異なっていた。

　個体間変異の大きさは，多くの形質で系統間に有意差があり，それらは主として自殖系統間の差異に起因していた。異型接合体の単交雑は，同型接合体の自殖系統より，同一環境内での個体間の形質発現が必ずしも安定しているとはいえなかった。

　環境間での表現型安定性と，個体間変異の大きさでみた同一環境内での表現型安定性は，異なった遺伝的支配を受けることが示唆された。