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Citation	Journal of the Faculty of Agriculture, Hokkaido University, 62(3), 211-221
Issue Date	1985-11
Doc URL	https://hdl.handle.net/2115/13022
Type	departmental bulletin paper
File Information	62(3)_p211-221.pdf

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GENOTYPE×ENVIRONMENT INTERACTIONS IN SINGLE CROSS MAIZE CULTIVAR "PIRIKA-SWEET" AND ITS PARENTAL INBRED LINES

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Received January 9, 1985

Introduction

When genotypes are compared over a range of environments, their relative ranks for a quantitative character frequently varies with environments. This implies the expression of genetic differences in response to environmental changes and can be manifested as a significant genotype × environment interaction. The genotype × environment interaction must be taken into account for selecting widely adaptable or stable genotypes, and for preparing more suitable conditions for given genotypes.

STEBBINS (1949) suggested the two ways by which a plant population achieves the tolerance over a range of environments. ALLARD and BRADSHAW (1964) defined these two ways as populational buffering and individual buffering, to apply them for plant breeding. According to their definition, 1) if a plant population is composed of various genotypes (e. g., three-way and double crosses or outbreeding cultivar), and individual genotypes adapt to a somewhat different range of environments, that population has the high populational buffering ability. On the other hand, 2) if a plant population is composed of the same genotype (e. g., single cross or self-fertilizing cultivar), and the genotype adapts to a wide range of environments, that population has high individual buffering ability.

It has been reported that there is no differences in the yield stability between single and three-way crosses in maize (*Zea mays* L.) (EBERHART and RUSSELL 1966, LUNCH *et al.* 1974). On the other hand, SCOTT (1967)

[J. Fac. Agr. Hokkaido Univ., Vol. 63, Pt. 3. 1985]

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reported that the yield stability is genetically controlled, thus selecting for stability is supposed to be effective to increase yield. EBERHART and RUSSELL (1969) pointed out that individual buffering is important and they suggested that it is a heritable character in certain genotypes.

The interest in our investigation lies on the genotype×environment interaction, which reflects the difference of buffering ability in genotypes to environmental changes. The purposes of this study were to elucidate the variations of individual buffering ability between a single cross maize cultivar and its parental inbred lines.

Materials and Methods

Single cross cultivar "Pirika-sweet" and its parents, V 574 and Ma 21547 were used. "Pirika-sweet" was developed by Tokachi Agricultural Experimental Station, Memuro, Hokkaido, and it was released in 1975 as a recommended cultivar in Hokkaido. The cultivar has desirable characteristics for processing, such as colorless silk, bright hernels and high productivity of available ears (NAKANO *et al.* 1975).

The seed parent V 574 is the inbred line introduced from Horticultural Research Institute of Ontario, Canada. It was derived from inbreeding of a progeny of Me 100×V 3. The pollen parent Ma 21547 was introduced from Massachusetts Agricultural Station, USA, and it has been used as the parental line of several commercial cultivars, such as "Golden Beauty" and "Hokkan No. 3".

The seeds for the experiments were provided from Tokachi Agricultural Experimental Station.

The experiments were carried out at the experimental farm, Faculty of Agriculture, Hokkaido University, Sapporo, and the experimental field of Tokachi Agricultural Experimental Station, Memuro, in 1981. Plants were grown under eight environments by combinations of seeding dates and plant densities at two locations (Table 1). The experimental design at each location was split-plots with three replications arranging the environments for main-plots and genotypes for sub-plots. Four seeds per hill were planted and thinned to one plant at the three or four leaf stage of growth. Other crop managements were practiced as usual manners at each location.

Data were recorded with five competitive plants, taken at random in each plot. Following characters were measured in individual plants at the mature stage; culm length, ear height, ear length, length and width of the ear leaf, leaf vein frequency and stomatal density on the abaxial surface of the ear leaf. The latter two, leaf vein frequency and stomatal density were

TABLE 1. Discriptions of the environmental conditions

Location	Seeding date	Plant density# Intra-row spacing	Symbol
Sapporo##	May 14	20 cm (6667/10 a)	S 1
		40 cm (3333/10 a)	S 2
	June 3	20 cm	S 3
		40 cm	S 4
Memuro###	May 14	20 cm	M 1
		40 cm	M 2
	June 4	20 cm	M 3
		40 cm	M 4

#: Row spacing is 70 cm in all enviroments.
##: The experimental farm, Faculty of Agriculture, Hokkaido University, Sapporo.
###: The experimental field, Tokachi Agricultural Experimental Station, Memuro.

determined under microscope by means described in the previous papers (NAKASHIMA *et al.* 1981, MIURA *et al.* 1983).

Models

When genotype×environment interaction is significant, the response of each genotype to environmental changes is estimated by the regression method, which was proposed by ALANIS and HILL (1966). It provides the evaluation for the differences of response to environmental changes between homozygous parental inbred lines and their heterozygous F_1 hybrids. The regression method involves the partition of a phenotypic value into genotypic, environmental and genotype×environment interaction effects.

The phenotypic value of a parental inbred line, P_1 at the j-th environment can be written as:

$$P_{1_j} = \mu + d + \varepsilon_j + \gamma_{d_j}$$

and the value of another parental inbred line, P_2 at the same environment is written as:

$$P_{2_j} = \mu - d + \varepsilon_j - \gamma_{d_j}$$

where, μ is the average mid-parent value in overall environments, d is the mean deviation of P_1 or P_2 from μ. ε_j is an additive environmental effect

estimated from the difference of mid-parent value at the j-th environment from μ. γ_{d_j} is used to specify the genotype × environment interaction effect on the homozygous parental genotype. When the interaction effect on F_1 hybrid from the cross between P_1 and P_2 is specified by γ_{h_j}, the phenotype of F_1 hybrid at the j-th environment can be written as:

$$F_{1_j} = \mu + h + \varepsilon_j + \gamma_{h_j}$$

where h is defined as deviation from the overall mid-parent value, μ. If the genotype × environment interaction effects on parental inbred lines and on their F_1 hybrid could be assumed to behave as linear regression on ε_j, γ_{d_j} and γ_{h_j} are rewritten as follows:

$$\gamma_{d_j} = \beta_d \varepsilon_j, \qquad \gamma_{h_j} = \beta_h \varepsilon_j$$

where β_d and β_h are linear regression coefficients of a parent and F_1 hybrid for environmental changes, respectively. These are used as stability parameters in the experiments.

The magnitude of heterosis at the j-th environment is estimated by following equation:

$$F_{1_j} - P_{1_j} = h + \gamma_{h_j} - d - \gamma_{d_j}$$

where, P_1 is taken as the parent with higher phenotype of the character in that environment.

Results

1. Individual characters

Phenotypic values of individual characters in each environment were given in Table 2. F_1 hybrid "Pirika-sweet" had significantly higher values of culm length, ear height, ear length and leaf length than those of both parents in most environments. F_1 hybrid had higher values of leaf width than both parents, but not significantly different from the better parent Ma 21547 in all environments. Thus, remarkable heterosis was not observed in this character. F_1 hybrid had intermediate values of leaf vein frequency and stomatal density as compared with both parents.

Ma 21547 had significantly higher stomatal density than V 574 in overall environments. But differences in both parents for other six characters were varied among environments.

2. Analyses of variance

The results of the analyses of variance for seven characters were given in Table 3. In the analyses, genotypes were regarded as fixed and environ-

TABLE 2. Individual characters of parental inbred lines and F_1 hybrid "Pirika-sweet" in each environment

Genotype	Environments								
	S1	S2	S3	S4	M1	M2	M3	M4	Mean
				——Culm length (cm)——					
V 574	113.6a#	115.6a	111.7a	119.2a	87.0a	92.1a	88.1a	79.9a	100.9
Ma 21547	123.1a	107.1a	116.8a	115.4a	107.7b	93.6a	91.7a	92.8b	106.0
F_1	184.3b	163.3b	181.0b	160.5b	139.7c	133.7b	142.8b	139.5c	155.1
				——Ear height (cm)——					
V 574	25.2a	25.2a	32.4a	33.7a	28.6a	30.3a	26.9a	22.6a	28.1
Ma 21547	36.7b	23.6a	36.1a	33.1a	31.0a	29.7a	29.3a	29.5a	31.1
F_1	62.6c	53.3b	66.1b	54.7b	49.1b	50.1b	54.1b	49.7b	54.9
				——Ear length (cm)——					
V 574	9.98a	10.06a	10.39a	10.94a	8.63a	9.17a	8.69b	9.16a	9.63
Ma 21547	11.48b	12.46b	10.64a	11.95a	8.44a	8.97a	7.01a	9.27a	10.03
F_1	13.35c	14.94c	12.55b	13.65b	10.42b	12.44b	11.75c	12.60b	12.71
				——Leaf length## (cm)——					
V 574	64.9b	63.6b	71.9b	68.6b	59.5a	60.5a	61.6a	68.6b	64.9
Ma 21547	47.9a	47.4a	57.8a	57.6a	54.3a	54.0a	55.3a	54.0a	53.5
F_1	74.6c	71.1b	83.8c	83.2c	81.4b	76.6b	76.8b	73.7c	77.9
				——Leaf width## (cm)——					
V 574	6.15a	5.96a	6.08a	5.89a	4.35a	4.29a	4.67a	5.41a	5.35
Ma 21547	6.59a b	7.27a b	7.73b	7.75b	7.58b	7.67b	7.70b	7.64b	7.49
F_1	7.43b	7.71b	8.29b	8.19b	7.61b	8.26b	8.25b	8.08b	7.98
				——LVF### (No./mm)——					
V 574	6.07a	5.93a	5.77a	5.70a	6.10a	5.80a	6.13a	6.45a	5.99
Ma 21547	6.37a b	6.40b	6.30a	6.80b	6.77b	6.60b	6.83b	6.63a	6.59
F_1	6.43b	6.37b	6.00a	5.93a	6.50a b	6.37b	6.33a b	6.60a	6.32
				——SD### (No./mm^2)——					
V 574	59.3a	55.1a	60.3a	61.6a	59.8a	60.4a	72.4a	68.3a	62.2
Ma 21547	71.6b	72.5c	75.4b	84.7c	89.2c	91.1c	92.5b	90.2b	83.4
F_1	64.6a	65.9b	66.6a	67.8b	69.9b	73.3b	75.6a	75.2a	69.8

#: Followed by the same letter in a column were not significantly different at the 5% level.

##: On the ear leaf.

###: Leaf vein frequency (LVF) and stomatal density (SD) on the ear leaf.

TABLE 3. Analyses of variance for individual characters

Source of variations	df	Mean squares						
		Culm length	Ear height	Ear length	Ear leaf			
					Length	Width	LVF	SD
Genotypes, G	2	10770**	5183**	67.4**	3572**	47.05**	8.48**	1283**
Parents, P's	1	300	110	2.0	1558**	55.24**	16.92**	2503**
F_1 vs. P's	1	21240**	10257**	132.9**	5586**	38.86**	0.04	64
Environments, E.	7	1956**	77**	12.9**	105**	0.75**	1.12**	140**
G×E interactions	14	178*	40	1.8**	28*	0.98**	0.39	18**
P's×E	7	134		2.3**	34*	1.58**		29**
F_1 vs. P's×E	7	222*		1.3	22	0.34*		8
Errors	48	74	30	0.6	12	0.13	0.26	7

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

ments as random effects.

There were significant main effects due to genotypes and environments on all characters. The differences between F_1 hybrid and its mid-parent in five characters, excluding leaf vein frequency and stomatal density, were highly significant. Furthermore, F_1 hybrid showed significantly higher phenotypes than its better parent for these five characters. Genotypic variations of culm length, ear height and ear length were mostly ascribable to the differences between F_1 hybrid and its parents. Leaf vein frequency and stomatal density of F_1 hybrid were either similar to those of its mid-parent or less than those of the better parent. Thus genotypic variations of these characters were ascribable to parental differences.

The environmental effects varied with characters. The values of culm length, ear height and ear length were higher in plants grown at Sapporo than at Memuro. Conversely, leaf vein frequency and stomatal density were higher in plants at Memuro than at Sapporo. Ear length and leaf width were increased in the later sown plants at both locations. Plant densities did not directly affect on any character, but there were interactions with the locations or seeding dates on some characters.

There were significant genotype×environment interactions for five characters excluding ear height and leaf vein frequency, showing the differences in genotypic response to environmental changes. The different response between F_1 hybrid and its mid-parent were found on culm length and leaf width. On the other hand, for other four characters including leaf width, significant genotype×environment interactions were mostly ascribable to the different response between parents.

3. Patterns of response

The pattern of response in each genotype for individual characters which showed significant genotype×environment interactions were shown in Fig. 1. The environmental index shown on abscissa were estimated by mid-parent values to compare the response of F_1 hybrid with that of its mid-parent.

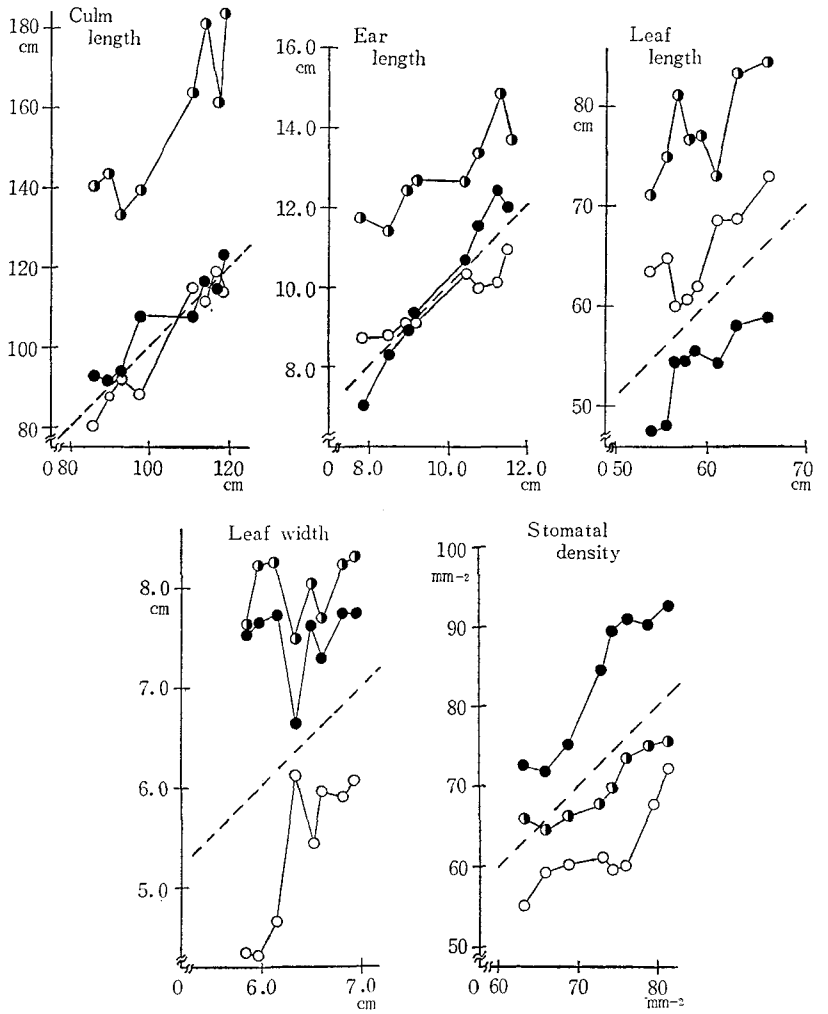

Fig. 1. Response patterns of genotypes to environmental changes in five characters which had significant genotype×environment interactions. Environmental index shown by broken line was estimated by mid-parent values.

○ : V 574, ● : Ma 21547, ◑ : F_1 hybrid "Pirika-sweet"

TABLE 4. Estimates of genetic parameters in parental inbred lines and F_1 hybrid for five characters which had significant genotype×environmentat interactions

Genetic parameters	Culm length (cm)	Ear length (cm)	Ear leaf		
			Length (cm)	Width (cm)	SD (No/mm²)
d	±2.5	±0.20	±5.70	±1.07	±7.22
h	+51.7	+2.88	+18.69	+1.56	−2.00
β_d	±0.138	±0.410	±0.088	±0.924	±0.272
β_h	+0.275	−0.174	−0.094	−0.777	−0.380

d; mean deviation of a parental inbred line from mid-parent over all environments, indicating additive genetic contribution to the parental inbred line.
h; mean deviation of F_1 hybrid from mid-parent, indicating dominance contribution to the F_1 hybrid.
β_d; linear additive genetic contribution of a parental line in response to environmental changes.
β_h; linear dominant genetic contribution of the F_1 hybrid in response to environmental changes.

The genetic parameters characterizing genotypic and genotype×environment interaction effects were given in Table 4.

The F_1 hybrid was less stable to environmental changes than both parents for culm length, but parents were not significantly different to each other. Magnitude of heterosis for this character increased in better environments, since h was positive and $\beta_d < \beta_h$. Patterns of response in parents were markedly different in ear length. Ear length of V 574 was more stable to environmental changes, but that of Ma 21547 varied from 7.0 cm to 12.5 cm among environments. Ear length of F_1 hybrid showed intermediate response in comparison with both parents. For both leaf length and width, the patterns of response of F_1 hybrid were relatively similar to those of the stable parent Ma 21547. Higher heterosis of these characters were appeared in poorer environments, since h's were positive and β_h's were negative. Response of stomatal density was significantly different between parents. The response of Ma 21547 was stable at Memuro, but that of V 574 was relatively stable at Sapporo. The negative heterosis in stomatal density increased when genotypes were grown at Tokachi which were regarded as better environments for parental phenotypic expressions of the character.

Discussion

From the results of the experiments, it was found that the characters independently responded to environmental changes. Thus, it was suggested that the suitable conditions for phenotypic expression were variable among characters. Furthermore, there were significant genotype×environment interactions in many characters. These interactions implies the differences in response among genotypes and the possibility of genetical control for individual buffering in homozygotes and heterozygote to environmental changes.

Different responses between parents to environmental changes were found in ear length, leaf length and width, and stomatal density. Ma 21547 was more stable in leaf length and width, in contrast, V 574 was more stable in ear length and stomatal density. The stability of F_1 hybrid "Pirika-sweet" varied with characters. For culm length, F_1 hybrid was less stable than both parents, but for leaf width, it was more stable than mid-parent. For ear length, leaf length and stomatal density, stability of F_1 hybrid was intermediate or higher than those of parents. Thus, the direction of dominance was lower stability in culm length, but higher stability in leaf characters. ROWE and ANDREW (1964) reported that there was no evidence of superior stability in F_1 hybrid as compared with the parental inbred lines, F_2 or back cross generations in maize. The facts that the direction of dominance for stability varied depending on characters were also reported in the experiments of inbred lines and their progenies in *Nicotiana rustica* (PERKINS and JINKS 1971) and in *Arabidopsis thaliana* (WESTERMAN 1971, WU 1975).

For leaf characters, especialy for leaf width, F_1 hybrid showed relatively resemble pattern of response to that of the stable parent Ma 21547. This suggests that individual buffering of F_1 hybrid seems to be partly a genetic property of the parental inbred line. The similar results were argued by EBERHART and RUSSELL (1966) in maize, PERKINS and JINKS (1971) in tobacco plants, and JOHNSON and WHITTINGTON (1977) in barley.

From these reports and the results mentioned above, two conclusions were obtained. First, heterozygote superiority in individual buffering of maize characters, proposed by SHANK and ADAMS (1960), is not common phenomenon in all of the characters. Second, the individual buffering of homozygous parental lines for a certain character is heritable to their heterozygous progenies.

In general, development of maize cultivars which have high yield and relatively high stability is fundamentally important for commercial production. From above discussion, it was suggested that individual buffering for plant

characters including yield components has genetic variations among inbred lines. Therefore, selecting of inbred lines with better individual buffering for yield components might be effective on breeding of desiable maize hybrids.

As shown in Table 3 and Fig. 1, the significant genotype × environment interaction for culm length was mostly ascribable to the different response between F_1 hybrid and both parents. This indicated that the magnitude of heterosis varied with environments. If environmental conditions, such as seeding dates, plant densities and other agricultural practices, are manageable (ALLARD and BRADSHAW 1964), it may be meaningful from standpoint of cultivation techniques to find out appropriate environmental conditions where the heterosis can be completely brought about. Then, it may also be effective to develop hybrids which possess a relatively high and stable yield in the poorer environments, as well as the capacity to respond to the better environments. At present, there is few informations concerning to these problems, thus further studies will be needed.

Summary

The experiments were conducted to investigate the variations of individual buffering between single cross maize cultivar "Pirika-sweet" and its parental inbred lines, under eight different environmental conditions at two locations, Sapporo and Tokachi in Hokkaido.

The results obtained were as follows;

There were significant genotype × environment interactions in many characters. These interactions implied the differences in individual buffering of genotypes. Individual buffering of "Pirika-sweet" varied with characters. "Pirika-sweet" was less stable than both parents in culm length, but more stable or intermediate between both parents in ear length and leaf characters. Leaf width of "Pirika-sweet" showed the similar pattern of response as the stable parent Ma 21547.

From these results, two conclusions were obtained. First, heterozygote superiority in individual buffering is not a common phenomenon for plant characters. Second, individual buffering of homozygous parents is heritable to their heterozygous progenies for certain characters.

Acknowledgment

The authors are indebted to Drs. T. HASEGAWA and S. SENDO of Tokachi Agricultural Experimental Station, Hokkaido, and Dr. H. TOZAWA of Division of Upland Farming, Hokkaido National Agricultural Experiment Station, for their helpful advice and supplying seeds used in the experiments.

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