Environmental and genotype-environment interaction effects on phenotypic variation for quantitative characters

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(Received May 15, 1991)

Abstract

A method for evaluating biological effects of an environment as affected by genotype-environment interaction was investigated. The effect of the j-th environment on phenotypic variation was estimated in terms of five parameters. e_j is the additive environmental effect assumed to act equally to all of genotypes. β_j is the linear effect on phenotypic differences among genotypes. δ_j^2 is the multiplicative effect including random effects on some particular genotypes. h_j^2 is the effect on genetic variation or heritability. $\bar{r}_j$ is the effect on repeatability in other environments. The genotype-environment interaction was taken into account in three parameters, β_j, δ_j^2 and $\bar{r}_j$.

Data on plant height in twelve inbred lines of *Nicotiana rustica* grown under 11 environmental conditions were analyzed. These five parameters were more fluctuated among years than among planting densities or sowing dates within years. The effect of the j-th environment on genetic variation was associated with the effect on phenotypic differences among inbred lines but not with that on repeatability. The method presented here was expected to be useful for evaluating several aspects of test environments and for identifying environments for effective selection.

Key words : genotype-environment interaction, heritability, *Nicotiana rustica*, selection.

Introduction

The existence of genotype-environment interaction, which has long been recognized, means that the effect of a particular genotype on the expression of phenotype is dependent on the growing environment and that there are genetic variations in adaptability to various cultivated conditions. In plant selection of widely adaptable genotypes, therefore, the interaction has been a major concern to plant breeders. The existence of genotype-environment interaction also implies that a given environment does not make the same contribution to the phenotypic expression when acting on different genotypes[9]. In other words, a given environment has more effect on some genotypes than it has on others.

Estimates of heritability and genetic gain are

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generally employed as a criterion for indentifying environments in which selection would be effective. But these estimates are not consistently associated with productivity levels over environments[1, 2, 5, 6, 8]. This inconsistency seems to be partly due to a deficiency of information on the environmental effects on phenotypic variation when genotype-environmet interaction affects.

The objective of this paper is to describe a method for evaluating some aspects of the effects of an environment on the phenotypic expression of quantitative characters. A population of *Nicotiana rustica* inbred lines is used to illustrate the analysis.

Materials and Methods

The PERKINS and JINKS model[7], originally proposed by YATES and COCHRAN[10], was applied. The observed value of a particular character, P_{ijk}, of the i-th genotype grown in the k-th replicate of the j-th environment can be written as

$$P_{ijk} = \mu + g_i + e_j + ge_{ij} + \varepsilon_{ijk}$$

where μ is the grand mean, g_i is the genotypic effect of the i-th genotype and e_j is the additive effect of the j-th environment, ge_{ij} is the effect attributable to genotype-environment interaction between the i-th genotype and the j-th environment, ε_{ijk} is the residual effect being regarded as the experimental error. The environmental effect e_j is used as a parameter measuring the additive effect which is assumed to contribute equally to all of genotypes grown in that environment.

To examine the contribution of the j-th environment to genotype-enviroment interaction, ge_{ij} can be regressed on g_i. Namely,

$$ge_{ij} = \beta_j g_i - \delta_{ij}$$

where β_j is a regression coefficient and δ_{ij} is a deviation from the regression line. A larger value of β_j than unity is expected when the j-th environment has a favorable influence on genotypes with larger g_i's, or an unfavorable influence on genotypes with smaller g_i's. Thus, phenotypic differences among genotypes may increase in the environment. δ_j^2, a variance of δ_{ij}, gives another parameter showing the genotype-environment interaction effect. The environment with a large δ_j^2 may be regarded to have random influences on some particular genotypes being independent of g_i.

Heritability h_j^2 is estimated from an analysis of variance table in each environment and used in evaluating the effect on the genetic variation.

A mean value $\bar{r}_j$ of correlation coefficients between phenotypes in the j-th environment and those in all of other environments is calculated. $\bar{r}_j$ can give a prediction of the relative rank among genotypes in the other environments[3]. Thus, $\bar{r}_j$ suits as a parameter by which an effect of the environment on repeatability of relative performance in genotypes can be examined. If $\bar{r}_j$ is high, genotypic differences observed in the j the environment are anticipated to be maintained in other environments because of the low level of genotype-environment interaction.

Table 1. The environmental regimes used in the *Nicotiana rustica* experiment

Code	Year	Seeding date		Transplanting date		Intrarow spacing[1]
1	1979	May	3	June	14	10cm
2	1979	May	3	June	14	20
3	1979	May	3	June	14	40
4	1980	April	14	May	22	15
5	1980	April	14	May	22	30
6	1980	May	6	June	14	15
7	1980	May	6	June	14	30
8	1981	April	14	May	16	15
9	1981	April	14	May	16	30
10	1981	May	6	June	2	15
11	1981	May	6	June	2	30

1) The interrow spacing is 70cm.

Data analyzed here was obtained from the field trials of *N. rustica* inbred lines carried out at Experimental Farm of Faculty of Agriculture, H okkaido University for three seasons. Twelve inbred lines were grown under 11 environmental conditions given in Table 1 with two replicates. Records of plant height were taken from ten competitive plants per plot at the harvesting time. In estimating h_j^2, β_j and δ_j^2, a transformed value into the logarithm was used for the purpose of inducing a reasonable degree of homogeneity of the experimental errors in analysis of variance.

Results

Analysis of variance given in Table 2 showed that environmental and genotype-environment interaction effects, as well as genotypic effect, were highly significant. Table 2 further revealed that the contribution of individual environments to the genotype-environment interaction could be partitioned into the linear and non-linear parts.

Table 2 . Analysis of variance for plant height of *N. rustica*

Source of variation	df	Mean square(×10⁻²)[1]
1 .Genotypes, G.	11	65.819**(5) [3]
2 .Environments, E.	10	47.734**(5)
3 . Between years	2	217.576**(3)
4 . Within years	8	5.273**(5)
5 .G × E interactions	110	1.195**(12)
6 . Heterogeneity of $\beta_j s^2$ [2]	10	3.481**(9)
7 . Between years	2	9.666* (8)
8 . Within years	8	1.935**(9)
9 . Deviations	100	0.966**(12)
10. Between years	20	2.515**(11)
11. Within years	80	0.579**(12)
12. Errors	132	0.249

[1] Evaluated in terms of the logarithm.
[2] The regression coefficient β_j of the phenotype in the j th environment on the genotype mean value through all environments.
[3] The item against which the test of significance was made was given in the parenthesis.
*,**:Significant at 5% and 1% levels,respectively.

ADDITIVE EFFECT

As shown in Table 3, the additive environmental effect in most parts varied among years and also tended to increase in the low density. The early transplanting in 1980 (codes 4, 5) was the most favorable, but the unfavorable conditions concentrated on the 1979 season.

Table 3. Five parameters estimating effects of the j-th environment on phenotypic variation for plant height of *N. rustica*

Environment code[1]		e_j	h_j^2	β_j	δ_j^2	$\bar{r}_j$
	1	−22. 4	93. 1	1. 35*	1. 87**	0. 837
'79	2	−18. 3	93. 8	1. 27**	0. 41	0. 897
	3	−17. 3	93. 0	1. 03	1. 17**	0. 811
	4	17. 4	89. 3	0.55**	1.36**	0. 748
'80	5	23. 0	85. 0	0.69**	1.00**	0. 823
	6	9. 7	79. 9	1.01	1.09**	0. 826
	7	13. 1	87. 2	0.97	1.10**	0. 843
	8	−3. 1	90. 7	0.88*	0.28	0. 900
'81	9	4. 7	93. 7	1.04	0.59*	0. 884
	10	−8. 8	93. 1	1.08	0.54	0. 883
	11	2. 0	92. 0	1.13*	0.26	0. 901
LSD 5 %		11. 2				

Note) e_j ; the additive environmental effect, assumed to act equally to all genotypes.
h_j^2 ; the effect on genetic variation or heritability.
β_j ; the linear effect on phenotypic differences among genotypes, see Table 2.
δ_j^2 ; the non-linear or random effect on some of particular genotypes evaluated by a deviation mean square from the regression.
$\bar{r}_j$; the effect on repeatability, evaluated by a mean correlation coefficient.
[1] Refe to Table 1.
*, ** : Significant at the 5 % and 1 % levels, respectively.

EFFECT ON GENETIC VARIATION

The estimate of heritability h_i^2 was used as a parameter of the environmental effect on genetic variation. h_i^2 varied from 79.9% to 93.8%, and differences among years were large. The high estimates indicated that plant height was mostly determined by genotypic effects.

LINEAR and MULTIPLICATIVE EFFECTS

The linear and multiplicative effects of each environment were estimated in terms of β_j and δ_j^2, respectively. β_j values showed that differences of plant height among genotypes extended when plants were grown under the environments included in 1979 and 1981 but reduced under the environments in 1980. The multiplicative effect was low under the four treatments in 1981.

EFFECT ON REPEATABILITY

The mean correlation coefficients in the four environments of 1981 were high and more than $\bar{r}_j = 0.88$, suggesting that the relative rank of genotypes observed in these environments tended to be maintained in other environments. The lowest value of $\bar{r}_j$ in the environment code 4 revealed that the early sowing under the high planting density of the 1980 season result in different responses of genotypes from the other environments.

RELATIONSHIP BETWEEN THE EFFECTS

Rank correlation matrices in all possible pairs of the parameters are presented in Table 4. The additive effect c_j was negatively associated with β_j and h_i^2. This indicated that the phenotypic differences among genotypes increased under unfavorable environments for plant height. It was confirmed from the negative correlation between δ_j^2 and $\bar{r}_j$ that the random effect due to genotype-environment interaction leaded a poor repeatability of relative performance of genotypes.

Table 4. Rank correlation matrices in all possible pairs of the parameters evaluating the environmental effects on phenotypic expression in plant height of *N. rustica*

c_j (1)	h_j^2 (2)	β_j (3)	δ_j^2 (4)	$\bar{r}_j$ (5)
(1)	−0.764**	−0.809**	0.082	−0.345
(2)		0.754**	−0.182	0.418
(3)			−0.182	0.482
(4)				−0.845**

Note) Each parameter was shown in footnote in Table 3.
**: Significant at 1% level.

Discussion

In plant breeding, heritability estimates are frequently employed as a criterion for identifying environments in which selection would be effective. This parameter is indelineating what degree of differences among phenotypes result from genetic causes[4]. The heritability estimated from separate analyses of variance tables in individual environments may be influenced by the genotype-environment interaction effect through the block interaction with genotypes as the error effect.

In the present data on plant height of *N. rustica* inbred lines, relationships between heritability and repeatability were not close (Table 4). This result suggested that the interaction of genotypes with micro-environmental variation within an environment was different from that with macro-environment. In addition, this confirmed the contribution of each environment to genetic variation and that to genotype-environment interaction were independent of each other. Thus, as ALLEN *et al.*[2] pointed out, the heritability estimated from single environment data may be deficient as a criterion for identifying environments when a genotype-environmet interaction is not negligible.

To measure the effect on genotype differences in phenotypes, we employed the regression coefficient. This parameter which was correlated with heritability (Table 4) varied among years rather than particular cultivation treatments (Table 3). This suggests that phenotypic differences among genotypes are affected by variation in unpredictable factors of the environment such as amount and distribution of rainfall and temperature rather than controllable factors like planting density and sowing date. From these results, the method presented here is expected to be useful for evaluating several aspects of test environments and for identifying environments for effective selection. However, it is emphasized that the population and environments tested here were limited, especially only one location data was analyzed. In addition, the standard error of r_j has still not been established while that of genetic variance can be calculated[4]. Therefore, the results of this experiment should be interpreted with causion and the method should be further examined for other types of genetic populations and environments.

Acknowledgments

The author is greatly indebted to Professors C. TSUDA and Y. SHIMAMOTO, Faculty of Agriculture, Hokkaido University, for their guidance.

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量的形質の表現型変異におよぼす環境効果と遺伝子型と環境との相互作用効果

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作物の量的形質発現に遺伝子型と環境との相互作用が存在するときに，個々の生育環境が表現型の変異におよぼす効果を5つのパラメータを使って評価した．

e_j；相加的環境効果．全ての遺伝子型に共通に作用．

h^2_j；遺伝変異の大きさにおよぼす効果．遺伝力．

β_j；遺伝子型との相互作用による相乗的効果のうち直線的な効果．

δ^2_j：上記相乗効果のうちランダムな効果．

$\bar{r}_j$；他の環境での再現性に対する効果．

ルスチカタバコ自殖系統の草丈のデータを用いて解析例を示し，広域適応性を目的とした育種選抜のための環境評価について論議した．

キーワード；遺伝子型と環境との相互作用，遺伝力，ルスチカタバコ，選抜

帯大研報 I, **17** (1991)：215〜219