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Genetic properties of four types of stability parameter *

C.S. Lin and M.R. Binns

Research Program Service, Research Branch, Agriculture Canada, Ottawa, Ontario K1A 0C6, Canada

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Summary. The genetic properties of four types of stability parameter for individual genotypes were investigated using a set of diallel cross data (28 genotypes × four locations × 3 years). The specific parameters studied were: the variance of a genotype across environments (T1); the genotype × environment (GE) interaction effect for a genotype, squared and summed across all environments (T2); the residual mean square (MS) of deviations from the regression of a genotype on an environmental index (T3); and years within locations MS for a genotype, averaged over all locations (T4). Each stability statistic was fitted to the additive model, based on the assumption that if the stability parameter is heritable, stability of F_1 is most likely to be the average stability of its parents. The results showed that T1 and T4 were additive, but T2 and T3 were not. A study of the consistency of stability rankings between two seeding rates over the same set of environments showed a similar pattern. It appears that stability parameters of types 1 and 4 are heritable, and thus useful for selection, while those of types 2 and 3 are nonheritable, and thus not useful.

Key words: Genotype-environment interactions – Regional trial – Diallel crosses

Introduction

Lin et al. (1986) studied the statistical relationship among nine conventional stability parameters and classified them into three types. A genotype is considered to be stable of type 1, if its variance over all environments is small; of type 2, if its environmental response is parallel to the mean response of all cultivars in the test; and of type 3, if its deviation mean square (MS) from the regression model (Finlay and Wilkinson 1963) is small. Lin et al. (1986) concluded that among these three types of stability, type 3 is the most problematical, because the residual MS from a regression model is merely an indicator of goodness of fit, and cannot be considered as a stability parameter. Their reason was that the regression model is a data-based descriptive model (not a predictive model based on external variables), and thus the residuals do not have a deterministic property that can be associated with genotypes.

Type 2 stability: since it uses the mean response as the standard, a stable genotype by this definition implies stability only with respect to the other genotypes in the test and it cannot be generalized. In contrast to both types 2 and 3, type 1 is a biologically meaningful parameter: it measures a genotype's homeostatic property to resist environmental change. However, this parameter has practical disadvantages. A breeder would like to find a genotype not only with good type 1 stability but also with high yield. However, type 1 stability is often associated with a relatively poor response in environments where other genotypes have high yields. Furthermore, although a high level of performance under a wide range of environments is desirable, this is difficult to achieve in practice. Even if it can be achieved, the effort is not entirely necessary, because several less widely adapted genotypes can be bred and then grown separately in different environments to achieve maximum production. Thus, the usefulness of type 1 depends largely on the range of environments under which the experiment is conducted. If the range is very large, such as a collection of sites from across the continental USA, type 1 stability may not be very meaningful, but if the range is small, such as a collection of sites from several counties within a state, then type 1 stability could be very important.

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In view of the theoretical and practical limitations of these three types of conventional stability parameters, Lin and Binns (1988) proposed a stability parameter (type 4) based on a genotype's years within location MS (as part of a genotype × location × year experiment). A genotype is considered to be stable if this MS is small. The idea is to separate environmental variation into predictable and unpredictable components, and then measure a genotype's stability with respect to the latter. Lin and Binns' (1988) reasoning was that predictable variation, such as genotype × location (mostly edaphic), can be controlled to some extent by selecting genotypes with specific adaptability to the region, while unpredictable variation, such as genotype × year (mostly climatic), cannot be controlled – one must rely on the homeostatic property of the genotype itself. Type 4 measures this property, which is independent of the regression analysis and also of the genotypic means.

Irrespective of how a stability parameter is defined, one of the most critical questions is whether it is genetic. If the characteristic measured by the parameter is nongenetic, it is not heritable and thus selection by such a parameter is fruitless. Lin and Binns (1988) studied this problem for type 3 and type 4, using two sets of data collected from regional trials in which two seeding rates were used within the same set of locations. Their assumption was that if the parameter is genetic, the resulting *stability ranking* for each seeding rate should be approximately the same, since both rates were subject to the same environments. Spearman's ranking correlation between the two seeding rates was significant ($p<0.05$) for type 4 but not for type 3. The inconsistency of type 3 was also confirmed by another set of data in which type 3 was assessed separately for each year. The resulting rank correlations among years were again not significant. These examples from both seeding rate and year studies support the theoretical argument that type 3 is only a measure of goodness of fit and cannot be considered as a stability parameter (Lin et al. 1986). Although type 4 stability was found to be consistent, this is not sufficient evidence to claim that it is genetic. To be able to claim this, the parameter must be examined with respect to the progenies of crossed material.

The experiment conducted by Tan and Tan (1980) for yield of smooth bromegrass (*Bromus inermis* Leyss) is ideally suited for such an investigation. Firstly, this set of data consists of a set of diallel crosses, which allows additivity of F_1 to be tested. Secondly, its data structure is genotype × location × year, and thus all four types of stability parameter can be investigated based on the same set of data. Our assumption is that if the *stability parameter* is heritable, the stability of F_1 is likely be the average stability of its parents (additive genetic effect), whereas if it is nonadditive, then it is probably nongenetic. Although in the latter case one still cannot exclude the possibility of inheritance through a non-additive genetic effect, this possibility could be tested in another experiment (such as in Lin and Binns 1988) examining the consistency, over the same set of locations, of the performance of the parameter. If such a test shows evidence of consistency, then the nonadditive genetic effect may be real, but if not, it is safe to conclude that the parameter is nongenetic.

The purpose of this paper is to investigate the additivity and consistency of four stability parameters, through crossed and non-crossed material, and to assess which of the four types of stability may be useful for breeding purposes. The validity of the conclusions for stability parameters of types 1, 2, 3 was further checked using diallel cross experiments reported in the literature. The merits of the type 4 stability parameter and the feasibility of breeding lines with high yield and high stability (of this type) are discussed.

Methods

Forage yield of 28 genotypes of smooth bromegrass, consisting of the progenies of a 7 × 7 half-diallel cross plus parental lines, grown in four locations in western Canada for 3 years, was analyzed. The combining ability analysis of this set of data was reported by Tan and Tan (1980). The mean data averaged over six replications for a 28 × 4 × 3 (genotype × location × year) experiment (W. K. Tan, personal communication) were used for the present analyses. Four types of stability parameter were calculated for each genotype, and these were then treated as data (stability) values for additivity analyses.

Let Y_{ij} be the stability value of F_1 for a cross between line i and line j. Then an additive genetic model can be written as:

$$Y_{ij}=u+g_i+g_j+e_{ij}\ ,$$

where u is the overall mean, g_i and g_j are the additive genetic effects of parental lines i and j, and e_{ij} is the deviation assumed to be normally and independently distributed with constant variance. Note that expect for the assumption about e, the above model is essentially the same as a combining ability model for a diallel cross: g represents the general combining ability (GCA) and e the specific combining ability (SCA) of the parents. Therefore, Griffing's (1956) method 2 can be used for the ANOVA.

The four stability parameters chosen for the present study are:

T1 – Variance of a genotype across environments (type 1).
T2 – Wricke's ecovalence (1962): the GE interaction effect for a genotype, squared and summed across all environments (type 2).
T3 – Eberhart and Russell's (1966) deviation parameter: the residual MS of deviations from the regression of a genotype on the environmental index, defined by the difference between location mean and the grand mean (type 3).
T4 – Lin and Binns' (1988) stability parameter: in a genotype × location × year experiment, the years within location MS for a genotype averaged over all locations (type 4).

Note that T1, T2, and T3 were calculated based on a 28 × 4 data structure (means over 3 years). Since the df associated with T1, T2, and T3 may be too small to give precise estimates, these three stabilities were also calculated based on a 28 × 12 data structure.

Table 1. Four types of stability parameter measured for Tan and Tan's (1980) diallel data for forage yield

Genotype (coded)	Mean (g/plot)	Stability parameter[a]						
		T1 (3)[b]	T2	T3 (2)	T4 (8)	t1 (11)	t2	t3 (10)
11[c]	3,501	4,051	149	14	528	16,379	909	83
12	3,819	2,091	293	105	752	12,284	1,036	95
13	3,719	2,700	4	2	679	13,531	357	36
14	3,200	3,714	148	44	666	16,467	741	64
15	3,512	1,972	83	8	978	13,743	3,198	305
16	3,691	3,017	110	54	622	14,027	733	73
17	3,509	2,695	8	4	1,035	16,361	1,533	149
22	3,518	1,806	594	190	717	11,159	2,183	182
23	3,142	1,469	274	27	454	8,040	1,471	61
24	3,502	3,245	61	22	596	14,500	372	36
25	3,557	2,891	78	39	766	14,798	685	67
26	3,676	2,412	22	5	696	12,802	338	32
27	3,500	2,371	39	12	1,076	15,722	1,135	111
33	3,285	2,104	181	59	569	10,863	1,709	138
34	3,685	3,808	142	33	1,033	19,689	1,743	135
35	3,392	2,368	66	24	620	12,065	547	48
36	3,591	3,232	30	6	628	14,718	404	39
37	3,484	1,778	166	25	1,045	13,696	1,903	186
44	2,791	4,148	548	241	510	16,522	2,844	284
45	3,412	4,359	189	2	569	17,627	903	69
46	2,825	2,944	50	24	539	13,145	385	38
47	2,980	3,170	69	29	853	16,333	1,071	100
55	3,155	3,423	496	247	524	14,458	5,530	516
56	3,265	2,330	340	144	592	11,722	1,792	157
57	3,641	2,931	159	80	1,121	17,762	1,061	85
66	3,840	3,864	238	84	638	16,694	1,416	135
67	3,634	3,799	215	76	910	18,675	1,513	124
77	3,240	3,215	248	122	1,483	21,509	3,816	346

[a] Divided by 10^3 in each column

[b] These numbers in parenthesis are the *df* associated with each estimate. No valid *df* for T2 and t2

[c] The parents were coded from 1 to 7 and a single cross is a combination of the two parental codes, with the female parent appearing on the left

The latter estimates are designated here by the letter "t" to distinguish them from the "T" series. It is important to note that these estimates of T1, T2, and T3 are independent of T4, but t1, t2, and t3 are not.

Since all stability statistics in the analyses are MS and since MS are distributed approximately as Chi-square, analyses for the additivity model were done also on square-root transformed data.

Results

Four types of stability parameter for Tan and Tan's (1980) diallel cross experiment are shown in Table 1. Their additive effects and the residual MS based on the diallel cross scheme are shown in Table 2. The general patterns of the results based on T and on t are about the same, and so are those based on the transformed and the untransformed data. The additive effect is highly significant ($P<0.01$) for T1 and T4, but not significant at all for T2 and T3. Although additivity of F_1 is a sure sign that the parameter is genetic, nonadditivity does not necessarily imply the reverse.

To assess if the nonadditivity of T2 and T3 is due to a complex of nonadditive genetic effects (e.g., dominance effect) or to random error, consistency of performance under the same set of locations was examined for sets 2 and 3 of Lin and Binns (1988), and Spearman's coefficients between the two seeding rates were estimated. These results together with those of T3, T4, previously reported, are summarized in Table 3. Except for the T2 correlation in set 2, which is significant, the general pattern of Table 3 is similar to that of Table 2: T1 and T4 are consistent over the same set of locations from one seeding rate to the other, but T3 is not, while the results are inconclusive for T2.

In an analysis of the *b*-value (regression coefficient), Tan and Tan (1980) reported that [MS (GCA of *b*)/MS (SCA of *b*)] for this set of data is 3.46. This suggests that although not as striking as T1 or T4, the *b*-value can be heritable too. Lin et al. (1986), discussing *b* and β $(=b-1)$, which they refer to as Group C stability parameters, said: "Group C can be interpreted as either Type 1 or Type 2, depending on how a standard stable genotype is defined.

Table 2. Additivity analyses of four types of stability parameter for Tan and Tan's (1980) diallel data

Stability parameter	MS_g (6)[b]	MS_e (21)	MS_g/MS_e	r[a] (26)
	Untransformed data[c]			
T1	1,587,800	344,993	4.6	−0.09
T2	20,516	26,354	<1	−0.29
T3	4,583	4,898	<1	−0.32
T4	193,236	20,898	9.2	0.24
t1	22,937,100	4,273,080	5.4	0.09
t2	1,894,940	1,251,340	1.5	−0.30
t3	17,602	10,923	1.6	−0.29
	Transformed data			
T1	142,326	30,343	4.7**	−0.08
T2	23,230	37,370	<1	−0.27
T3	13,493	17,805	<1	−0.28
T4	54,720	6,916	7.9**	0.28
t1	399,573	74,195	5.4**	0.10
t2	228,671	176,943	1.3	−0.28
t3	22,893	16,254	1.4	−0.29

** Significant at 1% (assessed for transformed data only)

[a] Simple correlation between the genotype mean and the corresponding stability parameter

[b] These numbers in parenthesis are the *df*

[c] All MS are divided by 10^6

Table 4. Analyses of additivity of F_1 for the three examples of a diallel cross experiment

	df	MS for stability parameter			
		T1	*b*-value	T2	T3
Grain yield of hard red spring wheat (Busch et al. 1976)[a]					
Additive (GCA)	7		0.0402		396,962
Residual (SCA)	28		0.0119		101,975
GCA/SCA		–[b]	3.38**	–	3.89**
Grain yield of maize (Dhillon and Singh 1977)					
GCA	19		0.2600		30,375
SCA	170		0.0390		19,707
GCA/SCA		–	6.7**	–	1.54
Weight gain of common carp (Lin et al. 1977)[c]					
GCA	3	711,202	0.1601	113,781	22,312
SCA	6	34,048	0.0061	57,811	128,863
GCA/SCA		20.9**	26.2**	1.97	<1

** Significant at 1% level

[a] MS of T3 are divided by 10

[b] Data not available

[c] MS of T1 and T3 are divided by 10^4 and 10^3, respectively

Table 3. Spearman's rank correlation coefficient between two seeding rates for Lin and Binns' (1988) sets 2 and 3

Stability	Set 2 (barley)	Set 3 (oat)
T1	0.85*	0.89*
T2	0.74*	0.60
T3	0.50	0.34
T4	0.76*	0.83*

* Significant at 5% level by *t* test

If stable genotypes are defined by having $b=1$ (Finlay and Wilkinson 1963) or $\beta=0$ (Perkins and Jinks 1968), Type 2 is implied; but if they are defined by $b=0$ ($\beta=-1$), Type 1 is implied." Since Tan and Tan's (1980) analysis is based on the *b*-value, type 1 is implied (the smaller the *b*, the greater the stability). Had the analysis been based on $|b-1|$, type 2 would have been implied (the closer *b* is to 1, the greater is the stability). The corresponding ratio based on $|b-1|$ is 1.05, which is not significant. Thus, *b* (as type 1) behaves like T1 and $|b-1|$ (type 2) like T2. This distinction between *b* and $|b-1|$ is similarly important in correlation studies of stability statistics (Lin 1989).

Conclusions and discussion

The conclusions that can be drawn from these analyses are that, of the four types of stability parameter, only types 1 and 4 are genetic and thus useful for selection, while types 2 and 3 are nongenetic and thus not useful. By the same token, when the *b*-value is used as a stability parameter, a genotype, if assessed as stable by the type 1 standard ($b=0$), is heritable, but if assessed as stable by the type 2 standard ($b=1$), it is not. The conventional practice of identifying an unstable genotype by testing the difference of *b* from 1 (e.g., Mahal et al. 1988; Chakroun et al. 1990) is thus misleading. Lin and Binns' (1988) proposal that the *b*-value should be used as an indicator to determine optimum ranges of locations, but not as a stability parameter, appears to be more sensible.

It is important to emphasize that although these conclusions were derived from a limited number of data sets, they are in complete agreement with the theoretical arguments presented earlier (Lin and Binns 1988). To check the validity of the conclusions with respect to types 1 (including *b*), 2, and 3, additivity was further examined using three diallel cross experiments reported in the literature: (i) grain yield of hard red spring wheat (Busch et al. 1976; Table 4); (ii) grain yield of maize (Dhillon and Singh 1977; Table 2); and (iii) weight gain of common carp (Lin et al. 1977; Table 1). Note that all crosses in (i) were F_2 and F_3 bulks, while the crosses in (ii) and (iii) were F_1. The additivity expressed by the GCA MS and the residual by the SCA MS are summarized in Table 4. Except in one case (T3 in the first example), all agree with the present conclusions.

Confirmation of the nongenetic nature of T2 and T3 prompted us to review two long-standing issues. One is that in spite of the numerous papers assessing genotype stability, few stable varieties have been developed through crossing and selection. The other is that, theoretically, genotypes that have a higher level of heterozygosity are presumed to be better buffered to environmental change than those having a lower level. However, experimental results reported in the literature are inconclusive on this subject (see, e.g., Patanothai and Atkins 1974; Busch et al. 1976). The lack of progress in stability breeding and the gap between theory and experiment are now seen to be attributable, at least in part, to the practice of using non-genetic stability parameters.

Type 1 and type 4 are both genetic parameters. Since they can be inherited additively in F_1, improvement of a genotype's stability through crossing is theoretically possible. The difference between type 1 and type 4 is that the former (a simple variance estimate or CV of the genotype across locations) measures the homeostatic property in terms of overall environmental variation, while the latter (the year within location MS averaged over locations) measures it only with respect to unpredictable variation, excluding the part (predictable) that is controllable. Thus, type 4 resolves one of the problems of type 1, namely, its impracticality mentioned earlier. Indeed, the strength of type 4 is that this parameter is not tied to the range of sites included in the test. In the literature, there are few examples where the highest yielding genotype is also the most stable by type 1 stability. In contrast, among the four sets of experiments we have studied so far with type 4 stability, we have witnessed two examples (set 2 and set 3 of Lin and Binns 1988) in which the highest yielding genotype is also the most stable. The implication is that breeding for high yield and high stability appears to be feasible if type 4 stability is used for selection. The only drawback of type 4 stability is that the parameter is more expensive to measure, because it requires a time factor in addition to genotype × location. Lin and Binns (1989) show that of the two available time factors, year and seeding time, the former is about twice as effective as the latter in generating unpredictable variation. A combined use of both factors for measuring type 4 is suggested if the test period would otherwise be deemed to be too long.

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