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THE SUITABILITY OF DIFFERENT STATISTICAL MEASURES TO ASSESS THE STABILITY OF RESISTANCE TO *PHYTOPHTHORA INFESTANS* (MONT.) DE BARY IN POTATO CULTIVARS IN FIELD CONDITIONS

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ABSTRACT

This study presents a comparison of several measures of stability applied for rAUDPC (relative area under the disease progress curve) values, which describes the rate of late blight development on plants of 22 cultivars examined in 13 environments. The stability variance (δ^2_i), coefficient of ecovalence (W_i), coefficient of variability (CV), environmental variance (S^2_{Yi}), coefficient of regression (b_i), nonparametric measures $S_i^{(1)}$ and $S_i^{(2)}$, and F statistic for the interaction G×E derived from the Sheffe-Caliński mixed model were among stability measures evaluated. The aim of the study was mainly to compare these measures of stability and select the most suitable one. The environmental variance S^2_{Yi} and coefficient of regression b_i are correlated with genotypic values and provide information of limited value. The coefficient of ecovalence W_i, stability variance δ^2_i and nonparametric measures $S_i^{(1)}$ and $S_i^{(2)}$ gave very similar results in terms of cultivar rankings. However, in the case of stability variance δ^2_i, the statistically justifiable division between stable and unstable reacting cultivars is enabled.

Key words: G×E interaction, stability parameters, potato cultivars, resistance to *P. infestans.*

INTRODUCTION

Each trait is shaped by genotype and environmental influences, but assessments carried out in different environments reveal that particular genotypes react specifically to changing environments. Genotype by environment (G×E) interactions are commonly observed and create difficulties both in the breeding of new cultivars (hampered selection) and in their subsequent production, due to limitations resulting from the adaptation of cultivars to specified conditions. However, cultivars with specific adaptation could be identified for specific environmental conditions.

The concept of interaction G×E is closely connected with the idea of stability adaptation to environmental conditions (Piepho, 1996; Mulema *et al.*, 2004/5; Forbes *et al.*, 2005). Statistical methods for assessments of interaction G×E are developed mostly using the data in the form of a two-way classification of genotype×environment (environments are sites in a single year, or sites-year combinations). Such assessments mainly concern stability of yield (Cygert *et al.*, 2003; Weber *et al.*, 2003; Bujak *et al.*, 2006; Oleksiak and Mańkowski 2006).

A number of statistical methods for stability evaluation have been developed, overviews of which can be found in the literature (Zobel *et al.*, 1988; Ukalska *et al.*, 2011; Bujak *et al.*, 2014). These methods usually refer to the dynamic concept of stability (Becker and Leon, 1988; Pietrzykowski *et al.*, 1996; Galek *et al.*, 2000), according to which the response of stable genotype to environmental changes does not deviate from the general response of all genotypes in the trial. The vast number of statistical methods for assessing G×E cause problems choosing the correct one and difficulty understanding stability and adaptability.

Developing potato cultivars resistant to *Phytophthora infestans*, the causal agent of late blight, is among one of the most important breeding aims. The genetic control of the late blight in the foliage can be achieved by two types of resistance. The first one is controlled by major genes originating from wild species e.g. *Solanum demissum* and *S. stoloniferum*. It is race-specific and provokes a hypersensitive response to incompatible pathotypes of the pathogen (Toxopeus 1956). Unfortunately, *P.infestans* easily adapts to factors limiting its development, such as host resistance based on R-type genes. The second type, which is believed to be more stable over years, is partial or field resistance, which is polygenic, non-race-specific (Umaerus *et al.*, 1983). Resistance expression may be largely modified by environmental influences and this applies to both types of resistance. Quantitatively manifested resistance to late blight is rarely analyzed in terms of G×E interaction effects (Haynes *et al.*, 1998; Haynes *et al.*, 2002; Forbes *et al.*, 2005; Tatarowska *et al.*, 2012).

From 2001 - 2004 the field experiments were performed in 4 locations, in which the resistance to late blight of 22 potato cultivars was assessed under natural conditions. For each cultivar, rAUDPC (relative area under the disease progress curve) values describing the rate of progress of the disease in foliage from 13 environments were obtained. These data were used in the stability analysis performed by the Scheffe-Caliński model (Caliński *et al*., 1998) and published by Tatarowska *et al*. (2012). The aim of this study was to compare various additional stability measures with measure obtained by the Scheffe-Caliński model in terms of their effectiveness in identifying cultivars with stable reaction to late blight development.

MATERIALS AND METHODS

The cultivars used in this study differed in terms of level of resistance to late blight and maturity. All cultivars were tested for field late blight resistance over a four-year period in 4 locations as described by Tatarowska *et al*. (2012). Repeated measurements of disease development were used for calculating the relative area under the disease progress curve (rAUDPC) for each cultivar (Fry, 1978). These results, obtained in a series of experiments in 13 environments (Tatarowska *et al*., 2012), were used to calculate additional parameters of stability: δ^2_i – stability variance (Caliński, 1967; Shukla, 1972; Kudła *et al*., 1987), W_i – coefficient of ecovalence (Wricke, 1965; Becker, 1981; Hühn, 1981; Pietrzykowski *et al*., 1996), CV – coefficient of variability (Francis and Kannenberg, 1978ab), S^2_{Yi} – environmental variance (Becker and Leon, 1988), b_i – regression coefficient (Eberhart and Russell, 1966) and nonparametric measures $S_i^{(1)}$ and $S_i^{(2)}$ (Nassar and Huehn, 1987). The values of $F_{G\times E}$ were obtained by using the Sheffe-Caliński mixed model (Scheffe, 1959; Mądry and Kang, 2005) and the Caliński-Kaczmarek joint regression model (Kaczmarek, 1986; Caliński *et al*., 1997; Mądry and Kang, 2005) implemented in Sergen software (Caliński *et al*., 1998).

The compared parameters were obtained by using MS Excel (2010) with the exception of the parameters δ^2_i, Wi, $S_i^{(1)}$, $S_i^{(2)}$ as well as Spearman correlation coefficients, which were calculated by using the package agricolae of R program (Mendiburu, 2015). The figure was prepared with the R program ggplot2 (Wickham, 2009).

RESULTS AND DISCUSSION

The values of the statistics and ranks of individual cultivars are given in Table 1. For some parameters, i.e. $F_{G\times E}$, δ^2_i, b_i, $S_i^{(1)}$ and $S_i^{(2)}$ their statistical significance is marked, but increasing values of all parameters indicate decreasing stability. In contrast, smaller values of rank sum indicate stability. The smallest sums were obtained for resistant cv Bzura (rAUDPC < 0.20), moderately resistant cvs. Jasia (rAUDPC = 0.26), Hinga (rAUDPC = 0.25) and Klepa (rAUDPC = 0.24). The highest sums were found for susceptible cvs. Albina, Mors, Irys (rAUDPC > 0.50) and for moderately resistant cvs Anielka, Beata, Rywal (rAUDPC range between 0.28 and 0.39) as well as for highly resistant cv Meduza (rAUDPC = 0.14) (Table 1).

However, rank sums provides hardly useful information on stability of resistance, when taking into account the correlations between parameters (Table 2) as well as correlation between sum of ranks and genotypic value, which was r_s=0.52 * (not shown in tables). The obtained stability measures were correlated with each other and with the parameter obtained previously by Tatarowska *et al*., 2012, which was F statistics for the G×E interactions ($F_{G\times E}$), which gives the significance of interactions effects contributed in the variation caused by each cultivar (for stable cultivar the interaction contribution should be insignificant).

The applied stability measures correlated with mean rAUDPC values and with each other in varying degrees (Table 2). Spearman's rank correlation between rAUDPC values and $F_{G\times E}$ was weak and insignificant while between rAUDPC and b_i was strong and significant. The correlation between rAUDPC and nonparametric statistics $S_i^{(1)}$ and $S_i^{(2)}$ were close to 0.5 and significant. The strongest correlations were those between genotype value and S^2_{Yi} or CV, the latter being negative.

The coefficients for correlations between stability measures were within the range from r_s = -0.70 (between CV and b_i) to $r_s = 1.00^{**}$ (between δ^2_i and W_i, and between both nonparametric statistics). Beside the latter value, strong correlations were also found between S^2_{Yi} and b_i as well as between δ^2_i or W_i and both nonparametric statistics. The values of $F_{G\times E}$ were highly correlated with δ^2_i and W_i. The S^2_{Yi} was moderately correlated with δ^2_i, W_i or CV. The b_i was weakly correlated with δ^2_i and W_i, and was not correlated with $F_{G\times E}$ (Table 2).

The vast majority of publications devoted to the study of stability raise these issues in relation to yield and the dynamic concept of stability (Adugna, 2008; Scapim *et al*., 2000; Farshadfar *et al*., 2012; Kılıç, 2012; Sabaghnia *et al*., 2012; Changizi *et al*., 2014; Flis *et al*., 2014; Temesgen *et al*., 2015). According to this concept, the stable reaction to environmental changes is observed, if this reaction is consistent with general response of all genotypes in the trial. In contrast, under static (or biological) concept of stability, the stable genotype shows no deviations from expected level of evaluated trait (Fasahat *et al*., 2015). In the case of resistance to late blight, the biological concept of stability seems to be an obvious choice. However, resistance under field conditions manifests mainly in a quantitative manner, and hence is subject to environmental influences. Applying the static stability concept in breeding may lead to the loss of valuable genotypes, which may express acceptable levels of field resistance under various environmental conditions. In the case of developing recommendations for cultivars for various agricultural conditions, using such a concept may be futile, since highly resistant cultivars are very rare and those available for farmers usually express different levels of quantitative resistance.

For the biological concept of stability two measures are available, namely environmental variance (S^2_{Yi}) and coefficient of variability (CV). In this study, low values of CV were related to high genotypic values of rAUDPC, indicating stability in the group of susceptible and moderately resistant cultivars (Fig. 1). Furthermore, the low rAUDPC values were only associated with the highest CV. This reduces the use of the CV in analyses of resistance stability.

The values of CV correlated highly and negatively with b_i, and positively and moderately with S^2_{Yi}, while correlations with other parameters were weak. In turn, the S^2_{Yi} correlated weakly only with $F_{G\times E}$, while with other measures moderately (r_s close to 0.5) or even very high, as for b_i. The values of S^2_{Yi} are quite clearly related to genotypic values.

The coefficient of regression b_i is believed to be suitable for assessment of either agronomic or biological stability (Finlay and Wilkinson, 1963; Eberhart and Russell, 1966). In the latter case, its value should not deviate significantly from zero. This was not found, since all coefficients of regression were significantly different from zero and positive (Table 1). This indicates an increase of rAUDPC values (greater susceptibility) in environments with higher infective pressure of *P.infestans*. However, the rate of increase was greater in susceptible than resistant cultivars. In addition, the variability of rAUDPC values was much less in the case of resistant cultivars (with low rAUDPC values), which is to some extent indicated by their respective S^2_{Yi} values. Furthermore, a positive and moderate correlation was found between b_i and mean rAUDPC values and the same was observed for environmental variance and mean rAUDPC (Table 2 and Fig. 1). This indicates some usefulness of b_i and S^2_{Yi} for arrangement of cultivars accordingly to decreasing resistance and simultaneous decrease of stability of resistance. Similarly, Pietrzykowski *et al*. (1996) and Becker (1981) found that both measures are highly correlated and can be interchangeably used.

The coefficient of ecovalence W_i and stability variance δ^2_i determine the contribution of individual genotype to interaction variance. Since δ^2_i is a linear combination of W_i, both measures gave similar results (Piepho, 1996, 1998; Piepho and Lotito, 1992). In this study, applying these measures produced identical ranking of cultivars. The study of Galek (2000), who evaluated the stability of resistance to powdery mildew and leaf rust in spring rye, confirmed similarity of the two measures. Both measures were very highly correlated with $S_i^{(1)}$ and $S_i^{(2)}$, and moderately correlated with $F_{G\times E}$ or S^2_{Yi} as well as with genotypic value (Table 2 and Fig. 1). A correlation between δ^2_i or W_i and regression coefficient b_i was not found.

A weak relationship between W_i and b_i was found by Becker (198l) and Pietrzykowski *et al*. (1996). Galek *et al*. (2000) found fairly strong correlation between W_i and b_i, if the resistance of spring rye to powdery mildew was evaluated, but for the other five evaluated traits this relationship was considerably weaker. Schott (1999) concluded that both parameters provide breeders similar information and can be used interchangeably.

Galek *et al*. (2000) examined stability of 6 traits of spring rye and found both high and low correlations between CV and W_i depending on the tested trait. In turn, the correlation coefficients between CV and b_i in research by Galek *et al*. (2000) were high and significant, with exception of a very weak (r = -0.11) correlation with the level of resistance to brown rust.

Completely different ranking of 20 spring rye lines in respect of stability of resistance was found when ranked by CV or b_i.

The nonparametric measures $S_i^{(1)}$ and $S_i^{(2)}$ were already applied for evaluating stability of resistance to late blight and were not found to be useful (Haynes *et al*., 1998). There are two tests of significance for these statistics (not shown in table). The first one, for sum of the test statistics, detected G×E interaction on ranking of cultivars, while the second one, which tests significance for individual values of $S_i^{(1)}$ and $S_i^{(2)}$, detected only significance (i.e. instability) for $S_i^{(2)}$ in the case of cv Anielka (Table 1). Hence, the interaction G×E was found, but could not be ascribed to a specific cultivar, with one exception. However, both measures produced almost identical results in terms of ranking of cultivars. The correlations between $S_i^{(1)}$ or $S_i^{(2)}$ and other parameters values were similar to those obtained with δ^2_i and W_i. Moreover, the correlation between $S_i^{(1)}$ or $S_i^{(2)}$ and genotypic values (i.e. mean rAUDPC values) were only slightly weaker than in the cases of δ^2_i and W_i (Table 2 and Fig.1)

Stability analysis is used primarily in relation to yield. The use of such analysis for resistance requires consideration of differences between the two traits. For example, while large numbers are desirable for yield, small numbers are desirable for rAUDPC. Moreover, the resistance is measured by rAUDPC and is a continuous trait, but in practice the classes of high, moderate and low resistance are distinguished.

This study included only 7 stability measures, which were compared with each other and with $F_{G\times E}$, which was the measure previously obtained by Tatarowska *et al*. (2012). It was found that some of these measures are not suitable for stability analysis. This was the case of the coefficient of variability CV, which in contrast to all other methods shows stability only in susceptible cultivars.

The applying of coefficient of regression b_i allowed only cultivars rank, starting from the stable resistant (or moderately resistant) cultivars and ending

Table 1. Stability measures (¢$^{2}_{i}$, CV, W_i, b_i, S^2_{Yi}, $F_{G\times E}$, $S_i^{(1)}$ and $S_i^{(2)}$) and genotypic values (mean rate of late blight development rAUDPC from 13 environments).

Cultivar	Genotypic mean of rAUDPC	$F_{G\times E}$#		δ^2_i		CV		W_i		b_i		S^2_{Yi}		$S_i^{(1)}$		$S_i^{(2)}$		Rank sum (without rank according to $F_{G\times E}$)
		value	rank	value	rank	value	rank	value	rank	value	rank	value	rank	value	rank	value	rank	
Bzura	0,131	*0.39*	*2*	0.005	3	37.0	18	0.061	3	0.66**	1	0.007	1	5.41	3	24.59	3	32
Meduza	0,140	*1.70*	*10*	0.015**	16	56.8	22	0.165	21	0.88**	8	0.019	14	9.44	21	64.58	20	122
Wawrzyn	0,153	*2.02*	*13*	0.007*	6	37.3	19	0.085	8	0.92**	10	0.016	8	6.82	8	34.09	7	65
Koga	0,172	*2.25**	*16*	0.008*	9	34.6	16	0.092	12	0.85**	5	0.015	4	7.67	12	42.44	12	71
Umiak	0,175	*0.53*	*4*	0.010**	12	38.3	21	0.117	11	0.90**	9	0.017	11	7.21	11	39.00	11	86
Grot	0,176	*0.54*	*5*	0.008*	8	33.2	15	0.089	7	0.86**	6	0.015	5	6.77	7	33.26	6	54
Dunajec	0,181	*2.99***	*20*	0.011**	14	38.0	20	0.123	13	0.71**	3	0.012	2	7.92	13	46.31	13	79
Jantar	0,222	*2.81**	*18*	0.010**	13	30.4	13	0.119	6	0.87**	7	0.016	9	6.59	6	34.64	8	60
Zeus	0,226	*2.18**	*15*	0.006	5	23.5	10.5	0.073	4	0.92**	11	0.016	7	5.95	4	26.36	4	45
Klepa	0,241	*1.27*	*6*	0.003	2	15.4	2	0.036	2	1.04**	16	0.018	13	5.08	2	19.74	2	39
Hinga	0,246	*1.30*	*8*	0.006	4	21.2	6	0.071	5	0.80**	4	0.012	3	6.08	5	29.58	5	32
Nimfy	0,256	*1.29*	*7*	0.008*	10	23.4	9	0.093	14	0.93**	12	0.017	10	8.31	14	49.40	14	84
Jasia	0,258	*0.36*	*1*	0.001	1	10.9	1	0.020	1	1.12**	17	0.020	15	4.82	1	16.92	1	37
Ania	0,268	*1.83*	*11*	0.008*	7	21.7	7	0.088	9	0.96**	14	0.018	12	6.92	9	34.76	9	68
Lawina	0,270	*0.52*	*3*	0.014**	15	28.6	12	0.154	15	1.25**	19	0.029	19	8.49	15	50.60	15	110
Anielka	0,277	*6.34***	*22*	0.022**	21	35.3	17	0.248	22	0.67*	2	0.016	6	9.62	22	75.74*	22	113
Beata	0,283	*2.96***	*19*	0.020**	18	32.5	14	0.219	19	0.94**	13	0.022	16	9.26	19	62.56	19	118
Vistula	0,283	*1.47*	*9*	0.009*	11	22.3	8	0.103	10	1.18**	18	0.025	17	7.05	10	36.36	10	85
Rywal	0,390	*2.16**	*14*	0.020**	19	23.5	10.5	0.219	20	1.03**	15	0.025	18	9.28	20	65.40	21	123
Mors	0,521	*1.85*	*12*	0.019**	17	17.2	4	0.209	17	1.42**	20	0.037	20	8.56	17	53.44	17	112
Albina	0,561	*5.74***	*21*	0.027**	22	19.1	5	0.298	16	1.53**	21	0.044	22	8.49	16	51.23	16	118
Irys	0,603	*2.67**	*17*	0.021**	20	15.9	3	0.239	18	1.55**	22	0.042	21	8.85	18	59.60	18	120

Data in the table are sorted in order of increasing mean rAUDPC value, i.e. decreasing resistance.

Significant: * at $P<0.05$ and ** at $P<0.01$

values obtained by Tatarowska *et al*. (2012)

with unstable ones. Similarly limited results were obtained by using environmental variance S^2_{Yi}.

The use of other measures, i.e. coefficient of ecovalence (W_i), stability variance (δ^2_i) and nonparametric measures ($S_i^{(1)}$ and $S_i^{(2)}$), gave very similar results in terms of cultivar ranking. For δ^2_i, $S_i^{(1)}$ and $S_i^{(2)}$ testing of statistical significance is available, which should give a statistically justifiable division between stable and unstable reacting cultivars. Such useful information was only obtained in the case of stability variance δ^2_i. Hence, stability variance may be regarded as the best among the compared measures. In addition, the stability variance values are moderately correlated with $F_{G\times E}$, and both these statistics show the contribution of each cultivar makes to the G×E interaction variance.

However, none of the parameters used in the presented comparisons provide detailed analysis of resistance stability, e.g. the distinguishing of cultivars with various types of unstable reaction, such as unstable, but with predictable reaction. Such information is only available with the use of more complex methods, which are offered by the AMMI or Scheffe-Caliński model, as described by Tatarowska *et al*. (2012).

Table 2. Spearman's coefficients of rank correlation between rAUDPC values and stability parameters for 22 potato cultivars evaluated in 13 environments in Poland.

	rAUDPC	$F_{G\times E}$	δ^2_i	CV	W_i	b_i	S^2_{Yi}	$S_i^{(1)}$
$F_{G\times E}$	0.33							
δ^2_i	0.57 **	0.63 **						
CV	-0.68 **	0.11	0.13					
W_i	0.57 **	0.64 **	1.00 **	0.13				
b_i	0.73 **	-0.05	0.27	-0.70 **	0.27			
S^2_{Yi}	0.77 **	0.08	0.54 **	-0.52 *	0.54 **	0.90 **		
$S_i^{(1)}$	0.45 *	0.52 *	0.90 **	0.23	0.91 **	0.20	0.50 *	
$S_i^{(2)}$	0.48 *	0.55 **	0.92 **	0.21	0.93 **	0.20	0.50 *	1.00 **

Significant: * at $P<0.05$ and ** at $P<0.01$

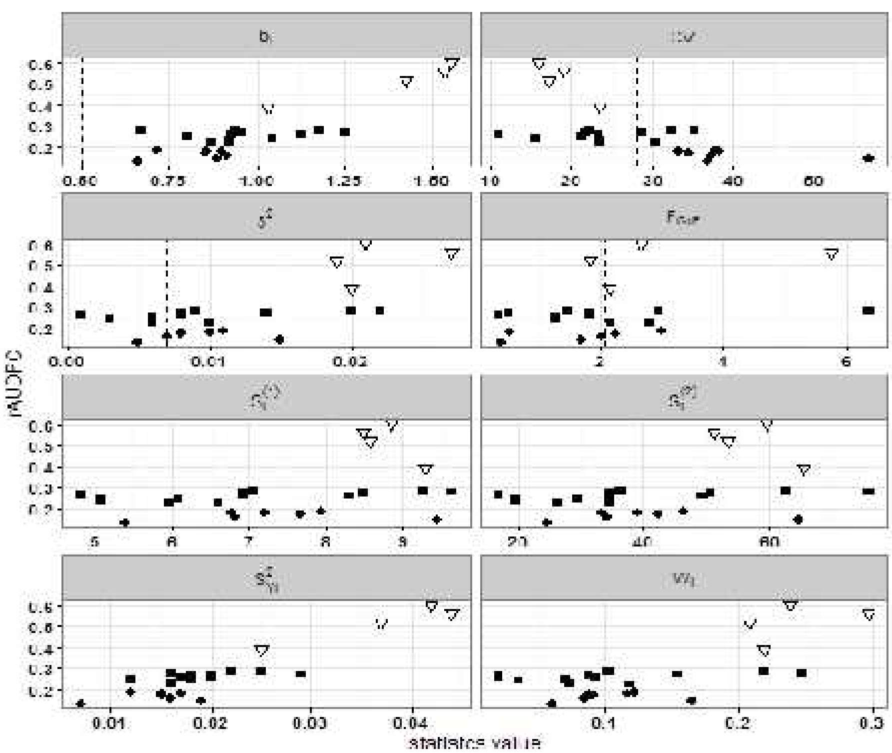

Fig. 1. Relations between specific statistic and cultivar mean rAUDPC values (genotypic value).
●- cultivar resistant to late blight (rAUDPC≤0.2) ♦ - cultivar moderately resistant to late blight (rAUDPC>0.2 and rAUDPC≤0.3)
▽- cultivar susceptible to late blight (rAUDPC>0.3) The vertical dashed lines separate low and insignificant values (indicating stable reaction of cultivar to late blight) from high and significant values (indicating unstable reaction).
In the case of CV, vertical line indicate mean value of this coefficient (low CV means stability).

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