

Study of Genotype x Environment Interaction for Forage Yield in Oat (*Avena sativa* L.) with Joint Linear Regression Analysis and AMMI Analysis.

Acciaresi H.A., ^{1,2} H.O Chidichimo ^{1,2} y C.B. Fusé ³.

1) Cerealicultura, Departamento de Producción Vegetal, Facultad de Ciencias Agrarias y Forestales, Universidad Nacional de La Plata, CC 31 (1900) La Plata, Argentina.

2) Comisión de Investigaciones Científicas de la Pcia de Bs. As. (CIC).

3) CONICET

Summary.

Improvement of forage yield in oat (*Avena sativa* L.) depends on thorough understanding of the influences of genotype, environment and the genotype x environment interaction (G X E). The objective of this study was to analyze G X E interaction in oat for biomass forage yield according two different models, joint linear regression analysis (JRA) and AMMI analysis. Twelve genotypes were grown in different environments during three years (1993-94-95) at the locations of La Dulce and La Plata, Buenos Aires Province, Argentina. The forage yield (dry matter yield Kg/ha) was determined at 60, 100 days after emergence and at ripening. Heterogeneity of regression in JRA was nonsignificant. Interaction sum of square accounted for by heterogeneity of regression were 12.08 % (three years mean). In contrast, the first principal component axis in AMMI was highly significant ($P < 0.001$). This first axis accounted for by 68.46 % of interaction SS (three years mean). The AMMI model was found to be more effective than JRA analysis in accounting for GXE interaction under low environmental diversity. The use of AMMI is recommended for the study of GXE effects in the oat breeding for forage yield.

Keywords. *Avena sativa*, GXE interaction, Forage Yield, AMMI and JRA analyses.

Introduction.

Genotype x environment interaction (G X E) limits the genetic advancing of plant breeding programmes, being extremely important to quantify its presence. This knowledge allows an accurate selection and evaluation of the entries under study.

Oat (*Avena sativa* L.) has become a very important forage cereal in Argentina, 70% of its production is used for this purpose. In recent years the sown land has grown (nearly two million ha) simultaneously with the number of commercial cultivars increment.

Joint regression analysis (JRA) has been a currently used methodology in G X E studies (Freeman, 1973, Wescott, 1986). The occurrence of significant regression concurrence has allowed to perform agronomic considerations on the studied genotypes and environments (Zobel et al., 1988). In recent years AMMI analysis (main additive effects and multiplicative interaction) came up as a very important method in G X E studies. This multivariate method was used in different crops (Zobel et al., 1988, Crossa et al., 1990, Crossa et al., 1991, van Oosterom et al., 1993).

G X E studies in oat were carried out in grain yield breeding programmes. Stability indexes such as stability variance of Shukla (σ_i^2), regression coefficient of Finlay and Wilkinson (b_i) and regression deviation of Eberhart-Russel (sd_i^2) (Helms, 1993) or determination coefficient (r^2) (Langer et al., 1978, Shabana et al., 1980) have been employed.

Nowadays there are no studies to evaluate the interaction incidence in oat breeding programmes to be used either as forage. G X E evaluation methods, such as JRA or AMMI have neither been used together in our country.

It was stated that AMMI analysis explains more variations of interaction sum of square (SS) than JRA as the environment diversity or the number of tested sites increase (Riggs, 1986, Zobel et al., 1988, Nachit et al. 1992).

When the environmental diversity or the number of tested sites are restricted in the plant breeding programmes, we propose that JRA can explain the variation of interaction SS as well as AMMI. According to this hypothesis, the objective of this study was to determine the effectivity of JRA and AMMI methods in the G X E quantification in the oat breeding program for forage yield.

The knowing of the G X E will be extremely useful because no such studies in oat have been performed up to now and they will allow the accurate methodology for its interpretation.

Material and methods.

Trials were carried out during 1993, 1994 and 1995 at La Dulce (38°45' S, 58°30'W) and La Plata (34°55' S, 57°57'W), which are within 520 km each other. The following cultivars were studied: Boyera F.A., Tambera F. A., Buck 152, Buck Epecuen, Cristal INTA, Millauquén INTA and Bonaerense Payé. Line 1, line 13, line 14, and line 35 were evaluated, they belong to Criadero A-1349 (INASE) Cátedra de Cerealicultura, Departamento de Producción Vegetal, Facultad de Ciencias Agrarias y Forestales (UNLP). La Plata. Argentina.

Two clippings of material were performed (1m²/plot). We determined dry matter yield (kg/ha) at first clipping (60 days after emergence), dry matter yield at second clipping (approximately 100 days after emergence), and total dry matter yield at ripening (T.D.M., kg/ha). A randomized plot design with four replicates and a plot size of 7.7 m² (seven 5.0 m rows spaced 20 cm apart) was used.

Six environments (combining years and location) for each evaluation were studied. The symbols for sites in the biplot (figure n°1 and figure n°2) was as follow: La Dulce 1993: (LD93), La Plata 1993: (LP93), La Dulce 1994: (LD94), La Plata 1994: (LP94), La Dulce 1995: (LD95) and La Plata 1995: (LP95). The symbols for cultivars and lines was as follow: Boyera F.A. (Boyera), Tambera F.A. (Tamb), Buck 152 (B. 152), Buck Epecuen (B. Epec), Cristal INTA (Cristal), Millauquén INTA (Millauq), Suregrain (Sureg), Bonaerense Payé (B.Payé), line 1 (L1), line 13 (L13), line 14 (L14), and line 35 (L35).

Joint linear regression analysis (JRA): The methodology of Freeman (1973) was used. The linear model is:

$y_{ijk} = \mu + G_i + E_j + b_i E_j + d_{ij} + r_{jk} + e_{ijk}$, where: y_{ijk} D.M.Y (kg/ha) of the i th genotype in the k th replicates of the j th environment; μ grand mean; G_i additive effect of the i genotype; E_j additive effect of j environment; b_i linear regression coefficient of the i genotype; d_{ij} deviation from regression; r_{jk} effect of the k th replicates of the j th environment; e_{ij} average of the random errors associated with the r th plot that receives the i th genotypes and j th environment. It is a mixed model, with genotypes as a fixed factor and environment and replicates as aleatory factors.

AMMI analysis: this analysis takes into account additive effects for the main effects and multiplicative effects for the G X E term. The model proposed is:

$Y_{ijk} = \mu + \alpha_g + \beta_e + \sum_n \lambda_n \gamma_{gn} \delta_{en} + \rho_{ge} + \epsilon_{ger}$ Where: additive parameters: μ grand mean, α_g grand mean genotype g deviation; β_e grand mean environment e deviation. Multiplicative parameters: λ_n eigenvalue of the principal component analysis (PCA) axis, n ; γ_{gn} and δ_{en} are the genotype and

environment PCA scores for the PCA axis n ; N is the number of PCA axes retained, ρ_{gr} residual of AMMI; ϵ_{gr} error term. This was a mixed model too.

The interaction SS was divided into N axes of principal components. Its degrees of freedom were calculated by the methodology of Gollob (1968):

$D.F = G + E - 1 - 2n$ where: G : n° of genotypes; n : n° of retained axes; E : n° of environments.

Results obtained by principal components analysis were detailed in a biplot (Kempton, 1984). JRA and AMMI analyses were carried out using SAS procedures (SAS Institute, 1988).

The criteria to compare the two models was based on: i) the statistical significance reached by the heterogeneity of regression in JRA and by the first PCA axis in AMMI (Yau, 1995), ii) the effectivity of the model measured through the explanation of the total SS and iii) the possibility that the model provides agronomically meaningful insights into the data structure. These aspects were evaluated by means of the significance of regression lines concurrence and the study of AMMI biplot.

Results.

Results for the first clipping were detailed in Table 1. A highly significant environment SS was observed ($f=53.03$ $p<0.001$). The genotype SS also recorded a highly significant variation ($f=15.50$ $p<0.001$). The JRA and AMMI analyses showed a highly significant $G \times E$ ($f=2.94$ $p<0.001$). Differences between both analyses came up when the interaction SS was partitioned. The JRA showed a nonsignificant heterogeneity of regression ($f=1.106$) and a highly significant deviation from regression ($f=3.114$ $p<0.001$). On the other hand, the AMMI showed a first PCA axis which accounted for 53.38% of the variation of the interaction SS ($f=5.75$ $p<0.001$). The second PCA axis explained 24.04% additional of the interaction SS ($f=2.98$ $p<0.001$). The residual of AMMI was highly significant ($f=2.789$ $p<0.01$). The JRA model accounts for 78.22% of the total SS, obtaining the heterogeneity of regression 20.0% of degrees of freedom. The AMMI model as a whole accounts for 85.20% of the total SS, being more effective than JRA model. The first PCA axis used 27.27% of degrees of freedom, being less parsimonious than JRA.

The results corresponding to the second clipping were detailed in Table 1. A highly significant environment SS was observed ($f=128.21$ $p<0.001$). The genotype SS was significant ($f=2.01$ $p<0.05$). The $G \times E$ was highly significant ($f=9.28$ $p<0.001$). Differences in the decomposition of the interaction SS according to the analysis employed appeared again. The JRA showed a nonsignificant heterogeneity of regression ($f=1.716$), explaining only 4.4% of the variation of the interaction SS. The deviation from regression was highly significant ($f=12.19$ $p<0.001$), accounted for 95.6% left from the interaction SS. The AMMI showed a first PCA axis that explained 87.6% of the interaction SS ($f=29.79$ $p<0.001$) and a second PCA axis which accounted for an additional 7.92% ($f=3.108$ $p<0.001$). The residual left by AMMI was nonsignificant ($f=0.846$). In this evaluation the model of JRA explained as a whole 42.97% of the total SS, while the model of AMMI captured 83.01%.

Respect to T.D.M (Table 1), a highly significant SS for environments and genotypes were observed ($f=36.56$ $p<0.001$ and $f=5.82$ $p<0.001$, respectively). $G \times E$ was highly significant ($f=2.63$ $p<0.001$) The decomposition of the interaction SS showed different performance according to the two analyses considered. The JRA recorded a nonsignificant heterogeneity of regression ($f=0.362$) explaining only 8.86% of the interaction SS. The AMMI showed a first PCA axis that explained 64.41% of the interaction SS ($f=6.22$ $p<0.001$) and a second PCA axis that accounted for 21.89% more ($f=2.44$ $p<0.01$). The residual left was nonsignificant. For this evaluation, JRA model captured 60.32% of the total SS respected 74.47% obtained by AMMI model, being again more effective than

Table 1: Joint linear regression analysis and AMMI analysis (two axes of PCA axis) of dry matter yield (kg/ha) (first and second clipping) and total dry matter yield for the different site and genotype. Years : 1993-1994-1995

Source	Clipping 1			Clipping 2			Total Production		
	D.F	SS (Y)	SS%	D.F	SS	SS%	D.F	SS	SS%
Total	287	9114.22		287	3535.70		287	8563.20	
Genotype	11	2689.14 *** §	29.50 a	11	597.73 ***	16.90	11	1570.98 ***	18.34
Environment	5	4209.32 *** #	46.18 a	5	851.88 ***	24.09	5	3455.78 ***	40.35
Block/Env.	18	285.75 ** ¶	3.13 a	18	23.92 n.s	0.67	18	340.32 **	3.97
GXE	55	867.26 *** ¶	9.51 a	55	1485.66 ***	42.01	55	1350.42 ***	15.77
H.R	11	198.52 n.s @	22.89 b	11	65.40 n.s	4.40	11	119.71 n.s	8.86
C.R	1	2.30 n.s ff	1.16 c	1	7.48 n.s	11.4	1	23.85 n.s	19.92
D.C	10	196.21 *** ¶	98.84 c	10	57.92 *	89.6	10	95.86 n.s	80.07
D.R	44	668.73 ** ¶	77.11 b	44	1420.25 **	95.5	44	1230.70***	91.14
PCA axis 1	15	462.98 *** ¶	53.38 b	15	1301.44 ***	87.6	15	869.83 ***	64.41
PCA axis 2	13	208.43 *** ¶	24.04 b	13	117.66 ***	7.92	13	295.71 ***	21.98
Resd(1-2)	27	404.27 ** ¶	22.58	27	66.55 n.s	4.48	27	184.87 **	13.69
Error	198	1062.74	14.79 a	198	576.50	16.30	198	1845.69	21.55

Y: Sum of Square (SS) = Actual values: Reported values x 10⁴.

*,**,*** : P < 0.05, 0.01 and 0.001, respectively. n.s: nonsignificant.

H.R: heterogeneity of regression. D.R: deviation from regression.

C.R: concurrence of regression. D.C: deviation from concurrence.

§: Tested against G X E Mean Square M.S.

#: Tested against Block/Environment M.S.

¶: Tested against error M.S.

@: Tested against Deviation from regression M.S.

ff: Tested against Deviation from concurrence of regression M.S.

SS%: Percentage of SS: a: % of SS respected Total SS. b: % of SS respected GXE SS. c: % of SS respected heterogeneity of regression SS.

JRA.

The concurrence of regression was nonsignificant in all evaluations, explaining only 10.8% of heterogeneity of regression SS (three years mean). The heterogeneity of regression accounted for 12.03% of the interaction SS (three years mean) while the first PCA axis explained an average 68.5% (three years mean). The residual left by AMMI captured 13.5% of the interaction SS (three years mean), while the residual of the regression obtained 89% (three years mean) of such SS.

The biplots for each clipping were detailed in Figures 1 and 2 (T.D.M. biplot not shown). It was observed that early genotypes (more D.M.Y at first clipping) have been very stable with little contribution to the interaction (Boyera F.A, Tambara F.A and Line 1). On the other hand, genotypes with more D.M.Y at second clipping recorded lesser stability, but with positive contributions to interaction (Cristal INTA, Millauquén INTA and Bonaerense Paye). As regards environments, it was observed that for the first clipping La Dulce (except in 1995) differed only in yield mean values, showing practically the same score of first PCA axis (positive). Conversely, La Plata had variation not only in the main effect, but also in the contribution to interaction. Due to this, the prediction of the performance of the different genotypes will be more difficult in La Plata than in La Dulce. In the second clipping both places showed a similar positive contribution to the G X E, with differences only in the D.M.Y. The differential performance obtained for 1995 could be due to the spring draught in both locations, appearing as negative effect on the G X E .

Discussion.

Results showed the comparative advantage of AMMI with respect to JRA. The heterogeneity of regression and inside it, the regression concurrence, did not explain the variation of the interaction SS in any of the tested evaluations, proving that the interaction was not a linear function of the environment. In this way the linear additive model of JRA could not make such interaction evident. Conversely, the AMMI on accounting significantly for the interaction SS, allowed to carry out an evaluation of genotypes and environments. Due to the multivariate nature of the G X E (Freeman, 1973) the multivariate methods are going to perform a better interpretation.

The use of biplots allows to identify stable and high yielding genotypes, quantifying each one's contribution to the G X E (Yau, 1995). This is so that the cultivar Tambara F.A and Boyera F.A and Line 1 came out in the first clipping with production values higher to the grand mean and with little contribution to the interaction. The use of biplots, allows to visualize genotypes yielding relatively better in sites having first PCA axis values of the same sign, but not in sites with first PCA axis values of opposite sign (Zobel et al. 1988). The performance was evident between the cultivars Cristal INTA, Millauquén INTA, and Bonaerense Paye and La Plata 1993 for second clipping.

The relation between cycle cultivar-trial location was an important contribution to the significance of the G X E, shown through the association between early cultivar and La Plata and late cultivar and La Dulce. According to this, the use of biplot increases the possibilities of studying the G X E in the processes of genotype selection and environments evaluation (Zobel et al. 1988).

The AMMI model explained between two to eight more times the variation of the interaction SS with respect to JRA. On the other hand, the first PCA axis captured five times more the variation of the interaction SS than the heterogeneity of regression. This performance could be due to the fact that AMMI uses a series of parameters to quantify the G X E, while JRA uses only one parameter (Gauch, 1996). It is also important to point out that in our case, two axes of the PCA axis have come up, and the incorporation of a greater number of them will improve the method's usefulness for the quantification of the G X E (Yau 1995).

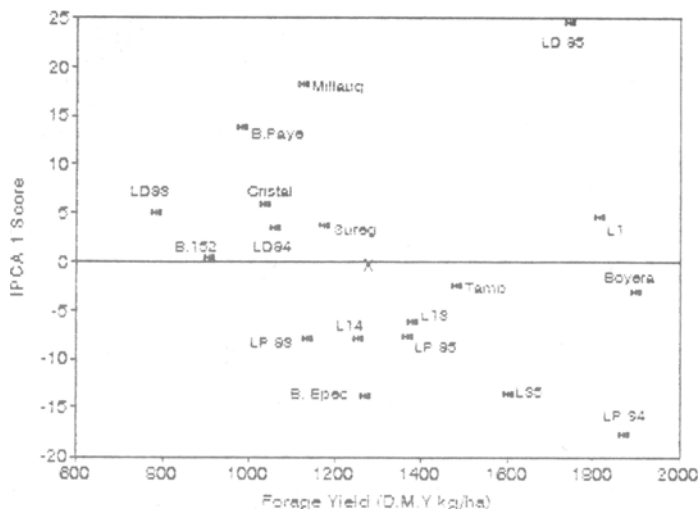


Figure n°1: Biplot of the forage yield mean (D.M.Y Kg/ha) and the first principal component axis scores (PCA axis 1) at the first clipping of 12 genotype and 6 environment. X represents the grand mean.

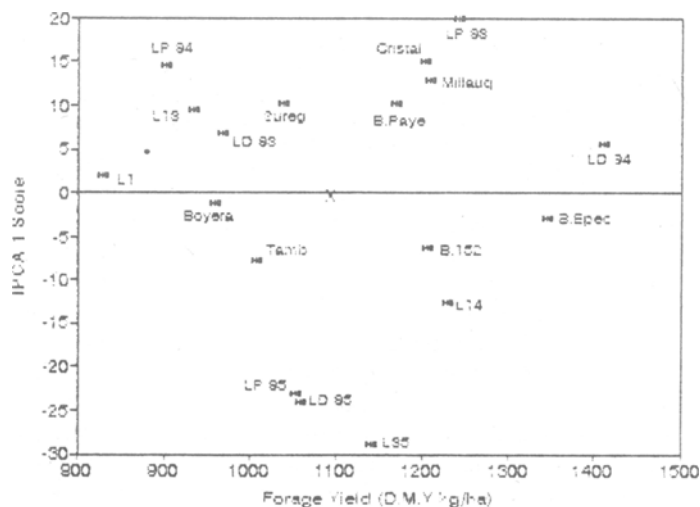


Figure n°2: Biplot of the forage yield mean (D.M.Y Kg/ha) and the first principal component axis scores (PCA axis 1) at the second clipping of 12 genotype and 6 environment. X represents the grand mean.

The importance of AMMI in studying the G X E has been pointed out when trials with a high number of environments or wide environment diversity were evaluated. On the other hand, the heterogeneity of regression was useful when facing the opposite situation (Riggs, 1986, Zobel et al. 1988, Nachit et al. 1992). The presence of a significant concurrence of regression indicates the existence of a high correlation between the regression coefficients and the genotypes means in all the environments (Eagles, 1977). This performance allows to establish similarities between genotypes in their interaction with environments, and similarities between environments in their effects on genotypes (Zobel et al., 1988). In agreement with the obtained data the above asseveration could not be confirmed due to the fact that in none of evaluations, the heterogeneity of regression and, inside it, the regression concurrence, explained significantly the variation of the interaction SS. Conversely, the AMMI by means of the biplot helped to discern the genotypes, environments, and interaction effects. This results shows the importance of AMMI as an appropriate method to understand the nature of the G X E . This is of extreme importance because in plant breeding programmes environment diversity can be frequently diminished.

The possibilities of using JRA in the present breeding program are restricted because the heterogeneity of regression did not explain the variation of the interaction SS satisfactorily though it was working with a low number of environments. The high residual left by this method showed that the data used in this trials do not agree with the model presented by JRA.

Conclusion.

The JRA did not explain the variation of the interaction SS, so agronomic considerations of genotypes and environments could not be inferred. Conversely, the AMMI analysis explained the presence of the G X E between the oat genotypes and the environments very effectively. This analysis explained a greater proportion of interaction SS, letting less residual than JRA. These features allow to obtain more information from data than with the use of JRA.

The use of AMMI analysis in the present plant breeding program will provide details about G X E overcoming the problem that causes its presence and making more efficient the process of selection.

Ammi model showed its effectiveness above JRA even when the number of evaluated environments has been low. It will be very important to continue incorporating production data so as to determine if the increase of number of environments improves AMMI performance in the knowing of the G X E .

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Received 19 September, 1996, accepted 20 February, 1997