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Genotype-environment Interaction in Tomato

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Summary. Twelve varieties of tomato of economic importance and their hybrids (including reciprocals) were studied in four environments: inside and outside of greenhouses and with and without plastic mulching. Seven characters were recorded per plant per environment: (1) total yield, (2) fruit weight, (3) locules/fruit, (4) fruits/cluster, (5) earliness in maturity, (6) earliness in harvesting and (7) leaves between clusters. There was an almost general tendency for hybrids to show higher values than the parentals for characters (1), (4) and (7); the opposite was true for (2) and (3), even when the differences were not statistically significant at the 5% level. Environments were always highly significant; the effect of the greenhouse explained most of the variation. Genotype-environment interaction by regression analysis showed that the performance of the hybrids was generally higher than that of the parents for characters (1), (4) and (7). Total yield was higher, in general, in the most protected environments. Locules per fruit was very constant but when interaction did exist, the number of locules was higher in the less protected environments. Hybrids interacted with environments more strongly than parent lines. Earliness was the most environmental dependent characteristic the choice of early harvesting being irrelevant. Some of the hybrids obtained seem promising from a commercial point of view.

Key words: *Lycopersicon esculentum* – Genotype environment interaction by regression analysis – Polyethylene – Plastic greenhouse – Polyethylene mulch

Introduction

Tomato culture in unheated polyethylene greenhouses has been a very important technological as well as economical advance; the rapid expansion of this method is a good proof of this assertion. To obtain the maximum benefit of this technique it is necessary to have varieties adapted to the new conditions; hence, a knowledge of the genotype-environment interactions is essential.

Genotype-environment interactions in tomato have been studied by some authors: Williams and Gilbert (1960) studied traditional greenhouse-open air, Baroncelli et al. (1972), autumm and spring sowings. Nevertheless, polyethylene greenhouse-open air effects have not been studied. Here, we will study the responses of a set of chosen varieties to these conditions, using as an additional treatment black polyethylene mulching.

Materials and Methods

Material

Twelve varieties from different origins and characteristics, well known in the zone where the experiment was carried out (Málaga, Southern Spain), were used: 'Resaplus N.V.F.' (Netherland), 'Florida MH-1' (USA), '428 VF' (USA), 'Early Pak 7' (USA), 'Pearson A 1' (USA), 'Royal Ace' (USA), 'Homestead' (USA), 'Grosse Fleisch' (Germany), 'Pakmor VF' (USA), 'Hellfrucht Fruhstamm' (Germany), 'Melillero' (Spain), and 'VFN 8' (USA). All possible hybrids among them were obtained (132 : 66 direct plus 66 reciprocals).

The 132 hybrids and their 12 parentals were sown early in May and cultivated in four environments: polyethylene greenhouse with and without polyethylene mulching (GP and GS respectively), and open air with and without mulching (AP and AS, respectively). Distance between rows was 1 meter and between plants within rows, 0.33 m. A total of 380 units of nitrogen, 300 of phosphorous (P_2O_5) and 600 of potassium (K_2O) were supplied in six applications. Plants were trained and pruned leaving only one stem per plant. Plastic mulch was performed using commercial polyethylene layers of 0.05 mm thickness.

Characters studied were: total yield per plant (g), mean fruit weight (g), number of locules per fruit, number of fruit per raceme, time to harvest the first third of the fruit produced per plant (origin of time arbitrarily chosen before beginning of the harvesting period; this character will be referred to here as 'early maturity'), fraction of the yield harvested in the first third of the productive period (g; this character will be referred to as 'early harvesting') and, finally, the number of leaves between racemes. The two measurements of earliness are justified because of their importance in greenhouse culture.

Statistical Procedure

The data were analyzed according to the following model:

$$x_{ijk} = m + g_i + h_j + (th)_{ij} + e_{ijk}$$

where the symbols represent: x_{ijk} the datum k within the environment j of the genotype i, m the grand mean, g_i the effect of the i genotype, h_j the effect of the j environment, $(th)_{ij}$ the interaction between the i genotype and the j environment and e_{ijk} the experimental error. Data were recorded from five nodes of four plants per genotype per environment. Direct and reciprocal were pooled because of the lack of significance of maternal effects (Cuartero and Cubero, unpublished). Parental lines were not included in the analysis of variance to avoid a possible difference in genetic buffering between lines and hybrids. Both kind of effects (g and h) were considered fixed. The 144 individual plots of every environment were fully randomized. To look deeper into both the environmental and the interaction effects, an orthogonal contrast was used to know their components:

Contrast	GP	GS	AP	AS
(1) Plastic-house-Open air	+1	+1	−1	−1
(2) Mulching-No mulching	+1	−1	+1	−1
(3) Interaction (1)–(2)	+1	−1	−1	+1

Genotype-environment interactions were also studied by mean of regression analysis, each environment being defined by the average of the twelve parental lines. These four values (abcisae) were plotted against each individual genotypic value (ordinatae), studying separately parental lines and hybrids, in order to compare their behaviour.

Results

Hybrid-Parental Differences

Table 1 shows the values of both the hybrids and the lines in each of the four environments. The large amount of variation between environments can be seen mainly in such important characters as total yield and earliness, the range of variation between environments being higher than that between genotypes. Protected environments have a positive effect on total yield, fruit weight, fruits/raceme and for the two measurements of earliness, and a negative one for locules/fruit and number of leaves between racemes.

Table 1 also shows the general lack of significance of the parent-hybrid differences; but there is an almost general constant tendency for them, hybrids showing higher values than parents for total yield, fruits/raceme and leaves between racemes, the opposite being true for fruit weight and locules/fruit (differences being almost nil in the less protected environments, namely for fruit weight). There are no parent-hybrid differences for early maturity, as early harvesting is not constant, hybrids being slightly earlier than parents only in the most protected environment.

It is obvious that there is no heterosis for total yield, at least from a statistical point of view. But the parent-hybrid differences are so constant that these differences can have an important economic value.

Analysis of Variance

Table 2 shows the analysis of variance. Environment effects are always highly significant, even in the case of

Table 1. Mean values and standard errors ($\bar{x} \pm S_{\bar{x}}$) of the 12 parent lines (lowest value) and their 132 hybrids (uppermost value). Hybrid-parental differences were not significant

Environments		Total yield (g)	Fruit weight (g)	Locules per fruit	Fruits per cluster	Earliness		Leaves between clusters
						Early maturity (days)	Early harvesting (g)	
GP	(1)	2289± 41	128± 3	5.30±0.12	4.02±0.10	22±0.35	1026±32	2.67±0.04
	(2)	2090± 72	135±12	5.56±0.46	3.69±0.38	22±1.06	1074±80	2.46±0.17
GS	(1)	2002± 36	114± 3	5.28±0.12	3.94±0.10	22±0.35	880±25	2.64±0.05
	(2)	1834±154	122±13	5.75±0.50	3.71±0.47	22±1.11	821±91	2.51±0.18
AP	(1)	1584± 30	104± 2	5.78±0.13	3.53±0.07	30±0.35	346±12	2.81±0.04
	(2)	1395± 82	107±10	6.14±0.50	3.14±0.31	31±1.03	312±48	2.72±0.16
AS	(1)	1249± 28	105± 2	6.01±0.15	2.97±0.07	31±0.34	272±22	2.80±0.04
	(2)	1096± 87	107±12	6.04±0.64	2.85±0.20	33±1.36	198±40	2.76±0.16

(1) Hybrids; (2) Parentals

Table 2. Analysis of the variance (mean squares and significance)[a]

Origin of variation	d.f.	Total yield (Kg/plant)	Fruit weight (× 10⁻³)	Locules per fruit	Fruits per clusters	Early maturity (days)	Early harvesting (Kg/plant)	Leaves between clusters (× 10)
Environments	3	27.67***	17.27***	16.78***	30.69***	3042***	18.81***	9.21***
A-G (Open-air greenhouse)	1	70.16***	39.31***	46.49***	69.95***	9092***	54.68***	26.98***
S-P (Soil-plastic mulching)	1	12.79***	4.99***	2.01 NS	14.16***	11 NS	1.59***	0.55 NS
Interaction	1	0.08 NS	7.12***	1.84 NS	7.96***	23 NS	0.18 NS	0.10 NS
Hybrids	65	0.25**	6.03***	13.81***	5.23***	34***	0.12***	15.60***
Environment × Hybrids (GE interactions)	195	0.14 NS	0.25 NS	0.61 NS	0.47*	15**	0.06*	0.62 NS
A-G × Hybrid	65	0.17 NS	0.26 NS	0.69 NS	0.82***	17**	0.08*	0.72 NS
S-P × Hybrid	65	0.13 NS	0.27 NS	0.51 NS	0.28 NS	13 NS	0.05 NS	0.58 NS
Interaction × Hybrid	65	0.11 NS	0.22 NS	0.63 NS	0.27 NS	24 NS	0.05 NS	0.58 NS
Error	264	0.13	0.29	0.85	0.39	11	0.05	0.76

[a] NS = $P > 0.05$; * $0.01 < P < 0.05$; ** $0.001 < P < 0.01$; *** $P < 0.001$

very stable characteristics (locules/fruit and leaves between racemes). The orthogonal contrast shows that differences between greenhouse and open air conditions have been the main cause of variation between environments, mulching not having been significant for locules/fruit, early maturity and leaves between racemes. Interaction between the two kinds of protection has been significant only for fruit weight under greenhouse conditions and for the number of fruits (slightly) in the open air.

Differences between genotypes were highly significant, as expected. Some of them seem promising for commercial practice in this zone.

Genotype-environment interactions were significant for early maturity, early harvesting and fruits/raceme. The component explaining this result is again the difference between greenhouse and open air conditions, mulching having no effect at all on interactions. Nandpuri et al. (1974) found in their study significant interaction for fruit weight; perhaps the difference in Autumm-Spring sowing is of a different nature than the greenhouse-open air one.

Genotype-Environment Interactions by Regression Analysis

In spite of some criticism about the linearity of the genotype-environment interactions when studied by regression methods (Knight 1973), many recent works point to the fitness of that hypothesis provided the experimental limits are not close to the viability limits (see, for example, Johnson and Wittington 1977, working on barley and using 17 different environments). Our results point in the same direction as will be shown here.

The seven characteristics studied in 12 parentals and their hybrids produce 84 graphs whose analysis of variance as well as their representation exceed the limits of this article (see Cuartero 1976). They can be classed for the purpose of this work in four different types, as shown in Fig. 1; an example is given for each type. In type 1 (Fig. 1a: total yield in 'Homestead') the

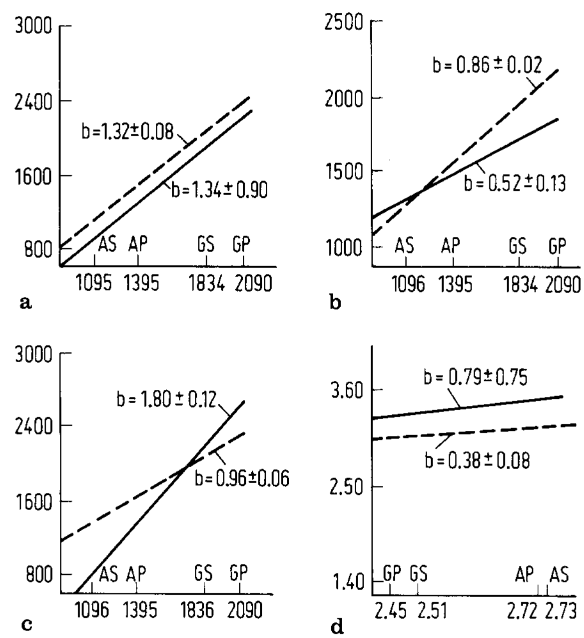

Fig. 1a–d. Types of environment-character regressions. Solid lines: parentals; broken lines: hybrids. Abcissae: Mean values of each environment; ordinatae: Individual values of parentals (solid lines) or hybrids (broken lines). **a** total yield in 'Homestead' (type 1); **b** total yield in 'Melillero' (type 2); **c** total yield in 'Grosse Fleisch' (type 3); **d** leaves between clusters in 'Melillero' (type 4)

Table 3. Frequencies of the different environment-character types of regression (see Fig. 1)

	1. Total yield [a]	2. Fruit weight [a]	3. Locules per fruit [b]	4. Fruit per clusters [a]	5. Early maturity [b]	6. Early harvesting [a]	7. Leaves between clusters [b]	Total
Type 1	7	5	4	7	2	4	7	36
Type 2	2	1	3	2	2	3	–	13
Type 3	2	–	2	1	4	1	2	12
Type 4	1	6	3	2	4	4	3	23

[a] Pattern of increasing values in the four environments is AS-AP-GS-GP
[b] Pattern of increasing values is GP-GS-AP-AS

regression lines of the hybrids are constantly higher than, those of the parents. The opposite happens in type 4 (Fig. 1 d: leaves between racemes in 'Melillero'). Types 2 and 3 represent the different behaviour of both hybrids and parentals in different environments; in type 2 (Fig. 1 b: total yield in 'Melillero') hybrids interact more with the environments than the parents; the reverse is type 3 (Fig. 1 c: total yield in 'Pearson').

Table 3 shows how these four types are distributed accordingly with the seven characters. Type 1 is the most frequent for three characters: total yield, fruits/cluster and leaves between clusters. Total yield and fruits/cluster show two type 2 cases, reinforcing the conclusion that their maximum expression is obtained in the protected environments. The other four characters, excepting early maturity, did not show a so neat behaviour; this one shows 8 cases of types 3 and 4, that

Table 4. Distribution of the significance of the 84 slopes of environment-character regression lines

P/H types	Total yield	Fruit weight	Locules per fruit	Fruits per cluster	Early maturity	Early harvesting	Leaves between clusters	Total
NS/NS	–	1	8	2	–	–	8	19
NS/S	8	9	1	7	10	6	8	44
S/NS	–	–	2	2	–	–	–	4
S/S	4	2	1	1	2	6	1	17

NS = not significant; S = significant (5% level); P = Environment-character regression of parent lines; H = Environment-character regression of hybrids
Example: 8 in 'total yield', second row (NS/S), means that there are 8 cases where the regression of the environment-genotype interaction is *not* significant for parentals but it is for hybrids

is, hybrids require a shorter period than parentals in the protected environments.

The significance of the slopes of the regression lines of the 84 graphs are summarized in Table 4. Figures in this table indicate the number of cases in which the slopes are significant for parentals and hybrids. Thus, for example, 9 NS/S cases for fruit weight means that in 9 out of the 84 graphs (Fig. 1), the slope of the regression line corresponding to parentals is not significant (NS), that of the hybrids being significant (S).

In 61 (44 NS/S plus 17 S/S) out of the 84 cases, the regression line of the hybrids have slopes significantly different from zero. For parentals this situation is only found in 21 cases (4 S/NS plus 17 S/S). The most frequent type is the NS/S one (more than the 50%), that is, no significance for parentals and significance for hybrids, a fact indicating that hybrids fit much better the lineal hypothesis to study genotype-environment interactions than parentals. In fact, we obtained much larger errors for parental than for hybrid regressions. Only in 7 out of the 84 cases was the standard error of the slope smaller for parentals than for hybrids, in 32 cases the former was more than five times that of the latter (Cuartero 1976).

Final Remarks

In short, the results suggest that response to different environments is much more regular in hybrids than in their parental lines. This is in agreement with Williams and Gilbert (1960). Hybrid development seems to be better canalyzed than that of the lines, confirming the idea expressed above that even when there are not statistical differences between parents and hybrids, these differences do exist. It is interesting to describe the behaviour of the characters studied.

Total yield is increased, in general, in the most protected environments. All the hybrids follow this rule, but only four parents showed significant environment-genotype regression (Table 4): 'Pearson' and 'Grosse Fleisch' gave type 3 and Melillero and 'VFN 8' gave type 2 graphs (Fig. 1).

Fruit weight significantly increases in the most protected environments for all hybrids but those of 'Resaplus' (the only NS/NS case, Table 4). On the other hand, only two parental lines ('Homestead' and 'Pakmor') show interaction with environments (Table 4, the two S/S cases).

Locules/fruit was very constant over all the environments (Table 4: the 8 NS/NS cases). Three parentals (S/NS and S/S) and two hybrids (NS/S and S/S) did interact with environments, number of locules increasing in the less protected ones (Table 1).

Hybrids interact with environments more strongly than parents for fruits/raceme (Table 4: 7 NS/S and 1 S/S vs. 2 S/NS and 1 S/S), the interaction meaning an increase of the number of fruits in the most protected environments. The biggest parent-hybrid differences were recorded for this character, hybrids being superior in all cases but for 'Hellfrucht Fruhstamm' (Table 3: type 3), a result explained by the fact that 'H. Fruhstamm' is the variety with the greater number of fruits/cluster among those studied.

Earliness is the most environmental dependent characteristic. The study by early maturity on early harvesting is irrelevant. Table 4 shows how all the hybrids have significant regression line slopes (NS/S and S/S cases). Early maturity in 'Melillero' and early harvesting in 'Pearson' show parent hybrid differences, in both cases parents being earlier than hybrids. Both parental lines are responsible for the interaction observed in Table 2. The hybrids coming from these parental lines would be useless under greenhouse conditions from an economical point of view.

Number of leaves between clusters scarcely show a interaction with environments (Table 4: 8 NS/NS cases). Where regression was significant, the number of leaves was smaller in the protected environments (Table 1).

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