Biometrical Analysis of a Mutant that Increases Shelf-Life of Tomato Fruits

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ABSTRACT

The nature and the magnitude of the genetic effects of a mutation, denominated ´firme‘, involved in the shelf-life trait expression, were studied through the generation-means and the Griffing’s approach. Plants of tomato (*Lycopersicon esculentum* Mill.) cv. ‘Santa Clara’, ‘firme’ mutant and the accesses BGH-6913, BGH-6914 and BGH6915 were crossed in a diallel cross, excluding reciprocals, and the F_2 and backcrossed populations were obtained for the first two parents. The results of the generation-means showed that the mutation increases shelf-life, the mean and the additive genetic effects being the main responsible for the character expression. The dominance deviation and epistasis, in turn, was of secondary importance. Similar results were obtained by the Griffing’s approach, where the mean squares of GCA effects were higher than those from SCA. The ‘firme’ mutant and BGH-6913 genotypes showed the largest magnitudes for GCA, being, therefore, of interest for intrapopulation breeding programs for genotypes with greater potential for post-harvest storability. The best combinations for obtaining gains in segregating progenies from biparental crosses, are ‘firme’ mutant x BGH-6913, BGH-6914 x BGH-6915 and ‘Santa Clara’ x BGH-6915.

KEY-WORDS: Tomato, *Lycopersicon esculentum*, ‘Firme’ mutant, Inheritance, Genetic effects.

INTRODUCTION

The ripening process of fruits such as tomatoes, and the characteristics of climacteric species, comprise a series of physiological and biochemical changes which make them attractive for consumption, and for the development of color, flavor, aroma and texture (Hobson and Grierson, 1993). Such changes are originated from different metabolic pathways (Gray *et al.*, 1994); however, evidences have shown ethylene as the gene expression coordinator related to the ripening process of climacteric fruits (Gray *et al.*, 1994; Lelièvre *et al*., 1997; Yang, 1985).

As for tomato fruit high perishability, several strategies have been used to prolong shelf-life and to minimize physical damages caused by handling (Mutschler *et al*., 1992). With the finding that ethylene plays fundamental role in tomato ripening, the practice of storing mature-green fruits with subsequent application of ethylene turning them ready for consumption was developed. However, Kader *et al.* (1977) point out that products of low quality are frequently obtained, once fruits are harvested at an immature stage.

The greatest advances in obtaining genotypes with increased post-harvest storability have been verified in the production of transgenics, via antisense RNA technology (Oeller *et al.*, 1991; Gray *et al.*, 1994), as well as by the development of hybrids with recessive mutations in the heterozygote condition (Steven and Rick, 1986). Recently, in the producing region of Viçosa (MG), cv. ‘Santa Clara’ plants exhibiting early foliar senescence, yellowish stigmas and fruits with yellow-cream and reddened color in the immature and mature stage respectively, which were shown firmer than the normal, were identified (Schuelter *et al.*, 1997). Later on, Schuelter (1999) verified that the mutant phenotype for morphologic characteristics was governed by a recessive gene with pleiotropic effects. The author verified that fruits of mutant plants, denominated 'firme' mutant, and the hybrid of the cross 'firme' mutant x cv. 'Santa Clara', presented lower rates of loss of firmness and fruits with increased shelf-life.

Though, as the inheritance of post-harvest storability of tomato plants has still not been completely understood, the objective of the present work is to study the nature and the magnitude of genic effects brought about by the mutation in shelf-life trait (SL) using generation-means and diallel analyses.

MATERIALS AND METHODS

Materials and growing conditions

Five accessions of tomato, one normal and four mutants with increased fruit shelf-life, from the collection of the Germplasm Bank at Federal University of Viçosa (BGH-UFV) were involved in a diallel producing all possible hybrid combinations, excluding the reciprocals. The involved parents were: P_1 - 'firme' mutant; P_2 - cv. 'Santa Clara'; P_3 - (BGH-6915, *alc* - alcobaça gene); P_4 - (BGH-6914, *rin* - ripening inhibitor gene); P_5 - (BGH-6913, *nor* - nonripening gene). Nevertheless, F_1 plants originated from crossing cv. 'Santa Clara' with 'firme' mutant were self-fertilized and backcrossed, to obtain the F_2 and the two backcross populations.

The genotypes of the segregating (F_2 and backcross) and non-segregating (parents and F_1) generations were evaluated at the Federal University of Viçosa, MG, experimental from winter to summer, 1997. The treatments were tested in a randomized completed block design with three replications. Each experimental plot of parental generations and F_1 consisted of 4 useful plants and those of segregating generations consisted of 62 F_2 plants, 31 BC_1 plants and 35 BC_2 plants. During the experiment, the growing conditions were maintained as recommended for a commercial tomato crop.

Evaluation of fruits

The shelf-life of fruits (SL) harvested in the breaker stage was determinated in storages at 25°C and 95% relative humidity. Fruits were examinated everyday and those which were commercially unacceptable due to change in pericarp coloration from reddish to grayish areas, to excessive softening and to the appearing of decomposer microorganisms were discarded. The SL character was expressed in days postharvest.

The fruit value from each evaluated plant was the mean of two stored fruits. Thus, in parental generation eight fruits for each replication were analyzed. Also, 16 F_1, 124 F_2, 62 BC_1 and 70 BC_2 fruits were evaluated.

Statistical analysis

Shelf-life data were analyzed using the generation-means methodology as described by Mather and Jinks (1982), and the diallel approach, proposed by Griffing (1956).

The original data and its logarithmic transformation were considered for the generation-means analyses. The original data were transformed to reduce a possible multiplicative effects of the genes controlling the character, in such a way that the results could be explained by the addictive-dominant model. According to Kearsey and Pooni (1996), epistasis can be caused by the measuring scale and data transformation can be efficient to minimize its effects.

Genetic parameters for six populations (two parentals, F1, F2 and two backcrosses), were estimated and interpreted based on means and variances of the evaluated generations. The shelf-life quantitative analysis based on variance allowed the estimate of genetic and environmental parameters, expressed by:

a) environmental variance,

$$\sigma^2_{e(F_2)} = \frac{1}{4}\left[\hat{\sigma}^2_{p(P_1)} + 2\hat{\sigma}^2_{p(F_1)} + \hat{\sigma}^2_{p(P_2)}\right] \quad ;$$

b) genotypic variance,

$$\hat{\sigma}^2_{g(F_2)} = \hat{\sigma}^2_{p(F_2)} - \hat{\sigma}^2_{e(F_2)} \quad ;$$

c) phenotypic variance,

$$\hat{\sigma}^2_{p(F_2)} = \hat{\sigma}^2_{g(F_2)} + \hat{\sigma}^2_{e(F_2)} \quad ;$$

d) variance due to additive genetic effects,

$$\hat{\sigma}^2_{a} = 2\hat{\sigma}^2_{p(F_2)} - \left[\hat{\sigma}^2_{p(BC_1)} + \hat{\sigma}^2_{p(BC_2)}\right] \text{ ; and}$$

e) variance due to dominance deviation,

$$\hat{\sigma}^2_{d} = \hat{\sigma}^2_{g(F_2)} - \hat{\sigma}^2_{a} \quad .$$

The proportion of the phenotypic variance explained by the additive genetic effects was also quantified, by calculating the heritability in the narrow-sense:

$$h^2_n = \frac{\hat{\sigma}^2_{a(F_2)}}{\hat{\sigma}^2_{p(F_2)}} = \frac{\hat{\sigma}^2_{a(F_2)}}{\hat{\sigma}^2_{a(F_2)} + \hat{\sigma}^2_{d(F_2)} + \hat{\sigma}^2_{e(F_2)}} \quad .$$

Through the analysis of the segregating and non-segregating generation means, it was possible to evaluate genetic effects involved in the determination of the shelf-life character. The adequacy of the additive-dominant model and the contribution of each genetic effect to total variation, non-orthogonal, associated to the used genetic model, were also estimated.

The Diallel model II approach (Griffing, 1956), which considers genotype fixed effects was used. Diallel analysis of variance was accomplished by the partition of treatments in general combining ability (GCA) and specific combining ability (SCA) effects, as proposed by Griffing (1956) and detailed by Cruz and Regazzi (1994). Statistical analyses were processed using GENES - Software for Experimental Statistics in Genetics (Cruz, 1997).

RESULTS AND DISCUSSION

The shelf-life trait generation-means analysis of six generations involving 'firme' mutant (P_1) x cv. 'Santa Clara'(P_2) are shown on Tables 1-6. The average shelf-life of 'firme' mutant fruits was superior to the others (Table 1), revealing a considerable mutation effect on enhancing this character expression. Besides, the variance in the 'firme' mutant population was superior to the other populations, demonstrating the occurrence of variability, which makes the selection of superior genotypes feasible.

The estimated genetic and environmental parameters based on variances showed that the dominance deviation variance is negative (Table 2). However, when the original data were logarithmically transformed, the estimates reached values close to zero. This type of variance being of reduced magnitude was considered null, and the heritability in broad and narrow sense estimates and the phenotypic variance of F_2 generation, were estimated considering only environmental and additive variances.

According to Ferreira (1995), besides experimental error, the negative dominance variance may also be explained by the inadequacy of the method to evaluate quantitative traits highly influenced by environment. In the present work, the negative estimate of this variance could be due to overestimation of the environmental variance, which was based on the pondered mean of the segregating generation variances, causing underestimation of the genotypic variance of quantitative traits. The fact that the logarithmic transformation of data has produced a value close to zero for dominance component suggests that it provided an adequate fit, turning thus the genetic inferences reliable. It is worth noting that the additive variance is obtained based on the variances of the segregating generations, when these are assumed as equal to environmental effects. Consequently, the removal of the addictive part of those underestimated genotypic variances can provide negative values for the dominance variance, whenever this underestimation is very large, to the point of the genotypic variance being smaller than its additive fraction. From a practical point of view, stands out the fact that parent P_1 has presented a very large environmental variance, larger than the variance of generations F_2, BC_1 and BC_2. This could be attributed to the fact that almost all fruits of cv. 'Santa Clara' were discarded at 14 days of storage, while the 'firme' mutant ones were, on the average, more long-lived, yet more heterogeneous for shelf-life.

The data of fruit shelf-life from non-segregating generations (Table 1) show that the F_1 hybrid is around the midpoint in relation to the parents, indicating the absence or presence of small dominance deviation. Hallauer and Miranda (1988) emphasizes that, if estimates of are $\hat{\sigma}^2_d$ in reality either very small positive values or zero, negative experimental estimates are not unexpected. This allows to hypothetize that for shelf-life trait, the overestimation of enrironmental variance associated to the absence of dominance deviation could be responsable for the negative estimates of the $\hat{\sigma}^2_d$.

Table 1 - Number of evaluated plants, means and variances of tomato fruit shelf-life (SL).

Generation	Number of plants	Means (m)	Variances (s^2)	V(m)
P_1	12	30.8	57.659	4.805
P_2	12	15.3	3.515	0.293
F_1	24	22.4	20.167	0.840
F_2	186	18.8	40.107	0.216
BC_1	93	21.3	32.225	0.346
BC_2	105	17.1	9.737	0.093

The original and transformed results allow the conclusion that 92.25% and 95.38%, respectively, of the total variation in the F_2 population was due to additive genetic effects, indicating that intrapopulation breeding strategies are better to increased postharvest conservation (Table 2). Nevertheless, the high heritability estimate demonstrates the viability of using simple breeding methods, as mass selection, for example, with great possibilities of gains from selection. Furthermore, it should be emphasized that the introgression of the shelf-life trait in populations of interest may be done by backcrossing, based on the premise of Schuelter (1999), in which the mutant phenotype for morphologic traits is governed by a recessive single gene.

Table 2 - Phenotypic, genotypic, additive, dominance and environmental variance estimates and narrow sense heritability for shelf-life (SL) trait, without and with logarithmic transformation.

Parameters	SL	Log. SL
Phenotypic variance	40.107	0.102
Genotypic variance	14.730	0.009
Additive variance	38.253	0.016
Dominance variance	-23.523	-0.006
Environmental variance	25.377	0.008
Narrow sense heritability	0.954	0.922

The estimates of genetic parameters based on the means of the six generations and the null hypothesis significance for each parameter of the complete model for explaining the shelf-life trait variability, with and without logarithmic transformation, are shown in Table 3. In these two cases, the mean, the addictive and epistatic effects (*ad* and *dd*) evaluated by the *t*-test, were significant, indicating the importance of those effects for the shelf-life trait expression. Through non-orthogonal partitioning of the sum of squares of the parameters (Table 4), it was verified that the mean and the additive genetic effect explained 86.15% and 97.91% of the available variability in the original and transformed data, respectively.

Table 3 - Estimates of genetic effects, obtained from the analysis of means of six generations (P_1, P_2, F_1, F_2, BC_1, BC_2) of tomato plants for fruit shelf-life (SL) trait, without and with logarithmic transformation.

Parameter	**SL**			**Log. SL**		
	Estimate	**Variance**	***t* test**	**Estimate**	**Variance**	***t* test**
m[1/]	21.480	6.481	8.44**	1.262	0.002	25.13**
a	7.708	1.274	6.83**	0.147	0.0003	8.99**
d	-11.524	41.923	-1.78^{ns}	-0.111	0.016	-0.89^{ns}
aa	1.562	5.207	0.68^{ns}	0.068	0.002	1.42^{ns}
ad	-6.979	6.855	-2.66**	-0.116	0.002	-2.71**
dd	12.460	18.936	2.86**	0.190	0.007	2.25*

[1/] *m* is the mean; *a* is the pooled additive genetic effect; d is the pooled dominance genetic effect; *aa* is the pooled additive x additive genetic effect; *ad* is the pooled additive x dominance genetic effect; and *dd* is the pooled dominance x dominance genetic effect

^{ns} and * and **: t-test nonsignificant and significant at P<0.05 and P<0.01, respectively.

Table 4 - Non-orthogonal partitioning of the sum of squares (SS) of parameters (*m*, *a*, *d*, *aa*, *ad*, *dd*)[1/], by the technique of gaussian elimination, for shelf-life (SL) trait, without and with logarithmic transformation.

Source of variation	**SL**		**Log. SL**	
	SS	**R^2 (%)**	**SQ**	**R^2 (%)**
a/ m, d, aa, ad, dd	46.622	34.09	80.757	11.10
d/ m, a, aa, ad, dd	3.167	2.33	0.786	0.11
aa/ m, a, d, ad, dd	0.468	0.34	2.030	0.28
ad/ m, a, d, aa, dd	7.104	5.19	7.357	1.01
dd/ m, a, d, aa, ad	8.198	5.99	5.041	0.69
Total	136.743	100.00	727.690	100.00

[1/] *m* is the mean; *a* is the pooled additive genetic effect; d is the pooled dominance genetic effect; *aa* is the pooled additive x additive genetic effect; *ad* is the pooled additive x dominance genetic effect; and *dd* is the pooled dominance x dominance genetic effect.

The results of the reduced model considering the original and transformed data, are presented in Tables 5 and 6. In these two cases, the mean was the parameter with the largest estimate and the genic effect, due to dominance, with the largest variance. All the estimated parameters, except *d*, differed significantly from zero at the 5% probability level, by the *t*-test.

Table 5 - Significant null of less parametrized models of the genetic parameters obtained from the means of six generations (P_1, P_2, F_1, F_2, BC_1, BC_2) of tomato plants for fruit shelf-life (SL) trait, without and with logarithmic transformation.

Parameter	**SL**			**Log. SL**		
	Estimate	**Variance**	***t* test**	**Estimate**	**Variance**	***t* test**
m[1/]	19.315	0.398	30.63**	1.275	0.0010	102.8**
a	4.489	0.285	8.40**	0.103	0.0001	10.00**
d	0.431	1.209	0.39^{ns}	0.003	0.0005	0.11^{ns}

[1/] *m* is the mean; *a* is the pooled additive genetic effect; *d* is the pooled dominance genetic effect

^{ns} and **: t-test nonsignificant and significant at P<0.05 and P<0.01, respectively.

Table 6 - Non-orthogonal partitioning of the sum of squares (SS) of parameters (*m, a, d*)[1/], by the technique of gaussian elimination for shelf-life (SL) trait, without and with logarithmic transformation

Source of variation	**SL**		**Log. SL**	
	SS	**R^2 (%)**	**SS**	**R^2 (%)**
m/ a, d	938.213	92.98	10573.557	99.06
a/ m, d	70.627	7.00	100.078	0.94
d/ m, a	0.154	0.02	0.012	0.00
Total	1008.994	100.00	10673.646	100.00

[1/] *m* is the mean; *a* is the pooled additive genetic effect; *d* is the pooled dominance genetic effect.

According to Cruz and Regazzi (1994), the adequacy of the model may be tested by the correlation between observed means and the estimated values by using the formula $Y_e = X\hat{\beta}$. These results are on Table 7, and it can be verified that the additive-dominant model allows for a prediction of the means. These correlate well with observed means, as shown 0.92 in magnitude, and 90% of coefficient determination, for the logarithm transformed values. The coefficient of determination for non-transformed values reached an 80% level. Thus can be inferred that the additive-dominant genetic model is suitable to explain the tendency of generation-means for the shelf-life trait, and the additive variability in F_2 is much higher than that attributed to the dominance deviations.

The analysis of the shelf-life trait average values in diallel crosses confirms the significance of mean squares due to GCA and SCA (Table 8). Such significance depicts the importance of additive and non-addictive genetic effects for the determination of the shelf-life trait. The data demonstrate that GCA mean squares were much higher than SCA mean square. In the case of autogamous, like tomato, inferences from mean square results are not recommended as an indicator for the predominance of gene action in the expression of the trait. This is because not always the GCA magnitude of the e being higher than the SCA magnitude indicate predominance additive gene action. Singh and Chaudhary (1985) suggest that is adequate to use the mean square of effects to evaluate the gene action related to the trait. Thus, considering the mean square of effects (Table 8),could be seen the predominance of the additive gene effects and its relation to the increasing in fruit shelf-life.

Table 7 - Observed and estimated means from the analysis of means of six generations(P_1,P_2,F_1, F_2, BC_1, BC_2) of tomato plants for fruit shelf-life (SL) trait, without and with logarithmic transformation.

Generation	**SL**		**Log. SL**	
	Observed mean	**Estimated mean**	**Observed mean**	**Estimated mean**
P_1	30.8	23.8	1.476	1.379
P_2	15.3	14.8	1.183	1.172
F_1	22.4	19.7	1.341	1.278
F_2	18.8	19.5	1.254	1.277
RC_1	21.3	21.5	1.315	1.328
RC_2	17.1	17.3	1.226	1.225
r (y_{obs},y_{est})	0.90		0.92	
R^2	0.80		0.84	

Table 8 - Analysis of variance for shelf-life (SL) trait, according to the model proposed by Griffing (1956), involving the parents and F_1 hybrids.

Source of variation	**d.f.**	**SS**	**MS**	**F**
Treatments	14	1953.924	139.566	9.37**
GCA	4	1503.409	375.852	25.24**
SCA	10	450.515	45.051	3.02*
Error	28	417.008	14.893	
Mean square effects				
GCA		17.188		
SCA		10.052		
Error		14.893		

* and **: F-test significant at P<0.05 and P<0.01, respectively.

The evaluation of parental GCA effects (Table 9) confirmed that positive $\hat{g}_i$ values were present in the 'firme' mutant, BGH-6913 and BGH-6914 genotypes. This indicates a tendency towards the increase of genetic contribution to shelf-life in crosses for the production of lines in advanced generations derived from parental self-fertilization. On the other hand, cv. 'Santa Clara' showed high negative value of $\hat{g}_i$, denoting, consequently, reduction in SL character contribution. The differential behavior of 'firme' mutant with regard to cv. 'Santa Clara', means that the presence of the mutation increases shelf-life and that this characteristic has great potential for future breedings.

Except for BGH-6915, the estimates of $\hat{s}_{ii}$ effects for the other genotypes were positive (Table 9). It means that negative heterotic values tend to happen in hybrids derived from 'firme' mutant, 'Santa

Clara', BGH-6914 and BGH-6913 parents, especially from the last one, due to largest positive $\hat{s}_{ii}$ estimate. These results confirm that the best strategy to prolong shelf-life in tomato plants is the use of these parents in intrapopulation breeding programs.

Estimates of $\hat{s}_{ij}$ effects indicate that the best hybrid combination happened with the pairs 'firme' mutant x BGH-6913, BGH-6914 x BGH-6915 and 'Santa Clara' x BGH 6915, whose values were 4.847, 3.503, and 2.713, respectively (Table 9). Thus, although BGH-6915 is inadequate for intrapopulation programs, it presented good capacity for the mentioned genetic complementation. Consequently, when aiming for superior segregants deriving from biparental crosses, the last two combinations should be worthy of attention.

Table 9 - GCA (gj) and SCA (sij) effects for shelf-life trait (SL).

	SCA					
	‘firme’ mutant	cv. ‘Santa Clara’	BGH-6915	BGH-6914	BGH-6913	GCA
‘firme’mutant	1.847	0.558	-4.088	-5.011	4.847	2.333
cv. ‘Santa Clara’		1.689	2.713	0.120	-6.771	-5.298
BGH-6915			-0.604	3.503	-0.919	-3.481
BGH-6914				1.619	-1.851	1.612
BGH-6913					2.347	4.833

CONCLUSIONS

The mutation identified in cv. 'Santa Clara' increases shelf-life, being the mean and the addictive genic effects the main factors responsible for the determination of the character.

The diallel analysis confirmed the great importance of addictive genic effects, indicating that intrapopulation selection can increase gains.

The analysis of the GCA effects indicate that the 'firme' mutant and the BGH-6913 access tend to increase the genetic contribution to shelf-life, which is confirmed by the high $\hat{s}_{ij}$ values. However, the combinations BGH-6914 x BGH-6915 and 'Santa Clara' x BGH-6915, along with 'firme' mutant x BGH-6913 should be chosen to obtain superior genotypes regarding post-harvest conservation, derived from biparental crosses.

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RESUMO

Análise Biométrica de um Mutante que Aumenta a Vida de Prateleira de Frutos de Tomateiro

O presente trabalho teve como objetivos estudar a natureza e a magnitude dos efeitos gênicos de uma mutação, denominada mutante 'firme', envolvida na expressão do caráter vida de prateleira, por meio da análise de gerações e do procedimento de Griffing. Plantas de tomateiro (Lycopersicon esculentum Mill.) do cv. Santa

Clara, do mutante 'firme' e dos acessos BGH-6913, BGH-6914 e BGH6915 foram intercruzadas, em esquema dialélico, sem a inclusão dos recíprocos, sendo que para os dois primeiros genitores obtiveram-se as populações F2 e de retrocruzamento. Os resultados da análise de gerações evidenciaram que a mutação identificada no cultivar Santa Clara promove o aumento da vida de prateleira, sendo a média e os efeitos gênicos aditivos os principais responsáveis pela expressão do caráter. Os desvios de dominância e a epistasia, por sua vez, apresentaram importância secundária. Resultados semelhantes foram evidenciados pela análise de Griffing, onde a média dos quadrados dos efeitos da CGC foram superiores ao da CEC. Os genótipos mutante 'firme' e BGH-6913 revelaram as maiores magnitudes para a CGC sendo, pois, de interesse em programas de melhoramento intrapopulacionais visando à obtenção de genótipos com maior potencial de conservação pós-colheita. Para a obtenção de ganhos em segregantes de cruzamentos biparentais, as melhores combinações são mutante 'firme' x BGH-6913, BGH-6914 x BGH-6915 e Santa Clara x BGH-6915.

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