A mixed model for the effects of single gene, polygenes and their interaction on quantitative traits.

2. The effects of the *nor* gene and polygenes on tomato fruit softness

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The effects of the *nor* gene, polygenes and their interaction on tomato fruit softness one (SF1) and nine (SF9) days after picking at “breaker” stage of ripening were studied using two experimental populations, each obtained from a different cross and comprised of F3 families derived from selfed heterozygous (*nor*+) F2 plants. The results were analysed using a mixed model for a single gene, polygenes and their interaction. A multiplicative *nor* × polygenes interaction was detected for SF1, and it was included in the model by log transformation. The multiplicative coefficients of the *nor* effect on family means were 0.76, 1.07, 1.23, and 0.77, 1.06, 1.22 for *nor/nor*, *nor*+, +/+, respectively, in population 1 and 2, each. “Net Polygenic Heritability” was estimated as 0.51 and 0.27 in two different populations. The corresponding multiplicative coefficients for SF9 were 0.62, 1.06 and 1.51 and 0.60, 1.07 and 1.56. After log transformation, a random *nor* × polygenes interaction was also found for SF9. It was concluded that a rather small experiment of the design used (13–21 families, 305–461 individuals) facilitated simultaneous detection of the effects of a single gene, polygenes and their interaction on quantitative traits, as well as characterization of the nature of the interaction. This provided better understanding of the genetic control, as well as improved estimates of genetic parameters than those obtained when lack of such interaction was assumed.

INTRODUCTION

Firmness and shelf life are among the most important characters of tomato fruits. Firmness has been described as a quantitative trait with continuous distribution (Al-Falluji, Trinklien and Lambeth, 1982). El-Sayed, Erikson and Tomes (1966), studied a cross between relatively soft parents and concluded that firmness 7 days after picking at the “turning stage” was controlled by one major gene and a few modifiers, with the softer parent being dominant. Al-Falluji, Trinklien and Lambeth (1982) found that the genetic control of firmness of fruits, four days after picking at the “turning stage”, followed an additive-dominant polygenic model, with an average additive effect twice as large as the average dominant one.

Several ripening mutants, *rin*, *nor* and *Nr*, which are inherited as single genes, affect some or all components of the ripening process. These mutants also affect the softening of the tomato fruit during ripening (Brady *et al.*, 1982) and their use

in breeding programs for extending shelf life, has been considered (Kopeliovich *et al.*, 1979).

A mixed model which includes the effects of a single gene, polygenes and their interaction, was proposed by Elkind and Cahaner (1986). They suggested an experimental design comprising of F3 families derived from F2 plants heterozygous for the single gene, in order to estimate the components of the model. This design was used in this study to estimate the effects of the *nor* gene, polygenes and their interaction on the softness of tomato fruits one and nine days after picking.

MATERIAL AND METHODS

Experimental populations

There were three parental populations: (P1) Normal ripening (+/+), soft fruit line 475 originated from a cross between “summer Marmand” and line 70T82-1 (California); (P2) Normal ripening (+/+), soft and high-sugar fruit line 493,

originated from 76T128-1 (California); (P3) Non-ripening (*nor/nor*), very firm fruit line 864, an F7 derived from the cross (66-1 × 97-1) × (Rutges-*nor* × 97-1). Experimental population No. 1 and No. 2 were comprised of 13 and 21 F3 families obtained by selfing plants heterozygous at the *nor* locus of the crosses P1 × P3 and P2 × P3, respectively.

Experimental procedures

The experiment was performed in a split plot design in two randomized blocks with one plot of 15 plants for each family per block. In order to identify the *nor* genotypes of the F3 plants, green fruits were picked from each of them, two weeks prior to the softness measurement experiment, and stored at room temperature (23 ± 5°C). Two and four weeks later they were sorted according to their colour, into three groups—red, yellow and green—which indicated +/+, *nor*/+ and *nor/nor*, respectively. Four fruits for softness measurement were harvested at “turning stage” (USDA color stage 3, Anon., 1975) early in the morning, placed in padded boxes and stored at 20 ± 2°C. The marking of the flowers at anthesis facilitated the harvest of fruits from plants of *nor/nor* genotype at a similar chronological age to fruits of *nor*/+ plants.

Measurement of softness

Universal Test stand Model LTCM-II of Chatillon (Anon., 1982) with DFG10 force measurement head was used in a non-destructive dynamic loading of a fruit placed on its side between two flat plates. Compression speed was 50 mm/min for a distance of approximately 0.5 mm, at temperature of 20 ± 1°C. Softness was calculated as the ratio between the deformation and the force, and converted to cm/kg units. Measurements were made one and nine days after picking, and designated SF1 and SF9, respectively. Fruit diameter, height, weight and final colour were also recorded.

Data analysis

The interpretation of results followed the outlines described by Elkind and Cahaner (1986). The heterogeneity of slopes was indicated by “SG/Family” plots, in which means of plants of each single gene (SG) genotype (i.e., *nor/nor*, *nor*/+ and +/+) were plotted against their family means. The null hypothesis of homogeneous slopes was tested by joint regression analysis, similar to the one used in genotype × environment interaction

(Yates and Cochran, 1938) by the following model:

$$Y_{ij} = \mu + \alpha_i + Y_j + \beta_i(Y_j) + e_{ij}; \quad (1)$$

where Y_{ij} is the mean softness of plants of *nor* genotype i of family j and Y_j is the mean of family j ; μ is the general mean; α_i is the *nor* genotype effect; β_i is the regression coefficient of *nor* genotype i ; e_{ij} is the error term. Y_{ij} was weighted by its standard error. The regression coefficients, as estimates of multiplicative coefficients (MC), were obtained by a model in which μ and Y_j were dropped. Data processing and some analysis were performed by SAS (1985a, b) on a VAX 750.

The Restriction Maximum Likelihood method was used in the analysis of variance by programme 3V of BMDP (Dixon *et al.*, 1985). The model used for the analysis was:

$$Y_{ijkl} = \mu + F_j + B_k + (FB)_{jk} + \alpha_i + (\alpha F)_{ij} + C_{ijkl} + e_{ijkl}; \quad (2)$$

where Y_{ijkl} is the mean fruit softness of plant l in block k of family j with *nor* genotype i . μ is the general mean; F_j is the effect of family j ; B_k is the effect of block k ; (FB) is the between plots effect as well as the family × block interaction; α_i is the *nor* genotype effect; (αF) is *nor* × family interaction; C_{ijkl} is the mean fruit calibre, used as covariate and e_{ijkl} is the effect of plants within *nor* genotype in a plot. The μ and α_i was regarded as “fixed”, while the rest of the effects were “random”. Hypothesis testing was accomplished by calculating the difference between $-2 \times \log$ of maximum likelihood of the complete model, and that of a model in which the tested component was absent. This difference is distributed as chi square with 1 degree of freedom (Dixon *et al.*, 1985).

LSF1 and LSF9 were obtained by natural logarithm (ln) transformation of variables F1 and SF9, respectively. The MC of a genotype was calculated by anti-log transformation of the genotype effect (the difference between genotype mean and the grand mean) on the log scale. “Net Polygenic Heritability” (NPH), representing the heritability in F3 generation due to polygenes and independent of the single gene effect (Elkind, 1987), was calculated for log of SF1 according to Cahaner and Hillel (1980).

RESULTS

Fruit softness 1 day after picking

SG/family plots for SF1 are given in fig. 1(a) and 1(b). The solid lines in the plot are those expected in the case of no single gene × polygenes inter-

Figure 1 SG/family plots of SF1 (a and b) and LSF1 (c and d) in populations 1 and 2, respectively. Means within family of the *nor* genotypes are *nor/nr* ■, *nor/+* ▲ and *+/+* ●. Observed regression lines ---, expected lines in the case of no-interaction —.

Table 1 ANOVA of joint regression analysis for heterogeneity of slopes of means of single-gene genotype within family on family mean, for SF1 and SF9 (cm/kg) and their ln transformation LSF1 and LSF9

		SF1		LSF1		SF9		LSF9	
Source	df	S.S.	<i>P</i> (<i>F</i>)	S.S.	<i>P</i> (<i>F</i>)	S.S.	<i>P</i> (<i>F</i>)	S.S.	<i>P</i> (<i>F</i>)
Population 1									
<i>nor</i> genotypes	2	273	0.001	1.28	0.001	1508	0.001	4.26	0.001
Families mean	1	130	0.001	0.52	0.001	208	0.001	0.43	0.001
Heterogeneity	2	7	0.054	0.00	0.656	43	0.003	0.01	0.650
Error	22	23		0.09		61		0.16	
Population 2									
<i>nor</i> genotypes	2	600	0.001	2.51	0.001	3936	0.001	9.56	0.001
Families mean	1	120	0.001	0.42	0.001	331	0.001	0.58	0.001
Heterogeneity	2	15	0.003	0.01	0.423	105	0.001	0.03	0.262
Error	38	41		0.17		194		0.38	

Table 2 Multiplicative coefficient (MC) and their standard errors (S.E.) for *nor* genotypes of SF1 and SF9 estimated by joint regression analysis and anti-log transformation

Genotype	Joint regression slope				Anti-log			
	SF1		SF9		SF1		SF9	
	MC	S.E.	MC	S.E.	MC	S.E.	MC	S.E.
Population 1								
<i>nor/nor</i>	0.71	0.28	0.37	0.36	0.76	0.01	0.62	0.01
<i>nor/+</i>	0.95	0.23	0.91	0.32	1.07	0.02	1.06	0.02
<i>+/+</i>	1.35	0.28	1.58	0.37	1.23	0.02	1.51	0.03
Population 2								
<i>nor/nor</i>	0.49	0.20	0.28	0.22	0.77	0.01	0.60	0.01
<i>nor/+</i>	1.03	0.17	0.91	0.18	1.06	0.02	1.07	0.02
<i>+/+</i>	1.46	0.21	1.74	0.23	1.22	0.02	1.56	0.04

Table 3 Analysis and estimates of variance components (σ^2) of the model of LSF1 and LSF9 (100 ln(cm/kg)) in F3 families experiment using Restricted Maximum Likelihood method

Variance source	LSF1*			LSF9*		
	σ^2	S.E.	<i>P</i> (χ^2)	σ^2	S.E.	<i>P</i> (χ^2)
Population 1						
Between Families	111	52	0.0020	90	45	0.0010
Block	13	23	0.1253	37	93	0.0503
Family $\times$ Block	13	14	0.1302	0	—	1
<i>nor</i> $\times$ Family	10	12	0.2017	32	20	0.0231
Error	218	19		252	22	
Population 2						
Between Families	40	17	0.0015	44	27	0.0431
Block	7	12	0.2713	50	77	0.1175
Family $\times$ Block	4	7	0.3428	20	13	0.0255
<i>nor</i> $\times$ Family	9	8	0.1936	52	19	0.0000
	183	13		220	16	

* The estimates are in $10,000 \times (\ln(\text{cm/kg}))^2$
 S.E. = standard error of the estimate.

action. The means of the *nor/nor* and *+/+* genotypes within a family deviated from these lines in a non-random fashion. In families with high SF1 mean, the deviations are mostly positive for *+/+* and negative for *nor/nor*, and the reverse was found for families with low SF1 mean. This trend indicated a multiplicative interaction between the *nor* gene and the families (*i.e.*, polygenes). The regression slopes of the three genotypes were heterogeneous in population 2, and also in population 1, where $P(F) = 0.0544$ was regarded as significant (table 1). The slopes of the regression were smaller than 1 for *nor/nor* and greater than 1 for *+/+* (table 2).

The multiplicative interaction was incorporated into the model by the use of log transformation. The regression slopes of the *nor* genotypes of the transformed variable, LSF1, were homogeneous (fig. 1(c) and (d), and table 1) and did not differ from 1. The multiplicative coefficients (MC) for the effect of the *nor* gene on the family means, estimated by anti-log, were 0.76, 1.07 and 1.23 in population 1 for *nor/nor*, *nor/+* and *+/+*, respectively. Almost identical MC's were calculated in population 2 (table 2). The SG/family plots of LSF1 in the two populations were also very similar (fig. 1). The *nor* × family interaction was not significant for LSF1 (table 3), indicating additivity between *nor* and the families mean (polygenes) after the multiplicative interaction was included in the model.

The estimate of the "between families" variance component for LSF1 in population 2 was half of the estimate of population 1 (table 3). The net polygenic heritability (NPH) estimates, based on "within families" and "between families" variance components, were 0.51 and 0.27 for populations 1 and 2, respectively. These values are the ratio of polygenic to total phenotypic variance in F3 generation.

Fruit softness 9 days after picking

SG/family plot for SF9 are presented in fig. 2a and 2b. Similar to SF1, but more pronounced multiplicative *nor* × family interaction was identified in the plot. The regression slopes were heterogeneous (table 1) in the two populations. The slopes were smaller than 1 for *nor/nor*, and greater than 1 for *+/+* (table 2).

The multiplicative interaction was incorporated into the model by a log transformation. The slopes of the transformed variable, LSF9, were found to be homogeneous (fig. 2(c), 2(d), and table 1) and did not differ from 1. The MC for the effect

of the *nor* gene on the family means, estimated by anti-log, were 0.62, 1.06 and 1.51 in *nor/nor*, *nor/+* and *+/+* respectively for population 1. The MC values for population 2 were almost identical (table 2). The *nor* × family interaction was significant for LSF9 (table 3), indicating the presence of random interaction in addition to the multiplicative one. The nature of the interaction was indicated by the random distribution of the *nor* genotypes within families around the lines of no-interaction (Fig. 2(c), 2(d)). The "between families" variance component for LSF9 in population 1 was twice as large as in population 2. The reverse situation was found with the "*nor* × family" component (table 3).

DISCUSSION

The nature of nor × polygenes interaction

Multiplicative interaction

The *nor* gene had a multiplicative interaction with the polygenes in both SF1 and SF9. Therefore, MC were estimated for both, and found almost identical in the two populations. The MC of a single gene genotype indicates the effect of the genotype on the family mean over all polygenic combinations. In population 1, the MC were 0.76 and 1.23 for SF1, and 0.62 and 1.51 for SF9, in the homozygote genotypes *nor/nor* and *+/+*, respectively. The MC of SF9 deviated from 1 almost twice as much as those of SF1, indicating a larger multiplicative interaction for the former. The MC has no units and it represents the factor for multiplying the family mean in the measured units, *i.e.*, cm/kg, to yield the expected value of the genotype in the same units. Furthermore, if the only interaction present is a multiplicative one, the ratio between the MCs can be used for predicting the performance of one single-gene genotype based upon the score of its isogenic line with another single-gene genotype. For example, if the ratio of MC of *nor/nor* to *+/+* was 1.62 (1.23/0.76) for SF1, and the score of *nor/nor* with a specific polygenic constitution (*i.e.*, genome) was 10 cm/kg, then the predicted value for its isogenic *+/+* would be 16.2 cm/kg.

Multiplicative interaction between the "*py*" gene and polygenes was described by King (1955) for body weight in mice, in which the homozygotes for "*py*" were half the weight of their normal litter-mates.

In the present study, MC for SF1 and SF9 were estimated by two methods. Estimates obtained by

Figure 2 SG/family plots of SF9 (a and b) and LSF9 (c and d) in populations 1 and 2, respectively. Means within family of the nor genotypes are nor/nor $\bullet$, nor/+ $\blacktriangle$ and $\blacktriangle$ and $\bullet$. Observed regression lines —, expected lines in the case of no interaction ---.

anti-log had smaller standard error than those obtained by regression, e.g., the standard error of regression estimate of MC of SF1 for genotype $+/+$ in population 1 was 0.28 vs. 0.02 of the anti-log estimate (table 2). Elkind (1987) simulated multiplicative interaction between a single-gene and polygenes in the F3 experimental design used in the present study and estimated MC by the two alternative methods. The estimates obtained by anti-log transformation had much smaller variance than those calculated from the regression. The latter was also affected by heterogeneity of variance, a single-gene genotype with larger variance will have greater slope. Therefore, based on smaller S.E. in the experiments, as well as in the simulation study, estimation of MC by anti-log seems to be more reliable than regression. The theoretical aspects of multiplicative interaction between polygenes, and the use of log transformation in quantitative genetic models, were discussed by Horner, Comstock and Robinson (1955). Log transformation was used for tomato fruit weight per locule to achieve adequacy of the additive-dominant model (Powers, 1951).

Multiplicative and random interaction

Analysis of SF9 indicated the presence of multiplicative as well as random interaction. After the multiplicative interaction was incorporated in the model, a random-nature interaction was also detected (table 3). In population 1 the variance component of the interaction was a third of the "between families", whereas, in population 2 it was somewhat greater than the "between families". Therefore, the random interaction between *nor* and polygenes constitute an important part in the continuous genetic variation of tomato fruit softness 9 days after picking.

The random interaction may result from the fact that some polygenes affecting SF9 were expressed solely in one *nor* genotype, while other polygenes were expressed in another genotype. Alternatively, linkage between polygenes and the *nor* locus will also result in such interaction.

The variance estimates of the random interaction provide information about the expected deviations from the single-gene and the family effects. For example, in a family from population 2 with mean LSF9 of 2.95 ln(cm/kg) the value for *nor/+* genotype is expected to be 3.02 (the effect of the genotype was 0.07, table 4). However, the random interaction variance was 0.0052 ln(cm/kg)² (table 3), therefore, the interaction standard deviation was 0.072 ln(cm/kg). Thus, 95 per cent

Table 4 Mean and standard error (S.E.) of the *nor* genotypes of LSF1 and LSF9 (ln(cm/kg)) in two populations

Genotype	LSF1		LSF9	
	Mean	S.E.	Mean	S.E.
Population 1				
All	2.64	0.03	2.89	0.04
<i>nor/nor</i>	2.37	0.04	2.42	0.07
<i>nor/+</i>	2.71	0.04	2.95	0.07
$+/+$	2.85	0.04	3.30	0.07
Population 2				
All	2.68	0.02	2.95	0.04
<i>nor/nor</i>	2.42	0.03	2.43	0.06
<i>nor/+</i>	2.74	0.03	3.02	0.06
$+/+$	2.88	0.03	3.40	0.06

of the families are expected to be distributed between 2.87 to 3.15 ln(cm/kg) (± 2 S.D.). Interpreting the random interaction in the softness units by anti-log transformation of two standard deviations (0.14) gives 1.15. This actually gives a multiplicative factor that is somewhat similar to MC, and can be used to calculate the random distribution borders due to the interaction for each family. Furthermore, using MC ratio to predict the expression of one *nor* genotype based on its isogenic SF9 value, will have even larger deviation because the random interaction acts independently on both genotypes. For example, if the ratio of MC of *nor/+* to $+/+$ of SF9 is 0.69 (1.07/1.56) and the softness is 30 cm/kg, the predicted softness for *nor/+* will be 20.7 cm/kg. But, due to random interaction, with 2 S.D. on the log scale of 0.20 which gave a factor of 1.23 on the softness scale, the distribution interval for 95 per cent of the families will be between 16.9 and 25.4 cm/kg assuming no experimental error, and between 16.6 and 25.7 cm/kg including the experimental error.

This study demonstrates the utilization of detection and estimation of random interaction in predicting the effects of single-gene and polygenes on a quantitative trait. Furthermore, estimates of single-gene effects obtained from an experiment such as F3 families can be useful even in the presence of interaction, while estimates based on isogenic lines are relevant only to specific genetic background studied.

*The effect of *nor* on softness*

The rank of means of the three genotypes of *nor* for SF1 and SF9, as was found in this study, is

consistent with findings of others (Brady *et al.*, 1982; McGlasson *et al.*, 1983; Ng and Tigchelaar, 1977). A more comprehensive comparison between these studies and the present one was not made because of differences in genetic backgrounds as well as in measuring methods and units.

The effect of *nor* on the ripening process (Brady *et al.*, 1982) is probably responsible for the effect of the gene on the softness in SF1 and SF9 measurements. It is known that the ripening process commences a few days before the "turning" stage (Davies and Hobson, 1981), at which the fruits for the experiment were harvested. This could also explain the increase in the effect of *nor* during ripening.

Net Polygenic Heritability (NPH)

The NPH estimated for LSF1 in this work were 0.51 and 0.26 for populations 1 and 2, respectively. If the heritability was to be estimated from the same F3 families by the standard procedure, *i.e.*, ignoring the gene *nor*, the heritability estimates would be 0.78 and 0.68, respectively. The relatively large effect of *nor* caused the increase in the heritability as well as the reduced difference between the populations. NPH provides an accurate estimate for the gain expected by selection of the polygenes, and it is not affected by the genetic variation due to the single-gene, which has heritability of 1.

Utilization of the *nor* gene in tomato breeding

Since fruits of *nor/nor* plants do not ripen at all (horticulturally), only the utilization of the heterozygote genotype (*nor/+*) for extending the shelf life, indicated by SF9 will be discussed. Mean SF9 of fruits of *nor/+* plants was about 30 per cent lower than that of fruits of normal plants (+/+) from the same family (MC 1.07 vs. 1.56, respectively, table 2). Furthermore, one can speculate that the increase in the MC from 1 to 9 days (SF1 to SF9) also indicates that the MC of *nor/+* fruits after additional storage period will be even greater. Extending the shelf life based on these results involves the combined use of the *nor/+* genotype with polygenes. The presence of multiplicative interaction indicates that the expected effect of the *nor* gene will be greater in a soft genetic background. However, overall extended shelf life might be obtained by a combination of polygenes for low SF9 expressed in all the *nor* genotypes in addition to polygenes that reduce SF9 specifically in the *nor/+* genotype. Softness after

nine days (SF9) of less than 21 cm/kg can be obtained only with *nor/+* and family mean less than 21 cm/kg (Figure 2a, 2b). But, within these families the one with the lowest family mean does not have the lowest SF9 for *nor/+* (fig. 2(a)). At present, the *nor* gene is not widely used in breeding because of its adverse effect on fruit colour and flavour (Kopeliovitch *et al.*, 1979). Future studies on the effect of the *nor* gene and polygenes on flavour and on colour accumulation in the fruit may increase the importance of this gene in tomato breeding.

CONCLUSIONS

The present study illustrates the ability of an experiment comprised of F3 families derived from F2 plants heterozygous for a single-gene, to simultaneously detect the effects of the single-gene, polygenes and their interaction on a quantitative trait. Furthermore, this design allows the nature of this interaction to be characterized, *i.e.* multiplicative, random and a combination of the two. The detection and characterization of a single-gene $\times$ polygenes interaction are important aspects in studying gene expression. It can also assist in studying genes transferred by advanced molecular techniques, since they can be easily identified and are inherited as single-genes. The results of this study also indicate that the *nor* gene can be useful in extending the shelf life of tomato, by using the *nor/+* genotype in an optimal polygenic constitution.

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