Original article

Studies of gene action and heritability of the percentage of fruiting in tomato, cultivar Nagcarlang under conditions of heat stress

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ABSTRACT

Poor fruit set induced by high temperatures is the main cause of yield losses in tropical and subtropical regions. The present study was aimed to estimate gene action and the heritability of fruit set in heat tolerant Nagcarlang cultivar. Thus, fruit set percentage was evaluated over the optimal and spring-summer periods of the F_1, F_2 populations and the backcrosses with each parent of the cross between Nagcarlang and the beat sensitive AN-104-1 inbred line. Mean percentage of fruit set of the F exceeded midparent values are not significantly different from those of Nagcarlang, indicating complete dominance from heat tolerance. Generation means analysis showed that a model including simple and additive dominance is not adequate to explain inheritance of percentage of fruit set. The best fitting model included epistatic interactions. Heritability estimated in the broad sense was intermediate. The narrow sense heritability was lower in springsummer periods. The low narrow sense heritability for percentage of fruit set suggest that simple plant selection in the F_2 for high temperatures tolerance from crossed involving Nagcarlang is not effective to predict the progress by selection in tomato crosses in order to obtain heat tolerant cultivars and the selection should be based on in more advanced generations.

Key words: high temperature, plant breeding, *Solanum lycopersicum*, heat tolerance

INTRODUCTION

High temperatures are one of the major abiotic stresses affecting that affect reproduction in tomato crops in the tropical and subtropical lowland and, therefore, fruit set, which causes considerable economic losses in the crop (1-5). Most of the commercial cultivars of tomato (*Solanum lycopersicum* L.) are susceptible to high temperatures, so small increases above the optimal growth temperature will consequently lead to a decrease in fruit production (1,4). This effect is aggravated if the high temperature is combined with excessive rainfall, increasing pest incidence, fundamentally, in open field conditions (6-9). Heat tolerance is a complex trait, and understanding the genetics of heat tolerance is difficult, excessive genes are responsible for heat tolerance; they are governed by multiple genes, affected by environmental conditions and have low heritability (5,10,11). Additive and non-additive genes have been reported to govern heat tolerance (12,13). Some authors suggested that fruit set is the most important parameter to in the evaluation of different tomato cultivars under heat stress, in such a way that those varieties showing greater fruiting capacity under high temperature and humidity conditions are the most suitable for tomato production in the tropics. Therefore, the availability of genetic variation in fruit set under heat stress may help selection for heat tolerance (5,10,11,14,15). Heritability analysis is important to determine the appropriate method of genetic improvement. Heat stress tolerance was found to have low heritability (10,11). The main objective of this study were to estimate gene action and heritability of fruit set over optimal and spring-summer periods for heat tolerance Nagcarlag tomato cultivar.

MATERIALS AND METHODS

Plant material

For the present study, crosses between `Nagcarlang´ (P_1), heat tolerant cultivar and a heat sensitive inbred line AN-104-1 (P_2) to produce the F_1 hybrid. Nagcarlang and AN-104-1 to obtained the segregating generations. The F_2 generation was obtained by self-pollinated of F_1, while the first generation of backcrosses with each parent (RC_1P_1 and RC_1P_2) were obtained by crosses between F_1 and the Nagcarlang and AN-104-1 parents, respectively. All the crosses were under controlled conditions in protected cultivation houses made. The six generations, including both parents, the F_1 and F_2 populations and the backcrosses with both parents were in this study used.

Experimental conditions

The research was developed at the central area of the National Institute of Agricultural Sciences (INCA), placed at km 3 ½ of Carretera a Tapaste, San José de las Lajas, Mayabeque. INCA is located at 23º00' north latitude and 82º12' west longitude, 138 m a.s.l. The six populations were sown in trays with 196 cells of 30 cm^3 of capacity, containing a mixture of sugarcane sludge: zeolite and Ferrallitic Red Compacted soil in a proportion 1:2:1. Later, the seedlings 25 seedlings from both parents and from F_1, 50 seedlings of each backcross and 130 seedlings from F_2 (population) were transplanted to gutters of asbestos-cement, covered by saran mesh, in the outdoors. The gutters contained a mixture of Ferralitic Red Compacted soil (eutric Ferralsol) according to the New Soil´s Genetic Classification [(16)] and sugarcane sludge in a proportion 3:1, following a Completely Randomized Design. It was used a planting distance of 0.90 x 0.25 m. The planting in the period spring-summer and the optimal period was carried out on April 17th, 2012, and on October 15th, 2013, respectively.

In Tapaste Weather Station were taken of the climatic variables behavior of maximum and minimum temperature, as well as, relative humidity and the rainfall, which influenced during the experiment development, which are shown in Table 1. The cultural attentions in all cases were carried out according to the Technical Instructions for Organoponics and Intensive Vegetable Gardens established for tomato [(17)].

Table 1. Climatological variables behavior that affected during the experiment development at Tapaste Meteorological Station

Year	Transplant day	Maximum temperature (°C)	Minimum temperature (°C)	Relative Humidity (%)	Total rainfall (mm)
2012	May 3	31.10±1.21	21.92±1.23	81.50±3.96	788
2013	Nov 7	27.87±2.00	17.76±2.83	80.75±4.51	320

The percentage of fruit set on clusters 2-6 the main stem was determined on each plant. This indicator was determined as the total number of fruits divided by the total flower number on clusters 2-6 the main stem. The means of fruit set of the six generation and their standard errors were used to estimate gene effects [(18)]. The mid-parent value m together with additive [*d*] and dominance [*h*] gene effects were estimated. The adequacy of such *mdh* additive-dominance model was tested by c2-test. If the data did not adequately not adequately fit the three component model, then model including additive x additive [*i*], additive x dominance [*j*], and dominance x dominance [*l*] terms of digenic epistatic interactions were then calculated: *mdhi*, *mdhj*, *mdhl*, *mdhij*, and *mdhil*. No degree of freedom is left in the six-parameter *mdhijl* model and therefore it was not calculated. Finally, the best-fit model was chosen as that in which expected means deviated least from the observed means of the generations as indicated by a higher probability associated with the corresponding c2-test. The significance of individual genetic parameter estimates was tested by t test and the t value was found by dividing each parameter estimate by its respective SE.

Broad and narrow sense heritability was estimated. Broad sense heritability was estimated as a ratio of genetic variance to total phenotypic variance, according to Allard [19], while narrow sense heritability was evaluated as a ratio of the additive variance to total variance [20]. These determinations were estimated using the following formulas:

$$H^2 = Vg/(Vg+Ve) \text{ being } Vg = [VF_2 - Ve]$$

$$h^2 = ((2VF_2)-(VBC_1-VBC_2))/VF_2$$

where:

H^2: broad sense heritability.

h^2: narrow sense heritability.

Vg: genetic variance

Ve: the environmental variance, estimated by the average of the phenotypic variance of the two parents and the F_1.

VF_2: Phenotypic variance of the F_2 population.

VBC_1: Phenotypic variance of the backcross with parent 1 (Nagcarlang).

VBC_2: Phenotypic variance of the backcross with parent 2 (AN-104-1).

RESULTS AND DISCUSSION

Table 2 shows the estimate of generation means for fruit set in the cross of Nagcarlang x AN-104-1 in Optimal and Spring-Summer periods. According to the results fruit set, which is the indicator of heat stress tolerance, was less in An-104-1 compared with the heat tolerant parental Nagcarlang in both periods. (99.43 and 75.27 % and 100 and 47.16 % in optimal and spring-summer period, respectively. However, percentage of fruit set on were not significantly different of midparent.

Table 2. Mean and variances of the families derived from the Nagcarlang/AN-104-1 cross in the inheritance study of the fruiting percentage

	Frui set (%). Optimal period			Frui set (%). Spring-summer period		
Populations	**Nu. plants**	**Mean**	**Variance**	**Nu. plants**	**Means**	**Variance**
P_1 (Nagcarlang)	25	99.43 a	3.27	23	100 a	0
P_2 (AN-104-1)	23	75.27 c	5.58	19	47.16 e	10.42
Midparent		87.34 b			73.58 c	
F_1	24	98.52 a	6.57	21	91.19 a	9.92
RC_1P_1	48	93.23 a	69.55	46	78.54 b	65.93
RC_1P_2	47	88.13 b	62.41	41	60.88 d	78.68
F_2	123	91.61 ab	118.15	126	76.86 bc	103.02

Different letters indicate significant differences for $p \leq 0.05$

The mean percentage of fruit set of the F_1 and BCP_1 exceeded the midparent and was not different from P_1 (Nagcarlang) indicating that gene(s) controlling percentage of fruit set variation are dominant towards Nagcarlang parent values. This difference is most marked in the spring-summer period [18]. In addition, the variance for the segregating generation were greater that the variance estimates of the parental and F_1 generation. In this population, the mean of BC_1P_1 was numerically similar to the means of F_1 and P_1 (Nagcarlang) in optimal period. However, it was different from P_1 in summer-spring period. The mean of BC_1P_2 was statistically higher than the mean of P_2 (AN-104-1) which also indicated the dominant nature of gene action.

Generation means analysis with simple additive and dominance effects was not adequate in explaining the inheritance of percentage of fruit set since the X^2 test showed significant differences in both periods (Table 3).

Table 3. Generational mean estimates and gene effect (± ES), Chi-square tests (X^2) in the *mdh* model for fruiting percentage determinations of the six Nagcarlang family x AN-104-1 populations

Mean components and scaling test *mdh*	**Frui set (%) Optimum period**	**Frui set (%) Spring-summer period**
Parental mean value (m)	85.37±1.67***	71.94±2.05***
Additive effects [d]	14.02 ± 0.63***	9.78 ± 0.66***
Dominance effects [h]		-0.91 ± 3.29***
X^2	(3g.l)	(3g.l)
p	0.000***	0.000***

Therefore, epistatic components were necessary to explain the observed generation means for the percentage of fruit set on both periods. The best-fit models including these epistatic components are given in Table 4. Mean components of the generations for percentage of fruit set in optimal and summer-spring period differed in that dominance effects were more important than additive effects for optimal period while the opposite was observed for summer-spring period. It should be noted that an important part of the variation is heritable, since the additive component presented a high value. These results were similar to those obtained before (15,24).

Table 4. Estimates of the effect of genes (± ES), Chi-square tests in the best fit of the fixed effects model for the determinations of the fruit set percentage of the six generations of the Nagcarlang x AN-104-1 family

Components of the mean and scaling test ***mdh***	**Optimum period**	**Spring-summer period**
Parental mean value (m)	87.33 ±1.91***	73.56 ±2.18***
Additive effects [d]	15.76 ± 1.65***	12.72 ± 0.69***
Dominance effects [h]	18.45 ± 0.83***	10.61 ± 3.63***
Additive x additive effects (i)	-11.46 ± 3.80**	-
Additive x dominant effects [j]	-	-
Dominant x dominant effects [l]	-	17.23 ± 3.63*
X^2	1.21 (2g.l)	1.94 (2g l)
p	0.18ns	0.27ns

ns: non-significant differences for p≤0.01. *, **, *** Significant differences for p≤0.1, p≤0.05 or p≤0.01, respectively

Regarding epistatic effects, the additive x dominance interaction component was highly significant in optimal period, which explained the great similarity in optimal period of BC_1 generations to their respective recurrent parents. The best fitting model for percentage of fruit set in optimal peridos was *mdhl* model, while the other period was a better fit to the *mdhl* model. This last model explained the existence of an over dominance effect, since the values of [l] and [h] presented opposite signs and were greater than zero, showing heterosis in this character, as well as an important additive effect as reported by (3,12,24). Similar results were found for the heat tolerance source CL5915 (10).

In both cases, high values of the additive component were found, indicating that selection can be made for this trait. However, the presence of high dominance effect, as well as epistatic interactions in this period, suggest that part of the genotypic variation is heritable and part is not, as suggested by other authors (3,5,15). The selection for high temperature fruit set can be effective in the selection of heat-tolerant lines in breeding programs if the selection be based on in more advanced generations, when the lines are homozygous (3,5,15).

The wide and narrow heritability values of fruit set percentage are shown in Table 5. The heritability values in the broad sense were intermediate (0.58-0.64), while in the narrow sense lower heritability values were found, being these lower in the spring-summer period evaluated.

Table 5. Broad (H^2) and in the narrow sense (h^2) heritability of fruit set percentage in \`Nagcarlang\`/ \`AN-104-1´ tomato population

% Fruit set	**H^2**	**h^2**
Optimal season	0.64	0.52
Spring-summer season	0.58	0.39

The heritability results indicate that a high degree of homozygosity is needed to predict progress by selection in tomato crosses to obtain high temperature tolerant cultivars, so that selection will be effective if it is done in more advanced generations ($>F_5$) as suggested by other authors using other sources of heat tolerance in the crop [(10,11)].

The wide heritability values found indicate that the fruit set percentage has a high environmental influence, mainly in the spring-summer period. The lower values of narrow heritability obtained correspond to the results of the heritability study in which the presence of dominance and epistasis effects was detected, although the portion of phenotypic variance due to additive variance (0.52) in the optimum period is still appreciable and could be exploited in tomato breeding programs. The heritability results indicate that a high degree of homozygosity is needed to predict progress by selection through crosses to obtain heat tolerant varieties, so that selection will be effective if carried out in more advanced generations ($>F_5$).

Similar results were obtained by [(3,10)]. Several authors report that percentage of fruit set is one of the most used indicators to evaluate heat tolerance in tomato due to its relation with crop yield [(4,5, 21-23)].

CONCLUSIONS

- The fruit set percentage inheritance was explained by *mdhi* and *mdhl* models, in the optimal and spring-summer periods, respectively, with additive, dominant and epistatic gene effects important.
- The heritability, in the broad sense, for the percentage of fruit set was intermediate, indicating environmental influence for fruit set. In the narrow sense, lower values lower values were obtained, being lower for the spring-summer period, which is explained by the presence of dominant and epistatic effects.

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