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Route Analysis Through Filial Generations of Modern Varieties of Tomato (*Solanum lycopersicum* L.)

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ABSTRACT

Objective: To measure the efficiency of using advanced generations of some commercial tomato hybrids for small farmers and to identify the most important yield components associated with yield.

Design/Methodology/Approach: Seven saladette-type hybrids of indeterminate growth were evaluated, as well as their respective generations F_2s and F_3s under greenhouse conditions. The evaluation of the three generations was carried out during the 2013 agricultural cycle. Three harvests were made at 82, 94 and 136 days after transplanting. The experiment was a randomized complete block design, with 4 replications and 10 plants per replication.

Results: Results indicated that there were significant differences for a few traits in F_2 and F_3. Path analysis showed that the total number of fruits had the highest direct and indirect effects on yield through generations.

Limitations of the study/implications: The usefulness of advanced generations of tomato commercial hybrids would depend on the genetic background of the parental lines that take part in such as hybrids, as some hybrids would present high inbreeding depression depending on the genetic composition of their progenitors.

Findings/Conclusions: Advanced generations of 'LORETO', 'CUAUHTÉMOC' and 'ESPARTACO' could be used by the small growers since low values of inbreeding depression were observed in F_2 and F_3 families.

Keywords: Inbreeding depression, production costs, path analysis, tomato breeding, farmers.

INTRODUCTION

In 2019, the principal countries producing tomatoes (*Solanum lycopersicum* L.) were China (31.8%), India (10.4%), United States (7.4%), Turkey (7.8 %), Egypt (4.5 %), Italy (3.6%), Iran (3.6%), Spain (2.6%), Brazil (2.4%) and Mexico (2.3%). The first three establish the global tendency in pricing and consumption (FAO, 2019). In Mexico, production grew at an average annual rate of 4.8% between 2006 and 2016 through the implementation of new technologies in commercial production systems, from open

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field farming to production in high-tech greenhouses with automated systems for irrigation, nutrition, phytosanitary control, and use of varieties with higher yield and resistance to diseases (FIRA, 2017). The Service for Agrifood and Fisheries Information (SIAP) in Mexico, reported that annual tomato production in 2018 was 3 780 950 tons with a yield of 76.83 t ha^{-1} (SIAP, 2019). Although it generates many jobs and high income for Mexican society, few government institutions work toward varietal development, which makes producers dependent on private transnational corporations to obtain germplasm (Martínez-Vázquez *et al*. 2016).

The high price of seeds forces small growers to use F_2 seeds from commercial hybrids to reduce costs, assuming that the yield and quality of the fruit will not be significantly affected in the next generations. Sahagún and Rodríguez (2011) point out that farmers should not plant the F_1 progeny because high heterogeneity and inbreeding depression have been observed in subsequent generations. In this regard, Poehlman and Allen (2003) observed that in autogamous species, segregation in the F_2 generation causes a reduction in yield per plant due to a high degree of heterozygosity in the population. In contrast, there is evidence of transgressive segregation in tomato (De Vicente and Tanksley 1993; Poehlman and Allen 2003; Shivaprasad *et al*. 2012), generating plants with larger fruit than their parents (Rodríguez *et al*. 2005) due to the positive or negative complementation of additive alleles, epistatic interactions of unique parental attributes, unmasking of recessive alleles form a heterozygous parent or any combination of these mechanisms (De los Reyes, 2019).

Charlesworth and Charlesworth (1987) suggest that inbreeding depression from endogamy in self-pollinating species is relatively low, since recurrent recessive deleterious alleles are eliminated. In this regard, it has been observed that the correlation in yield between F_1 and subsequent generations (F_2 and F_3) has not been well studied, and thus the effectiveness of using subsequent generations has not been defined. Therefore, the objectives of this study were to measure the efficiency of the use of advanced populations of some commercial tomato (*Solanum lycopersicum* L.) hybrids, and to identify the yield components that are most important for determining yield for commercial producers who will use them as selection indices.

MATERIALS AND METHODS

The tomato (*Solanum lycopersicum* L.) varieties evaluated were 'MOCTEZUMA', 'CUAUHTÉMOC', 'ESPARTACO', 'CID', 'SUN7705', 'LORETO' and 'RESERVA', of the Roma type and of indeterminate growth; as well as their respective F_2s and F_3s generations, under greenhouse conditions during three experimental cycles in Texcoco, Estado de México, Mexico (19° 30' N and 98° 53' W, and 2250 m altitude).

The evaluation of the three generations took place in the growing cycle of 2013. The seven F_1 hybrids and their F_2s and F_3s generations were sowed on March 22 of 2013 and transplanted on April 23 of 2013, in polyethylene bags (40×40 cm) filled with red tezontle (red volcanic rock) as a substrate. There were three harvests, at 82, 94 and 136 days after transplanting. The research was conducted under a randomized complete block experimental design, with four replicates and 10 individuals per replicate. Fertilization was carried out with a Steiner nutrient solution (Steiner 1984), the concentrations were modified according to the phenological stages and four irrigations per day were used during the growth cycle.

The phenotypic analysis consisted in the study of seven quantitative variables: total number of fruit per plant (TNF), yield per plant (YL) and average fruit weight (AFW) expressed in g, fruit diameter (FD) and fruit length (FL) expressed in mm, number of trusses per plant (NT), number of fruit per truss (NFT).

Specifically, for the TNF and the YL the total number of mature fruits for the three harvests was counted and weighed. The values of the fruit variables such as AFW, FD and FL, were obtained from a sample of five fruits from each plant per replicate (n=5).

The statistical analysis consisted of univariate analysis using the PROC GLM instruction in the statistical software SAS V9 (SAS Institute, 2002). Afterward, a means comparison was performed via the Tukey test (p=0,05). The inbreeding depression (DEP, in %) in F_2, was estimated with respect to F1 using $DEP=(F_1-F_2)/F_1$, while in F_3 the DEP was calculated on the average difference between the F_1 and F_3 generations, using $DEP=(F_1-F_3)/F_1$. In both estimates the final results were multiplied by -1 to indicate a decrease in the magnitude of the evaluated variable. Finally, a route analysis was carried out considering the total population of each variety according to the procedure described by Mcgiffen *et al*. (1994).

RESULTS AND DISCUSSION

The contrast analysis of the F_1 hybrid and its advanced generations is shown in Table 1. The majority of the F_1 genotypes showed insignificant differences compared to their advanced generations, which indicates that yield was statistically similar in F_2 and F_3 to that observed in F_1. By contrast, 'CID' and 'MOCTEZUMA' had significant differences for most of the variables. Magaña *et al*. (2013) and Hernández-Leal *et al*. (2013) studied the effect of inbreeding depression on modern varieties of tomatoes and discovered that some exhibited an inbreeding depression significant for yield and other yield-related characteristics, while other tomato varieties did not express this. Based on the data obtained, a tendency was observed that suggests that the degree of inbreeding depends to a large extent on the genotype or the variety, the environment, and the interaction of genotype by environment.

The percentages of inbreeding depression through the generations and the results of Tukey's test are presented in Table 2. Regarding YL, in general the values of inbreeding depression were higher in the F_2 generation than in F_3, where 'CID' ($F_{1:2}$=−45.3% and $F_{1:3}$=−47.2%), 'MOCTEZUMA' ($F_{1:2}$=−23.3% and $F_{1:3}$=−32.6%) and 'RESERVA' ($F_{1:2}$=−40.2%) exhibited significantly higher values. In this regard, Márquez (1988) points out that these differences in inbreeding depression through the generations are due to the different degrees of segregation in F_2. For TNF, the inbreeding values oscillated between −42.4 and 21.0%, where 'SUN7705', 'MOCTEZUMA' and 'CID' had the highest inbreeding depression values of the seven varieties. In NT, significant inbreeding depression was found in 'SUN7705'$F_{1:2}$,' MOCTEZUMA'$F_{1:3}$, 'RESERVA'$F_{1:2}$ and 'CID'$F_{1:3}$, with values of −17.8, −24, −16.3 and −29.4%, respectively. Quintana *et al*. (2010) observed increases in yield when a greater number of trusses were present.

The results of this study presented a similar pattern between yield and number of trusses, due to the negative effect on yield when the number of trusses decreased in F_2 and F_3.

Regarding the variables related to fruit size (AFW, FL and FD), the genotypes "RESERVA" and "CID" exhibited a significant inbreeding depression in these three traits. This similarity in inbreeding depression is because of the strong association present between fruit weight and fruit length and diameter (De Souza *et al*., 2012). Consequently, the results suggest that producers could use advanced generations of the 'LORETO' variety. On the other hand, "CUAUHTÉMOC" and "ESPARTACO" had a slight reduction through their generations, which suggests that the F_2 and F_3 generations could also be grown by small-scale farmers for commercial use.

Table 1. Mean squares of the orthogonal contrasts between the F_1 *vs*. F_2 and F_1 *vs*. F_3 in seven tomato varieties.

Varieties	YL	TNF	NT	NFT	AFW	FL	FD
'Sun 7705' *vs*.Sun 7705-F_2	91621.96	63.845*	1.08*	1.45	38.63	0.1861	0.0098
'Sun 7705' *vs*. Sun 7705-F_3	482947.92	68.56*	0.1596	0.1922	71.28	0.021	0.0265
'Loreto' *vs*. Loreto-F_2	3319.5	3.86	0.2016	0.2346	19.47	0.1405	0.0145
'Loreto' *vs*. Loreto-F_3	1.94	12.05	0.7938	7.76	244.65	0.0703	0.3042*
'Moctezuma' *vs*. Moctezuma-F_2	554615.12*	89.38*	0.9316	0.845*	120.51	0.045	0.005
'Moctezuma' *vs*. Moctezuma-F_3	1083995.60*	172.42**	2.92**	1.17*	18.21	0.005	0.012
'Cuauhtémoc' *vs*. Cuauhtémoc-F_2	139780.35	1.02	0.0091	4.21	229.52	0.2346	0.0265
'Cuauhtémoc' *vs*. Cuauhtémoc-F_3	999.05	20.0	0.7503	3.6	6.14	0.208	0.0666
'Reserva' *vs*. Reserva-F_2	1087222.58*	25.92	0.98*	0.72	634.39*	0.1275	0.8978**
'Reserva' *vs*. Reserva-F_3	478491.42	0.3281	0.0145	0.0025	485.32*	0.0221	0.3741*
'Espartaco' *vs*. Espartaco-F_2	407014	25.21	0.7626	0.0276	3.14	0.3698	0.0253
'Espartaco' *vs*. Espartaco-F_3	59726.59	6.75	0.0545	2.46	250.88	0.8581	0.1953
'Cid' *vs*. Cid-F_2	4228028.44**	320.05**	3.46	0.8911	1994.59**	0.1922	0.845**
'Cid' *vs*. Cid-F_3	4597421.65**	403.28**	4.70**	2.9	966.90*	3.58**	1.58**
CV (%)	25.69	18.73	11.79	15.62	13.06	8.49	6.22

*, ** Significant at $p \leq 0.05$ and 0.01, respectively. TNF=total number of fruits per plant; YL=yield per plant; NT=number of trusses per plant; NFT=number of fruits per truss; AFW=average fruit weight; FL=length of fruit; FD=fruit diameter.

Table 2. Phenotypic means and percentage reduction exhibited among tomato varieties throughout their generations.

Varieties	YL (g)	R (%)	TNF	R (%)	NT	R (%)	NFT	R (%)	AFW (g)	R (%)	FL (cm)	R (%)	FD (cm)	R (%)
SUN 7705	1870.4 a		23.6 a		4.5 a		7.3 a		113.2 a		5.5 a		4.0 a	
SUN 7705-F_2	1656.3 a	−11.5	18.0 b	−23.7*	3.7 b	−17.8*	6.4 a	−12.3	117.6 a	3.9	5.8 a	5.5	4.0 a	0
SUN 7705-F_3	1379.0 a	−26.3	17.8 b	−24.6*	4.2 ab	−6.7	7.6 a	4.1	107.2 a	−5.3	5.6 a	1.8	3.8 a	−5
LORETO	1815.6 a		20.0 b		4.1 a		7.2 a		124.4 a		5.4 a		4.2 a	
LORETO-F_2	12774.8 a	−2.3	21.4 ab	7	4.4 a	7.3	7.5 a	4.2	121.3 a	−2.5	5.1 a	−5.6	4.1 a	−2.4
LORETO-F_3	1816.6 a	0.1	22.5 a	12.5	4.7 a	14.6	9.1 a	26.4	113.4 a	−8.8	5.6 a	3.7	3.8 b	−9.5*
MOCTEZUMA	2261.7 a		27.9 a		5.0 a		8.1 a		118.0 a		5.6 a		3.9 a	
MOCTEZUMA-F_2	1735.1 b	−23.3*	21.2 b	−24*	4.3 ab	−14	7.5 b	−7.4*	110.3 a	−6.5	5.7 a	1.8	3.9 a	0
MOCTEZUMA-F_3	1525.5 c	−32.6*	18.9 b	−32.3**	3.8 b	−24*	7.4 b	−8.6*	115.0 a	−2.5	5.5 a	−1.8	4.0 a	2.6
CUAUHTEMOC	1457.9 a		15.3 a		3.2 a		6.4 b		111.9 a		5.6 a		3.9 a	
CUAUHTEMOC-F_2	1193.5 a	−18.1	16.0 a	4.6	3.1 a	−3.1	7.9 a	23.4	101.2 a	−9.6	5.2 a	−7.1	3.8 a	−2.6
CUAUHTEMOC- F_3	1435.6 a	−1.5	18.5 a	21	3.8 a	18.8	7.8 a	21.9	110.1 a	−1.6	5.9 a	5.4	3.7 a	−5.1
RESERVA	1835.5 a		21.3 a		4.3 a		7.3 a		106.2 a		5.4 a		3.9 a	
RESERVA-F_2	1098.2 b	−40.2*	17.7 a	−17	3.6 b	−16.3*	7.9 a	8.2	88.4 b	−16.7*	5.6 a	3.7	3.3 b	−15.4*
RESERVA-F_3	1346.4 ab	−26.7	20.9 a	−1.9	4.2 a	−2.3	7.3 a	0	90.7 b	−14.6*	5.5 a	1.9	3.5 b	−10.3*
ESPARTACO	2095.1 a		23.4 a		4.2 a		7.6 a		116.1 a		5.9 ab		3.9 a	
ESPARTACO-F_2	1644.0 a	−21.5	19.9 a	−15	3.5 a	−16.7	7.8 a	2.6	114.9 a	−1	5.4 b	−8.5	4.0 a	2.6
ESPARTACO-F_3	1922.3 a	−8.3	21.6 a	−7.7	4.0 a	−4.8	8.7 a	14.5	127.3 a	9.7	6.5 a	10.2	4.2 a	7.7
CID	3210.1 a		33.5 a		5.1 a		9.3 a		143.3 a		6.0 b		4.5 a	
CID-F_2	1756.2 b	−45.3**	20.9 b	−37.7**	3.9 ab	−23.5	8.6 a	−7.5	111.7 b	−22.1**	5.7 b	−5	3.8 b	−15.6**
CID-F_3	1694 b	−47.2**	19.3 b	−42.4**	3.6 b	−29.4**	8.1 a	−12.9	121.3 b	−15.4*	7.3 a	21.7**	3.6 b	−20**
LSD	1011.3		9.55		1.24		2.97		32.24		1.18		0.5768	

In the column, the means with the same letter between treatments are statistically equal (α=0.05); *, ** significant at p≤0.05 and 0.01, respectively; LSD=least significant difference. TNF=total number of fruits per plant; YL=yield per plant; NT=number of trusses per plant; NFT=number of fruits per truss; AFW=average fruit weight; FL=length of fruit; FD=fruit diameter, R=percentages of inbreeding depression.

The route analysis allows breeders to dissect the correlation coefficients in direct and indirect effects, and thus avoid erroneous conclusions about the components that truly present a significant effect on the yield (Mcgiffen *et al.*, 1994). Table 3 shows that TNF had the greatest direct and indirect effects on the yield through the generations, with values between 0.78 and 0.81. Similar results were reported by Monamodi *et al.* (2013), who found that the number of fruits and the weight of a single fruit influenced the yield with direct effects of 0.752 and 0.446, respectively. Sharma and Verma (2000) reported that the total number of fruits per plant had the greatest direct effect on the yield. The above results indicate that the total number of fruits per plant is an important yield component, which is why this variable can be used as an indirect selection criterion suitable for identifying high yield specimens.

The route analysis of each genotype shows that TNF did not always exhibit the highest direct effect on yield, since AFW in "ESPARTACO", reached a high direct effect (0.66) on yield (Figure 1). In general, AFW was identified as an important trait that affects yield followed by the number of fruits per plant, with values that range from 0.22 to 0.35.

Diverse studies report similar values in terms of average weight per fruit, positively affecting yield in 0.46 and 0.96 (Mcgiffen *et al.*, 1994; Meena and Bahadur, 2015). Therefore these previous estimations are comparable to those obtained in the present study.

In NFT, the direct effects were not significant and had values lower than 0.03. These low direct effects found for NFT on yield in the combined analysis were also obtained in the single analysis within each genotype. The effect of NT on yield was negative in F_1 for almost all the genotypes except "CID" and "ESPARTACO". However, the magnitude of the direct effect exhibited by NT on yield was not constant throughout the generations, exhibiting a reduction in F_2 and an increase in F_3 for the 'CID' (0.27 and 0.36) and 'MOCTEZUMA' (0.03 and 0.10) varieties, while for F_2 and F_3 in the 'RESERVA' (0.43 and 0.33) and 'SUN 7705' (0.69 and 0.31) varieties, the observed effect was inverse to that found in the previous varieties. Previous studies suggest that the number of trusses per plant (NT) has a strong and positive effect on the yield (Supe *et al.*, 1992; Rani *et al.*, 2008). Such a result in the study can be explained by the indirect effect exhibited by the total number of fruits on the correlation coefficient formed by the number of trusses and the yield.

Table 3. Direct and indirect effects of the yield components obtained under the combined route analysis.

Variable *vs.* Yield	Generation	Direct effect	p	Indirect effect						r	P
				TNF	NT	NFT	AFW	FL	FD		
TNF	F_1	0.78	**	–	−0.11	0.01	0.21	0.02	0.00	0.90	**
	F_2	0.81	**	–	−0.02	0.00	0.08	0.00	0.03	0.90	**
	F_3	0.79	**	–	−0.05	−0.01	0.08	0.00	0.02	0.84	**
NT	F_1	−0.14	**	0.63	–	0.01	0.13	0.01	0.00	0.63	**
	F_2	−0.02	ns	0.62	–	0.00	0.05	0.00	0.03	0.67	**
	F_3	−0.07	ns	0.61	–	0.00	0.03	−0.01	0.02	0.58	**
NFT	F_1	0.02	ns	0.45	−0.06	–	0.15	0.01	0.00	0.57	**
	F_2	−0.01	ns	0.37	0.00	–	0.02	−0.01	0.01	0.38	**
	F_3	−0.02	ns	0.25	−0.01	–	0.07	0.00	0.01	0.30	**
AFW	F_1	0.35	**	0.46	−0.05	0.01	–	0.03	0.00	0.79	**
	F_2	0.22	**	0.29	−0.01	0.00	–	0.05	0.07	0.62	**
	F_3	0.34	**	0.19	−0.01	0.00	–	0.03	0.05	0.60	**
FL	F_1	0.04	ns	0.33	−0.03	0.01	0.26	–	0.00	0.60	**
	F_2	0.12	**	0.02	0.00	0.00	0.09	–	−0.01	0.21	**
	F_3	0.06	*	0.02	0.01	0.00	0.19	–	−0.01	0.27	**
FD	F_1	0.00	ns	0.41	−0.05	0.01	0.30	0.03	–	0.69	**
	F_2	0.10	ns	0.27	−0.01	0.00	0.15	−0.02	–	0.49	**
	F_3	0.07	*	0.23	−0.02	0.00	0.21	0.00	–	0.49	**

ns=not significant; *, ** significant at $p \leq 0.05$ and 0.01, respectively; p=significant; r=correlation coefficient; TNF=total number of fruits per plant; NT=number of trusses per plant; NFT=number of fruits per truss; AFW=average fruit weight; FL=length of fruit; FD=fruit diameter.

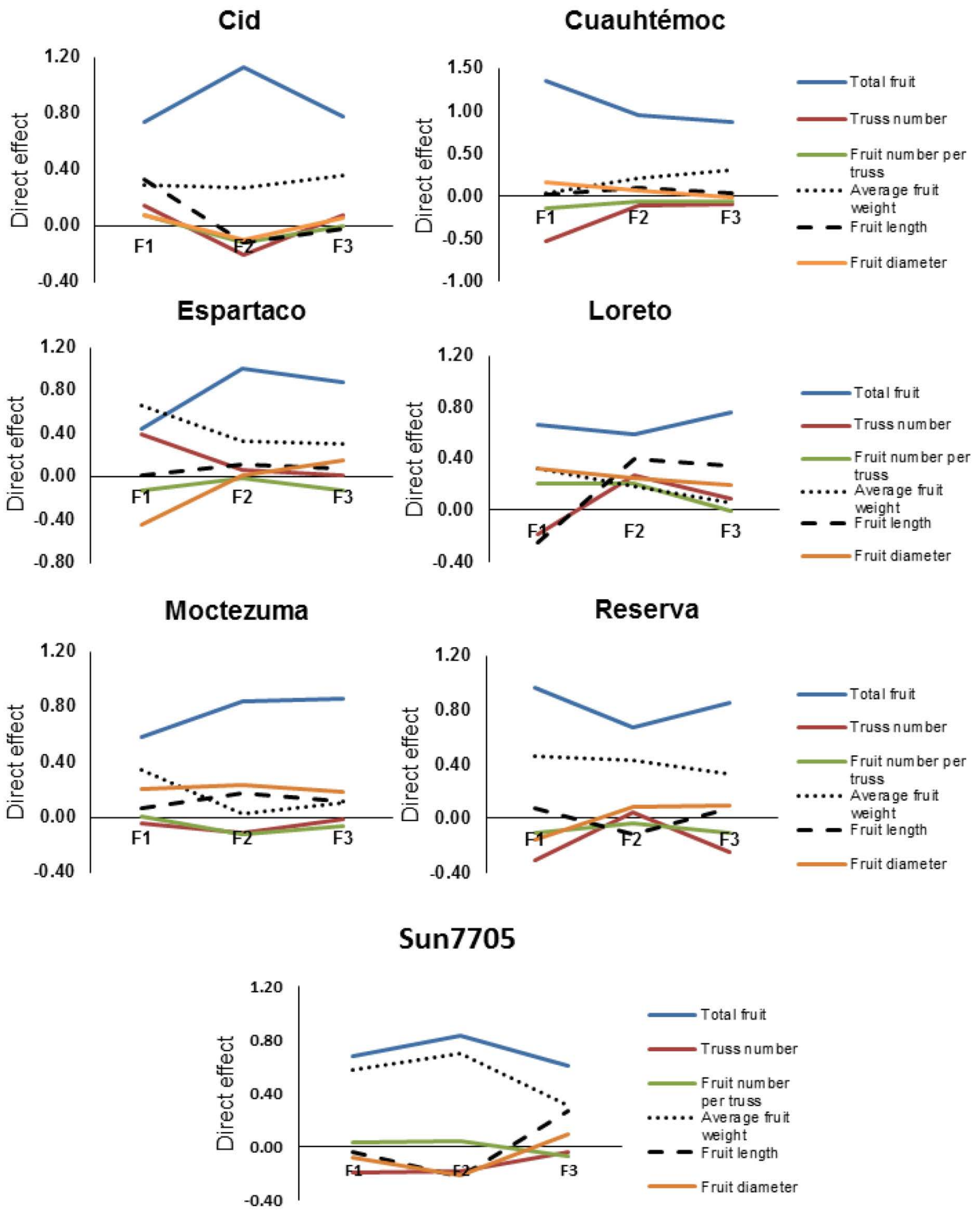

Figure 1. Direct effects of the six yield components evaluated in seven tomato genotypes.

The high direct and indirect effects of AFW and TNF across segregating generations found in most genotypes indicate that both traits can be used as a reliable indirect selection criterion to increase yield in populations consisting of 'CID', 'CUAUHTÉMOC', 'ESPARTACO', 'RESERVA' and 'SUN7705'.

CONCLUSIONS

Growers can use advanced generations of the 'LORETO' variety since the degree of segregation in F_2 and F_3 does not significantly differ from its parent. They can also use the 'CUAUHTÉMOC' and 'ESPARTACO' varieties because they presented low reduction in their productive behavior through their generations. Characteristics such as the total number of fruits and weight of fruit expressed higher direct effects on yield during the three generations, which indicates that these variables can be used as a reliable parameter for indirect selection to obtain high yield genotypes.

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