

Magnitude of Genotype × Environment Interactions Affecting Tomato Fruit Quality

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Abstract. There is a growing interest by consumers to purchase fresh tomatoes with improved quality traits including lycopene, total soluble solids (TSS), vitamin C, and total titratable acid (TTA) content. As a result, there are considerable efforts by tomato breeders to improve tomato for these traits. However, suitable varieties developed for one location may not perform the same in different locations. This causes a problem for plant breeders because it is too labor-intensive to develop varieties for each specific location. The objective of this study was to determine the extent of genotype × environment (G×E) interaction that influences tomato fruit quality. To achieve this objective, we grew a set of 42 diverse tomato genotypes with different fruit shapes in replicated trials in three locations: North Carolina, New York, and Ohio. Fruits were harvested at the red ripe stage and analyzed for lycopene, TSS, vitamin C, and TTA. Analysis of variance (ANOVA) revealed that there were significant differences ($P < 0.05$) among tomato genotypes, locations, and their interaction. Further analysis of quality traits from individual locations revealed that there was as much as 211% change in performance of some genotypes in a certain location compared with the average performance of a genotype. Lycopene was found to be most influenced by the environment, whereas TTA was the least influenced. This was in agreement with heritability estimates observed in the study for these quality traits, because heritability estimate for lycopene was 16%, whereas that for TTA was 87%. The extent of G×E interaction found for the fruit quality traits in the tomato varieties included in this study may be useful in identifying optimal locations for future field trials by tomato breeders aiming to improve tomato fruit quality.

The cultivated tomato (*Solanum lycopersicum* L.) is the second most commonly consumed vegetable crop after potato (*Solanum tuberosum* L.) in the world (FAOSTAT, 2008). In the United States, it is the most economically important vegetable crop with a total

farm value of \$2.36 billion (USDA-NASS, 2008) (http://www.nass.usda.gov/Data_and_Statistics/) and is fifth in crop value after maize, soybean, wheat, and cotton (FAOSTAT, 2008). There is a growing interest for improved tomato quality in the marketplace. Recently,

fruit quality has been the most important selection criterion for repeat buyers of tomato. Because of this, tomato breeders have placed significant efforts in improving tomato fruit quality traits, including lycopene content, TSS, vitamin C, and TTA content (Causse et al., 2002, 2007; Chaib et al., 2006). However, a tomato line with improved fruit quality in one location may not necessarily perform the same in another location; the phenomenon of performing differently by genotype in different locations results from G×E interactions. Environmental factors that may influence performance of a given genotype from location to location include soil, moisture, temperature, light intensity, humidity, rainfall, photoperiod, and cultural practices. These factors may play a role in gene regulation, which in turn can affect the expression of the genes controlling the trait of interest and ultimately result in different phenotypic expression among locations.

Greenhouse-grown round and cluster tomatoes were found to have higher lycopene content (30.3 mg·kg⁻¹) than field-grown tomatoes (25.2 mg·kg⁻¹) ranging from 5.7 to 47.8 and 4.3 to 31.5 mg·kg⁻¹, respectively, when 40 tomato varieties were evaluated (Kuti and Konuru, 2005). However, field-grown cherry tomatoes (91.9 mg·kg⁻¹) outperformed greenhouse-grown (56.1 mg·kg⁻¹) cherry tomatoes for lycopene showing a significant G×E interaction. Relatively less lycopene in greenhouse-grown cherry tomatoes was attributed to high temperature buildup in the greenhouse, which might have inhibited the lycopene biosynthesis. A significant G×E interaction was also found for lycopene and ascorbic acid content (vitamin C) when a diverse set of 14 varieties was evaluated in three environments (two field seasons and one greenhouse season) in Valencia, Spain (Rosello et al., 2011). A significant G×E interaction for total sugar was also found between field- and screenhouse-grown tomatoes when six varieties were evaluated (Cebolla-Cornejo et al., 2011). However, there was no G×E interaction for total organic acids, although a significant G×E for maleic acid was found. Although there was a significant G×E interaction for TTA, it was nonsignificant for TSS in yet another similar study (Causse et al., 2003). These studies indicated that there is a significant role of environment in determining the fruit quality of tomato.

In most cases, a significant G×E interaction is reported in quantitative traits. In tomato fruit, quality traits including lycopene, TSS, vitamin C, and TTA are quantitative traits (Causse et al., 2001, 2002; Fulton et al., 2002) that have continuous variation in segregating populations. The extent of G×E interactions for these traits is an important aspect that needs to be taken into account in breeding programs. This is because plant breeders need to develop the varieties that will perform consistently well across multiple environments. The objective of this study was to determine the extent of G×E interaction for tomato fruit quality including lycopene, TSS, vitamin C, and TTA content in three locations in the eastern United States.

Materials and Methods

Plant materials. A total of 42 diverse tomato varieties with different fruit shapes that were originally assembled by Dr. van der Knaap at Ohio State University (Rodriguez et al., 2011) were evaluated for fruit quality in three locations (North Carolina, New York, and Ohio) in 2010 with two replications per location. The tomato varieties have different origins and fruit shape characteristics, and they were obtained from a variety of sources. Details about each variety can be found at the Sol Genomics Network (<<http://solgenomics.net/>>) and at Rodriguez et al. (2011). The evaluation locations were Ohio Agriculture Research and Development Center, Wooster, OH, New York State Agricultural Experiment Station, Geneva, NY, and Mountain Horticultural Crops Research and Extension Center, Mills River, NC. All three locations are humid but temperature during the crop-growing season may vary. Soil types in North Carolina and Ohio were silty loam, whereas in New York, it was primarily Ontario loam. The experiment was laid out in a randomized complete block design and planted with two replications in the first week of June in each location. Fruits were harvested at the red ripe stage as described by the USDA (<<http://www.ams.usda.gov/AMSV1.0/getfile?dDocName=STELPRDC5050331>>) for further analysis.

Analysis of tomato fruits for quality traits. Pieces of eight to 10 freshly harvested, red ripe fruits per replicate were homogenized in a blender and aliquots of 50 mL were stored at -20 °C until assayed. Assays for vitamin C and lycopene were performed at the USDA-ARS Plant Genetic Resources Unit, Geneva, NY. Lycopene content was estimated using a Minolta Chroma Meter CR-300 (Konica Minolta Sensing Americas, Inc., Ramsey, NJ) (Hyman et al., 2004) using puree, and vitamin C was quantified using a Cosmo Bio Co. Ltd. (Tokyo, Japan) Vitamin C Assay kit (Prod. No. SML-ROIKO2-EX) as described previously (Labate et al., 2011). Although Hyman et al. (2004) used both whole fruits as well as puree to estimate the lycopene content, only puree was used to estimate the lycopene content in the present study. Assays for TSS and TTA were performed at the USDA-ARS Processed Foods Research Unit, Albany, CA. TSS was estimated with a refractometer. For

TTA assays, a fivefold dilution was made by adding 40 mL of water to 10 mL strained homogenate; this was then titrated with 0.1 N NaOH to pH 8.2 using a Metrohm 730 Sample Changer in conjunction with the 751GPD Titrino (Westbury, NY). Percent citric acid (the predominant acid) was estimated using the equation

$$\text{TA} \left(\frac{\text{g}}{100 \text{ ml}} \right) = \frac{(N) \times (V1) \times (\text{Eq wt}) \times 100}{V2 \times 1000}$$

where N equals the normality of NaOH (0.1), $V1$ is the volume of NaOH added to reach the titration point, Eq wt is the equivalent weight of citric acid (64 mg-mEq⁻¹), and $V2$ is the original volume of the sample (50 mL).

Data analysis. Data analysis was performed using SAS (Version 9.1.3) software (SAS Institute Inc., Cary, NC). Phenotypic data for the fruit quality traits were analyzed using PROC MIXED to determine differences among varieties. Location (L) was used as a random effect and genotypes (G) as a fixed effect in the model (SAS Institute Inc., 2007). The model used was:

$$Y = \mu + G + L + G \times L + \epsilon$$

Least square means (LSMeans) was determined and least significant difference (LSD) value was used to separate the LSMeans value for quality traits of the tomato varieties at the 0.05 P level. Pearson's correlation coefficients among quality traits were determined on a combined set of data as well as from each location using PROC CORR. Genetic correlations between fruit quality traits were determined on a combined set of data using the following formula (Falconer and Mackay, 1996; Kearsley and Pooni, 1996):

$$r_G = \frac{\text{Cov}_{xy}}{\sqrt{(\sigma_x^2 \sigma_y^2)}}$$

where r_G represents genetic correlation, x represents the first trait, y represents the second trait, and σ^2 is genetic variance. Cross products were generated using the multivariate ANOVA option of PROC GLM.

Broad-sense heritability (H) of the trait was estimated by the entry mean basis (Nyquist, 1991) as follows:

$$H = \frac{\sigma_g^2}{\sigma_g^2 + \left(\frac{\sigma_{ge}^2}{e} \right) + \left(\frac{\sigma_{re}^2}{r} \right)}$$

where H represents the heritability, σ_g^2 is genetic variance, σ_{ge}^2 is genotype-by-environment variance, σ^2 is error variance, r is number of

replications, and e is the number of environments. REML estimation in PROC MIXED produced variance components for heritability calculations. Data from three environments with two replications were used for the calculation of heritability.

Results

Analysis of variance of fruit quality traits.

There were significant differences ($P < 0.05$) among the genotypes for all four quality traits: lycopene, TSS, vitamin C, and TTA content in tomato fruits (Table 1). Over all locations, the average lycopene content ranged from 5.8 $\mu\text{g}\cdot\text{g}^{-1}$ to 27.7 $\mu\text{g}\cdot\text{g}^{-1}$ with an average of 15.6 $\mu\text{g}\cdot\text{g}^{-1}$ fruit weight (Table 2). On the basis of LSMeans for lycopene, the best performing genotypes were 'T1118' (27.7 $\mu\text{g}\cdot\text{g}^{-1}$) followed by PI 441739 (21.8 $\mu\text{g}\cdot\text{g}^{-1}$), and 'T749' (21.6 $\mu\text{g}\cdot\text{g}^{-1}$) (Table 1). As expected, the genotypes lacking the *phytoene synthase* gene ('Yellow Pear' and 'Yellow Plum') contained the least amount of lycopene. PI 441739 was one of the genotypes exhibiting the highest TSS together with 'Yellow Plum' (Table 2). The genotypes with lowest TSS were 'M82', 'T763', and 'Bellstar', among others. The best performing genotypes for vitamin C content included 'UPV24629', 'LYC 1922', 'Yellow Plum', and PI 441739. The genotypes with lowest vitamin C content were 'LYC2406', 'M82', and 'LYC1912'. The best performing genotypes for TTA content were 'UPV24629', PI 441739, and 'LYC 455', whereas the genotypes with the lowest TTA content were 'T749', 'Bellstar', and 'LYC1891' (Table 2).

There was also a significant difference ($P < 0.001$) among locations for all four fruit quality traits (Table 1). New York had the highest levels of lycopene, TSS, and TTA followed by Ohio and North Carolina, whereas Ohio had the highest level of vitamin C followed by New York and North Carolina (Table 2). In North Carolina, average lycopene content was 12.6 $\mu\text{g}\cdot\text{g}^{-1}$ ranging from 5.8 to 55.6 $\mu\text{g}\cdot\text{g}^{-1}$, whereas in New York, it was 5.8 to 54.0 with an average of 18.8 $\mu\text{g}\cdot\text{g}^{-1}$. In Ohio, average lycopene content was 15.4 $\mu\text{g}\cdot\text{g}^{-1}$ ranging from 5.8 to 45.6 $\mu\text{g}\cdot\text{g}^{-1}$ (Table 2). Average TSS in the present collection of tomato varieties was 4.2% with a range from 2.0% to 8.7% (Table 2). Average TSS in North Carolina was 3.7% with a range from 2.0% to 5.1%, whereas it was 4.7% with a range from 2.5% to 8.7% in New York. Average TSS in Ohio was 4.3 with a range from 2.7% to 5.9% (Table 2). Overall average vitamin C content was 70.3 $\mu\text{L}\cdot\text{mL}^{-1}$ with a range from 10.9 to 160.1 $\mu\text{L}\cdot\text{mL}^{-1}$ (Table 2).

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Table 1. Analysis of variance for fruit quality traits in a fruit shape diversity panel of tomato indicates that genotype-by-location interactions are significant for a subset of genotypes.

Effect	Numerator df	Denominator df	Lycopene	Total soluble solid	Vitamin C	Total titratable acid
Genotype	41	126	1.65*	8.4***	4.84***	14.88***
Location	2	126	11.8***	95.8***	160.63***	44.01***
Genotype*location	82	126	1.39*	2.35***	1.22 NS	1.94***

Note: *, **, and *** indicate significant F-values at $P \leq 0.05$, 0.01 and 0.001, respectively. NS = nonsignificant; df = degrees of freedom.

Table 2. Average (least square means) fruit quality traits in a fruit shape diversity panel of tomato in each of three locations.

Genotype	ID no. ^z	Lycopene				TSS (%)				Vitamin C				TTA (%)			
		North		New		North		New		North		New		North		New	
		Carolina	York	Ohio	Carolina	Ohio	York	Ohio	Carolina	Ohio	York	Ohio	Carolina	Ohio	York	Ohio	Carolina
Bellstar	G 33046	14.3	11.7	20.9	10.2	10.2	11.7	20.9	2.9	3.0	38.5	79.1	38.5	65.5	79.1	65.5	0.23
Cuor di Buei	G 33040	12.3	10.3	14.6	11.9	11.9	10.3	14.6	3.3	4.5	40.9	104.2	40.9	97.1	104.2	97.1	0.32
Determinato Tondino	G 33048	15.7	25.2	12.5	9.3	9.3	25.2	12.5	3.9	4.3	68.1	94.3	68.1	95.3	94.3	95.3	0.33
German Red Strawberry	G 33051	16.0	20.5	11.8	15.8	15.8	20.5	11.8	3.6	4.8	34.6	69.7	34.6	59.0	69.7	59.0	0.35
Grushovka	G 33052	16.4	23.9	11.3	14.1	14.1	23.9	11.3	4.2	3.7	37.4	70.7	37.4	68.7	70.7	68.7	0.31
Guajito	PI 636205	17.4	12.1	11.9	28.1	28.1	12.1	11.9	3.4	4.5	34.1	99.4	34.1	60.3	99.4	60.3	0.45
Howard German	G 33038	19.5	10.0	34.1	14.5	14.5	10.0	34.1	4.3	5.1	29.4	54.5	29.4	70.2	54.5	70.2	0.31
LYC1743	G 33055	18.7	9.1	35.5	11.4	11.4	9.1	35.5	3.1	3.0	52.5	100.8	52.5	107.2	100.8	107.2	0.30
LYC1891	NSL 321411	15.4	11.0	18.4	16.6	16.6	11.0	18.4	3.2	3.6	40.9	62.7	40.9	66.0	62.7	66.0	0.28
LYC1892	G 33053	16.2	16.2	21.6	10.7	10.7	16.2	21.6	3.6	4.8	43.2	103.4	43.2	99.1	103.4	99.1	0.41
LYC1899	PI 647533	13.4	12.0	17.0	11.1	11.1	12.0	17.0	3.6	3.5	49.6	60.9	49.6	90.3	60.9	90.3	0.31
LYC1912	PI 438877	14.9	14.1	14.7	15.9	15.9	14.1	14.7	4.7	4.1	41.2	46.8	41.2	63.2	46.8	63.2	0.30
LYC1918	PI 303810	13.5	7.7	21.8	11.1	11.1	7.7	21.8	2.7	3.6	29.8	60.4	29.8	74.7	60.4	74.7	0.30
LYC1922	G 33058	17.2	8.9	36.2	6.3	6.3	8.9	36.2	3.9	4.5	45.2	95.2	45.2	155.6	95.2	155.6	0.42
LYC2406	G 33059	12.4	8.6	14.6	14.0	14.0	8.6	14.6	3.6	3.7	31.9	53.2	31.9	52.1	53.2	52.1	0.27
LYC438	G 33060	10.3	7.3	9.9	13.6	13.6	7.3	9.9	3.9	4.8	55.3	83.2	55.3	120.2	83.2	120.2	0.36
LYC449	PI 636277	12.6	7.4	14.5	15.8	15.8	7.4	14.5	4.1	4.5	26.9	62.0	26.9	62.4	62.0	62.4	0.37
LYC455	G 33062	13.5	10.4	10.9	19.2	19.2	10.4	10.9	3.9	5.0	34.0	64.8	34.0	74.6	64.8	74.6	0.45
M82	G 33067	19.8	19.6	23.7	16.1	16.1	19.6	23.7	3.1	2.9	40.4	47.4	40.4	60.4	47.4	60.4	0.31
Orange Strawberry	G 33054	6.2	6.6	5.8	6.1	6.1	6.6	5.8	4.3	4.8	50.5	102.3	50.5	107.9	102.3	107.9	0.29
PI441739	PI441739	21.8	14.8	28.1	22.6	22.6	14.8	28.1	4.1	5.6	44.6	111.2	44.6	120.4	111.2	120.4	0.47
Sausage	G 33056	19.1	8.7	24.1	24.5	24.5	8.7	24.1	3.3	5.0	36.2	60.2	36.2	59.2	60.2	59.2	0.27
Spitz	G 33063	16.3	7.7	22.3	18.9	18.9	7.7	22.3	3.1	5.3	35.7	65.1	35.7	96.4	65.1	96.4	0.28
T1003	G 33041	12.8	8.6	14.6	15.2	15.2	8.6	14.6	4.4	4.4	67.7	65.8	67.7	88.3	65.8	88.3	0.38
T1118	G 33064	27.7	17.0	48.3	17.6	17.6	17.0	48.3	3.7	5.0	31.9	79.8	31.9	119.0	79.8	119.0	0.30
T1121	G 33065	15.6	7.0	16.6	23.3	23.3	7.0	16.6	3.4	5.1	40.8	72.4	40.8	112.1	72.4	112.1	0.30
T1355	G 33066	16.9	9.1	20.0	21.5	21.5	9.1	20.0	3.2	4.1	40.5	67.4	40.5	118.8	67.4	118.8	0.33
T39	G 33049	12.8	8.0	20.4	10.0	10.0	8.0	20.4	3.5	4.2	38.4	76.5	38.4	85.6	76.5	85.6	0.34
T533	G 33075	20.7	15.3	17.8	28.9	28.9	15.3	17.8	3.2	4.0	48.7	69.5	48.7	65.7	69.5	65.7	0.31
T749	G 33069	21.6	22.7	11.1	31.0	31.0	22.7	11.1	3.4	4.4	21.4	63.4	21.4	77.8	63.4	77.8	0.24
T750	G 33070	18.6	13.4	21.0	21.3	21.3	13.4	21.0	3.7	4.8	47.2	67.7	47.2	76.7	67.7	76.7	0.34
T763	G 33071	15.6	15.8	17.3	13.7	13.7	15.8	17.3	2.4	2.8	23.5	66.2	23.5	90.5	66.2	90.5	0.28
T764	G 33072	19.4	24.1	26.0	8.1	8.1	24.1	26.0	3.6	4.1	45.6	85.6	45.6	90.4	85.6	90.4	0.36
T848	G 33073	14.8	7.6	23.0	13.8	13.8	7.6	23.0	4.2	4.5	41.1	84.1	41.1	111.1	84.1	111.1	0.40
T864	G 33074	15.5	9.6	21.8	15.1	15.1	9.6	21.8	3.4	4.4	45.2	85.9	45.2	109.2	85.9	109.2	0.30
T932	G 33061	17.2	13.8	24.5	13.1	13.1	13.8	24.5	4.4	5.3	39.7	72.2	39.7	72.9	72.2	72.9	0.31
T954	G 33076	17.2	12.2	17.9	21.5	21.5	12.2	17.9	3.8	4.3	39.2	85.9	39.2	77.6	85.9	77.6	0.28
TresCantos	PI 339938	16.1	11.0	16.0	21.4	21.4	11.0	16.0	3.9	4.5	48.0	64.0	48.0	114.0	64.0	114.0	0.35
UPV24514	G 33077	19.4	31.4	14.9	11.9	11.9	31.4	14.9	4.1	5.0	45.3	82.0	45.3	96.7	82.0	96.7	0.37
UPV24629	G 33078	8.9	7.9	10.1	8.7	8.7	7.9	10.1	4.3	5.4	86.9	151.8	86.9	128.0	151.8	128.0	0.57
Yellow Pear	G 33017	5.8	5.8	5.8	5.8	5.8	5.8	5.8	3.5	4.9	55.9	90.1	55.9	94.3	90.1	94.3	0.30
Yellow Plum	PI 303811	5.8	5.8	5.8	5.8	5.8	5.8	5.8	4.2	7.3	53.5	91.7	53.5	132.1	91.7	132.1	0.40
LSN(0.05)		9.5	16.5	16.5	16.5	16.5	16.5	16.5	1.0	1.0	35.5	35.5	35.5	35.5	35.5	35.5	0.09

^zID number is assigned by USDA-ARS, Plant Genetic Resources Unit, Geneva, NY.^yAverage of three locations.^xLycopene expressed in mg·kg⁻¹.^wTotal soluble solids (TSS) (%).^vVitamin C (μL·mL⁻¹).^uTotal titratable acid (TTA) content (%).

LSD = least significant difference.

In North Carolina, average vitamin C content was $42.9 \mu\text{L}\cdot\text{mL}^{-1}$ with a range from 10.9 to $91.3 \mu\text{L}\cdot\text{mL}^{-1}$, whereas in New York, it was 77.9 with a range from 38 to $155.9 \mu\text{L}\cdot\text{mL}^{-1}$. In Ohio, average vitamin C content was 90.2 ranging from 37.9 to $160.1 \mu\text{L}\cdot\text{mL}^{-1}$ (Table 2). Overall average TTA content was 0.36% ranging from 0.15% to 0.84%. In North Carolina, average TTA was 0.34% ranging from 0.20% to 0.58%, whereas it was 0.40% ranging from 0.15% to 0.84% in New York. In Ohio, average TTA was 0.35% ranging from 0.22% to 0.69% (Table 2).

There was a significant ($P < 0.05$) G×E interaction for all traits but vitamin C (Table 1) indicating that some of the genotypes performed better than others in certain location. Furthermore, there was not a clear pattern of performance of genotypes over locations (Table 2), supporting the significant G×E interactions found in ANOVA (Table 1).

Because there was a significant G×E interaction found for all traits except vitamin C in the present study, we were interested to determine the level of interactions and report it in terms of percentage change with respect to average performance of each genotype. Average performance of each genotype was determined using observations from all three locations with two replications. Any genotype from each location with a value of less than 100% indicates poor performance, whereas a value of greater than 100% indicates better performance than average of a genotype. Based on the complete information on such location-specific changes in performance, there was as high as 211.3% and as low as 36.7% change in performance across the locations of some of the genotypes (Table 2). For example, 'LYC1922' performed extremely well in New York for lycopene content producing 211.3% more lycopene relative to its overall average across the locations. The same variety performed extremely poor in Ohio producing only 36.7% of its overall average. This indicated that 'LYC1922' was very unstable or a highly environment-sensitive variety for lycopene production. Other environment-sensitive varieties for lycopene included 'LYC1743', 'Howard German', 'T1118', and 'LYC1918' among others. All of these varieties performed very well for lycopene production in New York, whereas performed poor in Ohio. On the other hand, the least sensitive varieties to the growing environment were 'Yellow Plum' and 'Yellow Pear', among others for lycopene production, which performed almost equally across the location (Table 2). For TSS production, 'LYC1743', 'Yellow Plum', 'T763', 'Spitz', 'T1355', PI441739, 'German Red Strawberry', 'T848', 'Guajito', and 'Sausage' were the most environment-sensitive varieties producing up to 145% more than average TSS in New York. Similar to lycopene, the best performing and environment-sensitive varieties were grown in New York, whereas poor performing were in Ohio. 'LYC449', 'LYC2406', 'Determinato Tondino', and 'T954' were the most stable varieties producing almost average levels of TSS across the locations (Table 2).

Most of the varieties grown in Ohio produced a higher level of vitamin C and those in North Carolina produced less consistently as evident by nonsignificant G×E interaction. 'LYC1743', 'T1355', 'T763', 'Grushovka', 'T864', PI441739, 'Bellstar', 'German Red Strawberry', and 'LYC449' were the most environment-sensitive varieties. 'Bellstar' and 'Grushovka' produced the highest level of TTA in Ohio, whereas others were better in New York. The most stable varieties for TTA production across the locations were 'LYC1899', 'Tres Cantos', 'LYC1891', 'M82', and 'Guajito' (Table 2).

Trait-wise, the most environment-sensitive trait was lycopene content, which was changed by 134% ranging from 117% to 160% on average, whereas the least affected trait was TTA, which changed only by 45% across locations on average. TSS was changed by 47% and vitamin C was changed by 61% on average (Table 2).

Heritability estimates. Broad-sense heritability estimates on an entry-mean basis indicated that lycopene had a relatively low heritability (15.8%), whereas other traits had relatively high heritabilities (72.1% to 87%) (Table 1). Low heritability of lycopene indicated that lycopene content was largely influenced by the environment, which is consistent with significant G×E interaction results. Similarly, TTA had a high heritability of 87% indicating that this trait was least affected by the growing environment. This was also in agreement with percentage change in the value across locations because it was the trait least affected by the environment (Table 2).

Correlation analysis. Pearson's correlation coefficient analysis among the quality traits was performed to see if the traits were consistently related across the locations and in a combined set of data. Lycopene was positively correlated with TSS but there was no correlation with vitamin C and TTA in a combined set of data. A significant negative genetic correlation was found between lycopene and TSS and vitamin C and TTA. Contrary to this, significant phenotypic and genetic correlations among TSS, vitamin C, and TTA were found in a combined set of data. However, no correlations of lycopene were found across the locations with any other traits when analyzed separate from each location (Table 3), indicating that we need to assess the genotypes for lycopene independently. However, other traits including TSS, vitamin C, and TTA were positively correlated to each other, indicating that measurement of one trait may provide information on others to some extent. Although positive in all cases, the correlations were not strong. It should also be noted that the correlations were consistent across the locations (Table 3). Among the three locations, New York had the strongest correlation coefficients compared with other locations for quality traits, whereas Ohio had the weakest.

Discussion

There was a significant G×E interaction for all traits except vitamin C in the present

study, which is not surprising. There are a number of past studies that demonstrated significant G×E interactions of quantitative traits, particularly when the field trials were grown over diverse environments (Acuna et al., 2008; Shi et al., 2000; Taghouti et al., 2010). In the present study, not only were the traits quantitative (Carli et al., 2011; Fulton et al., 2002; Lecomte et al., 2004), but also the locations were extremely diverse. For example, the summer was unseasonably cool and wet in Geneva, NY, leading to delayed fruit maturity, whereas in Mills River, NC, the growing conditions were typical, which is warmer than New York. This might be attributed to have less lycopene from North Carolina because high temperature has been attributed to have reduced lycopene (Kuti and Konuru, 2005; Rosello et al., 2011). Weather-related information of all three locations can be found online (<<http://nc-climate.ncsu.edu/cronos?station=FLET&temporal=daily>>; <<http://www.oardc.ohio-state.edu/newweather/dailyinfo.asp?id=1>>; <<http://www.nysaes.cals.cornell.edu/weather/reports/>>).

Like in the present study, a significant G×E interaction for lycopene, TSS, and TTA has been reported (Causse et al., 2003; Cebolla-Cornejo et al., 2011; Kuti and Konuru, 2005). The variation for TSS and lycopene under controlled conditions was attributed to temperature and light intensity (Cebolla-Cornejo et al., 2011). They believe that there is more variation for temperature in the protected cultivation of tomato as a result of reduced air flow, which is not the case in field conditions. However, contrary to the present findings, a nonsignificant G×E interaction for vitamin C (Rosello et al., 2011) and TSS (Causse et al., 2003) has also been reported.

Significant genotypic differences for lycopene, TSS, vitamin C, and TTA indicated that some of the genotypes could be used as parents to improve the quality traits. Comparing the fruit quality trait profile in the present study with similar past studies, some of the lines in our panel were found to be better for lycopene (Cox et al., 2003), whereas in others, it was otherwise (Martinez-Valverde et al., 2002; Rosello et al., 2011). Finding a wide variation for any trait is expected if large numbers of genotypes are evaluated in the study.

The main objective of the present study was to determine the extent of variation on fruit quality including lycopene, TSS, vitamin C, and TTA in tomato varieties resulting from a G×E interaction. We observed as high as 211% change in the performance of some of the varieties as a result of location in tomato. A positive change with this magnitude may be useful for tomato breeders aiming to develop niche-specific varieties with improved fruit quality. In fact, the nature of horticultural crops is niche-specific (Palada et al., 2008), and there is much variation in crop types among agroecological niches.

Broad-sense heritability estimates provides an indication about a trait and its interaction with growing environment (Kearsey and Pooni, 1996). In the present study, other

Table 3. Pearson's correlation coefficients among fruit quality traits of tomato in combined and each location.²

Trait	Combined				North Carolina			New York			Ohio		
	Lycopene	TSS	Vitamin C	TTA	TSS	Vitamin C	TTA	TSS	Vitamin C	TTA	TSS	Vitamin C	TTA
Lycopene		0.18***	0.04 NS	-0.001	0.09 NS	-0.06	-0.01	0.10	-0.07	-0.07	0.00	-0.15	-0.17
Total soluble solids	-0.71***		0.45***	0.54***		0.30**	0.47***		0.37***	0.55***		0.25*	0.38***
Vitamin C	-0.73***	0.53***		0.33***			0.29**			0.46***			0.23*
Total titratable acid	-0.51***	0.53***	0.84***										

²Data below diagonal in combined set of data are the genetic correlations among fruit quality traits.

Note: *, ** and *** indicate significant correlation coefficient at 0.05, 0.01, and 0.001 *P* levels, respectively. NS = nonsignificant.

TSS = total soluble solid; TTA = total titratable acid.

than lycopene, heritability estimates were high for tomato fruit quality traits. Based on heritability and G×E interaction, lycopene was the most environment-sensitive trait, whereas TTA content was the least sensitive. The greater the level of environmental sensitivity, the less likely it will be to control and predict the variability based on genetic information alone. The corollary to this observation is that changes made to traits that are less sensitive to environmental changes (e.g., TTA content) will have a much greater probability of persisting even when the variety is grown in a different location. However, lycopene content will not be consistent across diverse locations. Contrary to the present findings, heritability for lycopene has been reported as high as 78.1% (Prema et al., 2011). However, heritability for TSS (77.9%), vitamin C (74.7%), and TTA (79.4%) were close to what we found in the present study (Prema et al., 2011). High heritabilities for lycopene (92%) and vitamin C (94%) have also been reported in yet another study (Dar and Sharma, 2011).

Consistent correlations were found between the quality traits across the locations. However, magnitudes of correlation coefficients differed. This was not unexpected because there was a significant G×E interaction for all quality traits except vitamin C in the present study. Similar to the present findings, lycopene was not correlated with TTA and vitamin C but there was a positive correlation between TTA and TSS (Saliba-Colombani et al., 2001). In this study, they did not find any correlation between lycopene and TSS, which contradicts the present findings. However, a positive correlation between TSS and lycopene has been reported in another study (Chen et al., 1999). In agreement with the present findings, there was no phenotypic correlation between lycopene and vitamin C, whereas the genetic correlation was negative ($r_G = -0.14$) (Adalid et al., 2008; Rosello et al., 2011; Rousseaux et al., 2005). Whereas there was a positive phenotypic correlation between lycopene and TSS, the genetic correlation was negative. It indicated that there was an influence of environment on determining the lycopene. This was in agreement with low heritability and a significant G×E interaction.

Marker-assisted selection (MAS) is the ultimate goal of our research, which will entail the use of genomics resources in our tomato improvement program. The ongoing Solanaceae Coordinated Agricultural Project (SolCAP) is developing ~8000 single nucle-

otide polymorphism molecular markers from the whole genome of tomato (<<http://solcap.msu.edu/>>). This will be an extremely valuable resource with which to identify molecular markers significantly associated with candidate genes, which will eventually be used in MAS. A study of genetic regulation of G×E interaction will explore the long-known phenomenon of G×E interaction at the molecular level. Available genomics resources such as the Solanaceae Genomics Network (<<http://solgenomics.net/>>), SolCAP (<<http://solcap.msu.edu/>>), and other genomics resources will be crucial to these investigations.

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