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POSTER PAPER

Effect of Recent Genetic Improvement on Some Analytical Parameters of Tomato Fruit Quality

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Abstract: Poor flavor in tomato fruit is a serious consumer concern. It could be said that tomato flavor has declined as variety selection and tomato production has placed emphasis on yield, fruit size, firmness, disease resistance, and processing performance and not on aspects of organoleptic fruit quality. Consumers frequently associate recent varieties with a lack of flavor, although such an association has not been proven. We have reviewed the scarce available literature on the influence of recent genetic improvement on quality attributes of tomato. As a case study, we have analyzed several parameters related to fruit quality in some traditional Spanish cultivars and commercial F1 hybrids of tomato. Organic acids and sugars were determined by high performance liquid chromatography (HPLC). Sodium (Na),

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potassium (P), and phosphorus (K) were analyzed by atomic absorption spectroscopy. Levels of respiration and ethylene production were measured, and fruit firmness was determined using a texture analyzer. All determinations were performed at two maturity stages, representing two frequent consumption stages. Differences between traditional cultivars and hybrids were found for respiration rates, ethylene production, P and K fruit contents. We also found important differences between "old" and "modern" cultivars for their organic acids profile. All cultivars showed similar levels of malic and succinic acids, but the modern hybrids showed a ~75% higher content of citric acid. This could be due to the F1 hybrids carrying chromosomal segments recently introgressed from wild *Lycopersicon* species. The influence of recent genetic improvement on quality attributes of tomato fruit is discussed.

Keywords: Analytical parameters, improvement, quality, tomato

INTRODUCTION

Tomatoes are one of the most popular items of fresh produce in supermarkets. The major complaint by consumers regarding fresh tomatoes is the lack of characteristic taste and flavor (Tandon et al. 2003; Causse et al. 2003). It could be said that tomato flavor has declined as variety selection and tomato production has placed emphasis on yield, fruit size, firmness, disease resistance, and processing performance and not on aspects of organoleptic fruit quality. Consumers frequently associate recent varieties with a lack of flavor, although such an association has not been proven.

Tomato Breeding and Quality

It is difficult to measure the contribution of plant breeding to the improvement of crop production. The most direct estimate of breeding progress is provided by the evaluation of cultivars from different eras, in common environments. However, this estimate is confounded by co-adaptation of new varieties with changing management practices. Reliable estimates have also been derived using data obtained from long-term annual records of cultivar performance relative to a check cultivar under the assumption that genotype × environment interaction involving the checks and other cultivars does not play a major role (Grandillo, Zamir, and Tanksley 1999).

Tomato breeding has played a major role in developing varieties adapted to the new agricultural and processing technologies. In tomato, to date more than 25 major genes for disease resistance have been reported, and many recently developed cultivars now possess multiple disease-resistance attributes. For example, as early as 1953, breeders at the University of Florida had accomplished the combination of more than five disease resistances in the cultivar Manalucie (Scott 1998). In the breeding programs, exotic germplasm has been almost exclusively used as the source for disease- and

insect-resistance genes. The use of such unadapted material (wild tomato species) to improve a cultivar can be difficult because of linkage drag, the transfer of linked, undesirable loci with the gene(s) of interest. For example, most modern cultivars possess nematode resistance conferred by the Mi-1 gene. The Mi-1 is contained within a large introgressed chromosomal segment from the wild species *L. peruvianum*, a species with small ($\sim$1 cm) and inedible green fruits. The amount of introgressed DNA varies among cultivars and lines, with the line Motelle generally thought to have the smallest introgressed region, a 650-kb segment (Seah et al. 2004). Tanksley et al. (1998) identified some negative effects (e.g., softer fruit, lower pH, larger stem scar) associated with the gene $Tm2^a$ (resistance to ToMV) when introgressed from the wild species *L. peruvianum* into a cultivated tomato.

Linkage drag can be especially problematic when genes from multiple sources are pyramided into an elite line. When too much unadapted DNA is introgressed into a cultivar, important agronomic traits can degrade to unacceptable levels. Modern hybrid cultivars of tomato have several introgressed DNA segments from different wild species. This could partially explain why today the quality of modern cultivars is criticized. The advent of molecular mapping techniques can significantly reduce the amount of wild germplasm introduced into a line (Frary et al. 2003).

Quality Characteristics Present in the Wild Tomato Species

However, valuable quantitative trait loci (QTL) alleles from wild species have been detected, which can now be systematically and efficiently introgressed in elite germplasm with marker-assisted selection for the development of future improved varieties. In independent studies utilizing different wild donor species, a variety of beneficial QTLs affecting fructose to glucose ratio (Levin et al. 2000), fruit color, soluble solids content (Bernacchi et al. 1998; Fulton et al. 2002), epidermal reticulation, fruit shape (Monforte et al. 2001), and acid content (Yates et al. 2004) have been identified. For example, lines with introgressions from the wild species *L. hirsutum* produced fruit significantly reduced in weight but with increased brix values, higher total sugars, more acids, greater viscosity, a significantly smaller stem scar, firmer fruit, and better external color. Similarly, lines with introgressions from *L. peruvianum* showed increased acid content, lower fruit weight, less puffiness, a thinner pericarp, more lycopene content, and a significant increase in soluble solids (Yates et al. 2004). Another example is TA1150, a tomato nearly isogenic line (NIL) that contains a chromosome 1 introgression (56 cM) from the wild species *L. chmielewskii* in the *L. esculentum* cv. E6203 background. This introgression has been reported to cause a significant increase in soluble-solids content, which is of paramount importance for processing tomatoes. In addition to high brix, TA1150 has orange fruit that are slightly pear shaped, firmer, and have a thicker pericarp and smaller stem scar than E6203. However, for effective

use in processing tomato improvement, the favorable traits contained within the introgression (high solids, firmness, thick pericarp, and small stem scar) must be uncoupled from orange fruit color (Frary et al. 2003).

"Old" and "Modern" Tomato Cultivars

The tomato was probably domesticated in Mexico; its transfer of varieties to Europe was made by early Spanish explorers. Spain and Italy were the first European countries where the tomato gained commercial importance. After its introduction, a wide array of local cultivars were developed, organoleptic quality being one of the main criteria of selection. Tomato is the main vegetable crop in Spain. Although production is almost exclusively based on modern hybrid varieties, there are still several traditional tomato landraces that are renowned for high quality. These landraces have no genes recently introgressed from wild species.

The objectives of this study were to review available literature on the influence of recent genetic improvement on quality attributes of tomato and to compare as a case study the quality characteristics of several traditional landraces with those of modern elite lines of tomato.

Quality in tomato is a difficult issue. Despite advances in tomato flavor analysis, breeders and molecular biologists still lack a clear genetic target for selection and manipulation of tomato quality (Tandon et al. 2003). Considerable progress has been made in the identification of important components in tomato and the determination of their concentration in fresh fruit, but sensory studies have still not clearly established the importance of analytical parameters in tomato quality. We know that sugars and total acid content are key components of flavor (Fulton et al. 2002), but even for sugar and acids, additional information is still required regarding the optimal ranges and ratios required for good flavor (Causse et al. 2003). Some studies point to total sugar and acid content as critical to fresh tomato flavor, whereas others emphasize the importance of a balance of soluble solids and titratable acidity. One study suggests that consumer acceptability increases with increasing sugar concentration but that there is an optimal level of acidity (Tandon et al. 2003).

MATERIALS AND METHODS

Plant Material and Experiment Design

As a case study, we have compared two modern elite lines of tomato (commercial F1 hybrids Bond and Ulises) with six traditional cultivars: three varieties of the "Muchamiel" type (Much4, Much18, Much30) and three varieties of the "De la Pera" type (Pera5, Pera16, Pera25). The two

modern hybrid cultivars carried at least seven genes for disease resistances, most of them coming from several wild species of *Lycopersicon*, whereas the "old" traditional cultivars carried not a single resistance gene from wild species.

Each local cultivar and hybrid was grown in the open air in three randomly distributed blocks of 10 plants per block at an experimental field located in Orihuela (Alicante, Spain). Fruits were harvested at two ripening stages, turning (<10% of the surface showing red colour) and red (>90% showing red colour). All determinations were performed at these two maturity stages, representing two frequent consumption stages. A total of 96 tomato fruits were individually analysed (8 genotypes × 2 ripening stages × 6 fruits per block).

Analytical Determinations

To measure ethylene production and respiration rate, tomato fruits were individually sealed in 500-mL glass jars fitted with a silicon septum for 1 hour. After this time, a 1-mL gas sample of the jar atmosphere was withdrawn, and the ethylene concentration was determined using a Hewlett-Packard gas chromatograph model 5890 (Wilmington, DE) equipped with a flame ionization detector and a stainless steel column packed with 80/100 mesh activated alumina. Column temperature was 90°C, and injector and detector temperatures were 150°C. Results were expressed as nanoliters of ethylene per gram of fruit per hour (nL g^{-1} h^{-1}). A second milliliter of the jar atmosphere was used to measure the respiration rate, by determining the CO_2 concentration using a Shimatzu GL 14A gas chromatograph (Kyoto, Japan) equipped with a catarometric detector (Amoroós et al. 2004). Column temperature was 50°C. Results were expressed as milligram of CO_2 per kilogram of fruit per hour (mg kg^{-1} h^{-1}). Flesh firmness was determined at two zones on the equatorial surface of the fruit (from which the peel had been previously removed), using a Penefel penetrometer manufactured by Copa-Technologie (Saint Etienne du Gres, France). The force required to penetrate a distance of 6 mm into the flesh was determined using a 0.5-cm diameter punch. Results were expressed in Newtons per centimeter^2.

To determine sugars and organic acids, 5 g of tomato mesocarp from each fruit were homogenized with 10 mL of deionized water using a Polytron homogenizer (IKA Labotechnik) and centrifuged at 10,000 × *g* for 10 min. An aliquot of 10 μL of the supernatant was used to quantify sugars and organic acids using an HPLC system (Hewlett-Packard, series 1100, Waldbrom, Germany) equipped with a Supelcogel C-610H (30 cm × 7.8 mm) column (at 30°C), a refractive index indicator (for sugar analysis), and an absorbance detector (210 nm UV, for acid analysis). The elution system consisted of 0.1% H_3PO_4, running isocratically at a flow rate of 0.5 mL min^{-1} (Serrano et al. 2005). Two separate extractions were made from each fruit, and for

each extraction, sugars and organic acids were determined in duplicate. A calibration curve was used to determine the concentration of individual sugars and organic acids in the samples. The following standard curves were used: sorbitol, sucrose, fructose, glucose, and malic, oxalic, citric, tartaric, ascorbic, succinic and fumaric acids from Sigma (Poole, Dorset, England). Results were expressed as grams per 100 g of fresh weight (%). The rest of each fruit sample was dried and mineralized by microwave acid digestion using HNO^3, according to Kalra, Maynard, and Radford (1998). Potassium (K), Phosphorus (P), and Sodium (Na) were measured by absorption atomic spectrometry.

Data Analysis

The data was first subjected to a variance components analysis (ANOVA with a nested or hierarchical design) to estimate the amount of variability provided by each of the three factors in the experiment (variability among cultivars, between maturity stages within each cultivar, and among fruits of the same cultivar and maturity stage). A multifactor analysis of variance was also performed to identify the significant factors and interactions between the factors.

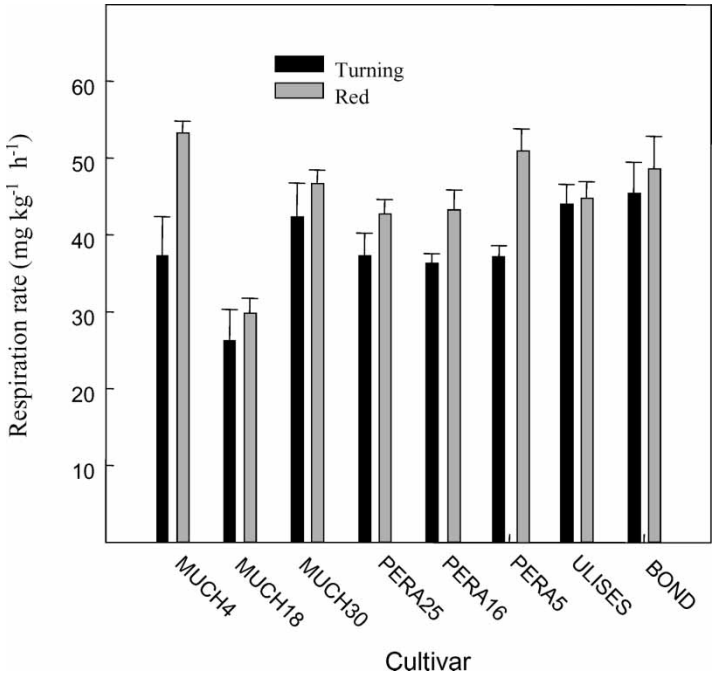

Figure 1. Respiration rates (mg CO_2 kg^{-1} h^{-1}) for the eight tomato cultivars at two maturity stages. Vertical bars represent standard errors.

RESULTS AND DISCUSSION

Respiration Rate, Ethylene Production, and Flesh Firmness

Some of the introgressed wild genes could have effects on the tomato post-harvest behavior. The comparison of the respiration rates of the traditional cultivars with the modern lines (Figure 1) showed that the values from the hybrids Bond and Ulises were within the range of those from the traditional cultivars. However, a differential behavior between the two types of cultivars was that the hybrids showed similar respiration rates at the two maturity stages, whereas the six traditional cultivars experienced an increase in CO_2 production at the red maturity stage, that was significant for four cultivars. Bond and Ulises showed a high ethylene production at the two maturity stages (Figure 2), but only Much4 and Much30, at the red stage, reached similar values. Values for flesh firmness were similar in all the cultivars. Hybrid cultivars have a longer shelf life than traditional varieties, and this differential behavior for the ripening process could be related to differences in fruit quality, but more investigation is needed before drawing conclusions.

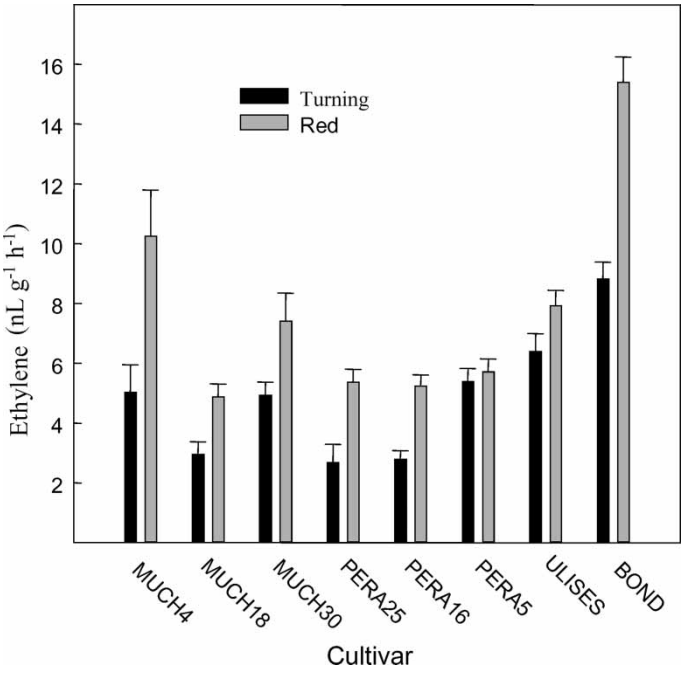

Figure 2. Ethylene production (nL g^{-1} h^{-1}) for the eight tomato cultivars at two maturity stages. Vertical bars represent standard errors.

P, K, and Na Fruit Content

The contribution of each factor to the total variability for the P, K, and Na fruit content is presented in Table 1. The variance component associated with the variability among cultivars was important for all three elements (48.8% to 69.9%), indicating that there were strong differences among cultivars. This was confirmed by the multifactor ANOVA analysis, which showed no interactions among factors, allowing us to state that the effect of the genotype (cultivar) was highly significant ($P < 0.001$). The modern lines Bond and Ulises showed the higher contents in P and K and the lowest in Na (Table 2). The maturity stage had very little effect in the P, K, and Na fruit concentration, but the variability among fruits of the same cultivar and maturity stage was somewhat high (19.5 for K to 36.6 for Na), suggesting that a higher number of fruits should be analyzed in future studies if we want to be able to detect fine differences among cultivars.

Sugars

Although sorbitol, sucrose, fructose, and glucose were quantified by HPLC, only the concentrations of fructose and glucose were important, because those of sorbitol and sucrose were extremely low (Table 2). The maturity stage had no effect on the level of sugars content in the tomato fruits. Although small differences could be detected for fructose fruit content among cultivars, the variability was only important for glucose (23.3% variance component associated with cultivars). However, there were no interactions, and there were no clear differences between old and modern cultivars; Ulises and Pera25 were the varieties with the higher glucose content. The importance of fruit sugar content, especially for the processing tomato, has justified extensive research to improve this quality parameter. However, there is a clear difficulty in achieving significant improvement because of the polygenic nature of the trait, the large effect of the environment, and the

Table 1. Variance components for Na, K, and P content (g/kg^{-1} D.M.), and glucose, fructose, and total sugars content (%) for each level of variation, calculated from an ANOVA with a hierarchical design

Source of variation	D.F.	Na (%)	K (%)	P (%)	Glucose (%)	Fructose (%)	Sugars (%)
Cultivars	7	48.8	69.9	64.0	23.3	5.6	13.5
Maturity stages	9	14.6	10.5	7.8	3.3	8.3	6.0
Fruits	78	36.6	19.5	28.2	73.4	86.1	80.5
Total	100	100	100	100	100	100	100

Table 2. P, K, and Na fruit content (g kg^{-1} D.M.) and glucose, fructose, and total sugars content (% of F.W.)

Variety	K	P	Na	Glucose	Fructose	Sugars
Bond	22.4 a	1.94 ab	1.07 c	1.32 bcd	1.68 abc	3.00 abc
Ulises	19.8 ab	2.03 a	1.21 b	1.51 a	1.75 ab	3.26 ab
Pera5	17.2 d	1.52 cd	1.21 ab	1.13 de	1.60 bc	2.73 cd
Pera16	17.6 d	1.42 de	1.27 ab	1.32 bcd	1.71 abc	3.03 abc
Pera25	17.0 d	1.59 c	1.23 ab	1.50 a	1.86 a	3.34 a
Much4	18.9 c	1.82 b	1.30 a	1.22 cde	1.69 abc	2.92 bcd
Much18	20.1 a	1.37 e	1.24 ab	1.04 e	1.48 c	2.53 d
Much30	19.0 bc	1.45 de	1.26 a	1.39 bc	1.87 a	3.26 ab

Note: Figures in the same column followed by the same letter are not different according to the Duncan's test ($P < 0.05$).

negative relationship between sugar content and fresh yield (Tandon et al. 2003; Lecomte et al. 2004).

Organic Acids

We have found important differences between old and modern cultivars' organic acid profiles. The acids present in higher concentrations in tomato fruit were citric and malic acids. All cultivars showed similar levels of ascorbic, oxalic, tartaric, malic, and succinic acids, but the hybrids showed a ~75% higher content of citric acid (Figure 3). The variance component associated with differences among cultivars was very high (70.6%) for the citric acid (Table 3). Although fumaric acid is present at very low

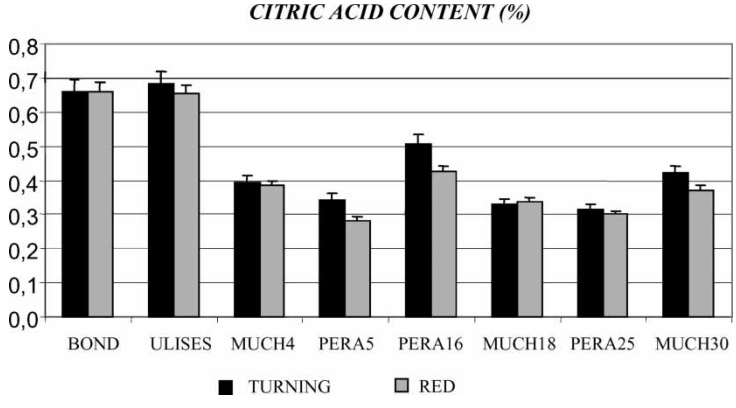

Figure 3. Citric acid content (%) of the eight cultivars at two ripening stages. Vertical bars represent standard errors.

Table 3. Variance components for acid content (%) for each level of variation, calculated from an ANOVA with a hierarchical design

Source of variation	Cultivars	Maturity stages	Fruits	Total
D.F.	7	9	78	
Ascorbic (%)	0.0	1.3	98.7	100
Citric (%)	70.6	0.0	29.4	100
Fumaric (%)	39.5	2.2	58.3	100
Malic (%)	14.2	19.9	65.9	100
Oxalic (%)	9.7	0.2	90.1	100
Succinic (%)	7.0	16.3	76.7	100
Tartaric (%)	14.2	20.1	65.7	100

concentrations in tomato fruit, there were also striking differences among cultivars. The traditional varieties showed a mean content of 0.058 mg kg^{-1}, with no significant differences among them, whereas the modern hybrids showed a mean content of 0.17 mg kg^{-1}. The higher acid contents of the two hybrids, containing introgressions from several wild species, is in accordance with the results found by other authors (Fulton et al. 2002; Yates et al. 2004). Maturity stages had only an important effect for malic and succinic acids. Total acid content is very important in tomatoes, not only as a key component of flavor, but also because it can change the volatility of aroma compounds, and a low pH assures the safety of the processed product (Fulton et al. 2002).

Correlation Analysis

A low number of significant correlations among the analyzed parameters was detected. The most important and significant correlations were those of citric acid with fumaric ($r = 0.55$) and tartaric ($r = 0.47$). Fulton et al. (2002) reported positive correlations between malic acid and citric acid ($r = 0.28–0.42$), but we have found in our cultivars a low and nonsignificant correlation. For maximum effect on both acidity levels and pH, selection for citric acid has been proposed to be most effective, although selection for malic acid would modulate pH with lesser effects on total acid content (Fulton et al. 2002). We have also found interesting correlations between citric acid content and K and P fruit content ($r = 0.56$ and $r = 0.64$, respectively). Citric acid was also negatively correlated with Na content ($r = -0.33$). As expected, K and Na fruit content were negatively correlated ($r = -0.48$), whereas K and P were positively correlated ($r = 0.47$). Glucose and fructose showed a strong correlation ($r = 0.86$), and the other parameter most closely correlated with glucose was citric acid ($r = 0.43$). The most correlated with fructose was tartaric acid ($r = 0.50$).

CONCLUSIONS

We have found important differences between old and modern cultivars for their respiration rates; ethylene production; K, P, and Na contents; and organic acids profile. Although possessing much more introgressed wild DNA, the modern hybrid cultivars showed higher contents (K, P, acids) or similar (glucose, fructose) than the traditional varieties. However, we have found in previous work that traditional cultivars have a higher content in volatile compounds (Ruiz et al. 2005). Quality in tomato is a difficult issue, and sensory studies have not clearly established the importance of analytical parameters in tomato quality. Considerable progress has been made in the identification of important components in tomato and the determination of their concentration in fresh fruit, but additional information is required regarding the optimal ranges and ratios for sugar, acids, and other parameters required for good flavor (Causse et al. 2003). The understanding of the effect of genetic improvement on tomato quality is still hampered by the lack of knowledge about how to define parameters related to fruit quality.

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REFERENCES

Amorós, A., Zapata, P., Pretel, M.T., Botella, M.A., Almansa, M.S., and Serrano, M. (2004) Role of naphthalene acetic acid and phenothiol treatments on increasing fruit size and advancing fruit maturity in loquat. *Scientia Horticulturae*, 101: 387–398.

Bernacchi, D., Beck-Bunn, T., Eshed, Y., Lopez, J., Petiard, V., Uhlig, J., Zamir, D., and Tanksley, S.D. (1998) Advanced backcross QTL analysis in tomato, I: Identification of QTLs for traits of agronomic importance from *L. hirsutum*. *Theoretical and Applied Genetics*, 97: 381–397.

Causse, M., Buret, M., Robini, K., and Verschave, P. (2003) Inheritance of nutritional and sensory quality traits in fresh market tomato and relation to consumer preferences. *Journal of Food Science*, 68: 2342–2350.

Frary, A., Doganlar, S., Frampton, A., Fulton, T., Uhlig, J., Yates, H., and Tanksley, S.D. (2003) Fine mapping of quantitative trait loci for improved fruit characteristics from *Lycopersicon chmielewskii* chromosome 1. *Genome*, 46: 235–243.

Fulton, T.M., Bucheli, P., Voirol, E., Lopez, J., Petiard, V., and Tanksley, S.D. (2002) Quantitative trait loci (QTL) affecting sugars, organic acids and other biochemical properties possibly contributing to flavor, identified in four advanced backcross populations of tomato. *Euphytica*, 127: 163–177.

Grandillo, S., Zamir, D., and Tanksley, S.D. (1999) Genetic improvement of processing tomatoes: A 20-year perspective. *Euphytica*, 110: 85–97.

Kalra, Y.P., Maynard, D.G., and Radford, F.G. (1998) Microwave digestion of tree foliage for multi-element analysis. *Canadian Journal of Forest Research*, 19: 981–985.

Lecomte, L., Duffé, P., Buret, M., Servin, B., Hospital, F., and Causse, M. (2004) Marker-assisted introgression of five QTLs controlling fruit quality traits into three tomato lines revealed interactions between QTLs and genetic backgrounds. *Theoretical and Applied Genetics*, 109: 658–668.

Levin, I., Gilboa, N., Yeselson, E., Shen, S., and Schaffer, A.A. (2000) Fgr, a major locus that modulates the fructose to glucose ratio in mature tomato fruits. *Theoretical and Applied Genetics*, 100: 256–262.

Monforte, A.J., Friedman, E., Zamir, D., and Tanksley, S.D. (2001) Comparison of a set of allelic QTL-NILs for chromosome 4 of tomato: Deductions about natural variation and implications for germplasm utilization. *Theoretical and Applied Genetics*, 102: 572–590.

Ruiz, J.J., Alonso, A., García-Martínez, S., Valero, M., Blasco, P., and Ruiz-Bevia, F. (2005) Quantitative analysis of flavour volatiles detects differences among closely related traditional cultivars of tomato. *Journal of the Science of Food and Agriculture*, 85: 54–60.

Scott, J.W. (1998) University of Florida tomato breeding accomplishments and future directions. *Proceedings Soil and Crop Sciences Society of Florida*, 58: 16–18.

Seah, S., Yaghoobi, J., Rossi, M., Gleason, C.A., and Williamson, V.M. (2004) The nematode-resistance gene, Mi-1, is associated with an inverted chromosomal segment in susceptible compared to resistant tomato. *Theoretical and Applied Genetics*, 108: 1635–1642.

Serrano, M., Guillén, F., Martínez-Romero, D., Castillo, S., and Valero, D. (2005) Chemical constituents and antioxidant activity of sweet cherry at different ripening stages. *Journal of Agricultural and Food Chemistry*, 53: 2741–2745.

Tandon, K.S., Baldwin, E.A., Scott, J.W., and Shewfelt, R.L. (2003) Linking sensory descriptors to volatile and nonvolatile components of fresh tomato flavor. *Journal of Food Science*, 68: 2366–2371.

Tanksley, S.D., Bernachi, D., BeckBunn, T., Emmatty, D., Eshed, Y., Inai, S., Lopez, J., Petiard, V., Sayama, H., Uhlig, J., and Zamir, D. (1998) Yield and quality evaluations on a pair of processing tomato lines nearly isogenic for the $Tm2^a$ gene for resistance to the tobacco mosaic virus. *Euphytica*, 99: 77–83.

Yates, H.E., Frary, A., Doganlar, S., Frampton, A., Eannetta, N.T., Uhlig, J., and Tanksley, S.D. (2004) Comparative fine mapping of fruit quality QTLs on chromosome 4 introgressions derived from two wild tomato species. *Euphytica*, 135: 283–296.