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Genotype x environment interactions in eggplant for fruit phenolic acid content

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Abstract

Eggplant fruit are a rich source of phenolic acids that contribute to fruit nutritive value and influence culinary quality. We evaluated the influence of production environments and stability of diverse genotypes across environments for eggplant fruit phenolic acid content. Ten *Solanum melongena* accessions including five F_1 hybrid cultivars, three open-pollinated cultivars and two land race accessions, plus one *S. macrocarpon* and one *S. aethiopicum* accession, were grown at two locations under greenhouse and open field environments. Twenty phenolic acid conjugates were identified in fruit flesh and assigned to six classes that included hydroxycinnamic acid amides, caffeoylquinic acid esters, hydroxycinnamoylquinic acid esters, malonylcaffeoylquinic acid esters, di-hydroxycinnamoylquinic acid esters, and other hydroxycinnamic acid conjugates. There were significant differences among the 12 accessions for total phenolic acid conjugate content and all individual classes. Analysis of fruit phenolic acids demonstrated that there were no significant differences among the environments for any of the variables. However, the environment x accession interaction was highly significant for all phenolic acid classes. Broad-sense heritability estimates for all six phenolic acid classes were high, ranging from 0.64 to 0.96. Stability analysis demonstrated widespread instability for phenolic acid content across environments. Stability of the predominant CQAE class positively influenced stability of total phenolic acid content for some but not all cultivars. High heritability, coupled with highly significant cultivar x environment interactions suggests that stability estimates may improve the efficiency of breeding new cultivars with predictable performance across environments.

Key words: fruit quality, heritability, hydroxycinnamic acids, Solanum melongena

Introduction

Eggplant (*Solanum melongena*) is an economically important Solanaceous crop native to southern India. Considerable diversity for plant habit and fruit shape, size and color exists in the eggplant types typically produced in Europe, America, Asia and Africa. Cultivated relatives of *S. melongena*, including the scarlet eggplant (*S. aethiopicum*) and the Gboma eggplant (*S. macrocarpon*), contribute additional diversity to the genepool for crop improvement. In addition to morphological diversity, eggplant genetic resources are a rich source of variation for secondary metabolites that influence fruit quality and nutritive value. Phenylpropanoids are stress inducible secondary metabolites with important physiological roles in vegetative and reproductive plant tissues that also influence crop nutritive value. In eggplant fruit, phenolic acid conjugates influence fruit culinary quality and are the major source of dietary phenolics (Winter and Herrmann, 1986). Several studies have evaluated diverse eggplant germplasm for total fruit phenolics content (Hanson et al., 2006; Prohens et al., 2007; Raigon et al., 2008). In a study of *S. melongena* and allied eggplant species, Stommel and Whitaker (2003) and Wu et al. (2013) documented extensive variation in content of individual fruit phenolic acid conjugates.

Phenolic acid conjugates are among the most abundant dietary polyphenols and are highly bioavailable (Manach et al., 2004). Bioactive properties of these compounds are of considerable interest for human health (Bravo, 1998). Phenolic acid conjugates are recognized as antioxidants and have anti-inflammatory properties demonstrated *in vitro* and *in vivo* (dos Santos et al., 2006: Prior, 2003; Sato et al., 2011). Studies have

also reported hypotensive, anti-carcogenic and anti-diabetic effects for these compounds (Ong et al., 2012; Suzuki et al., 2006; Yang et al., 2012)

Polyphenol oxidase mediated browning of cut eggplant fruit surfaces due to oxidation of phenolic compounds poses a seeming contradiction for development of eggplant cultivars with improved culinary quality and nutritive value. However, Prohens et al. (2007) reported wide variation for browning of cut eggplant fruit surfaces and total phenolics content with only 15% - 23% of the total variation for browning attributed to phenolics content. Variation reported for polyphenol oxidase activity among eggplant accessions (Dogan et al., 2002; Mennella et al., 2012) further suggests that high quality cultivars with low fruit flesh browning and increased nutritive value due to elevated phenolic acid conjugate content, can be developed.

Secondary metabolites such as phenylpropanoids are stress inducible and susceptible to numerous environment stimuli (Dixon and Pavia, 1995). In addition to diversity for phenolic acid conjugate content between eggplant genotypes, we have observed considerable variation within as well as between plants of an accession (Prohens et al., 2013; Stommel and Whitaker, 2003; Whitaker and Stommel, 2003). Luthria et al. (2010) also reported significant plant to plant variation in 5-caffeoylquinic acid content for plants from single cultivars grown under similar conditions. The observed variation arises from the joint action of genotype and environment. A genotype x environment interaction is defined as the change in the relative performance of a character of two or more genotypes that is quantified in two or more environments. Significant genotype x environment interaction results in changes in rank order for genotypes between environments and probable changes in size of the genetic,

environmental and phenotypic variances between environments. When genotype x environment interaction is significant, stability of performance over a range of environments or years can be measured using stability indices (Pritts and Luby, 1990). Stability indices are used practically to make varietal recommendations to growers and by breeders to evaluate the stability of a character in multiple genotypes across multiple environments that may influence the character of interest. Partitioning genotype x environment interaction into stability statistics for each genotype evaluated provides a useful measure for selecting stable genotypes (Fernandez, 1991).

The objectives of this research were to 1) measure the response of a diverse group of eggplant cultivars representing hybrid and open pollinated cultivars, landraces and exotic cultivated eggplant relatives within and across environments for phenolic acid conjugate content, 2) estimate broad-sense heritability for individual and total phenolic acid conjugates in this germplasm and 3) determine stability of individual and total phenolic acid conjugates at two locations under greenhouse and open field production conditions.

Materials and Methods

Plant Material. Twelve eggplant accessions were utilized in this study. These included five *Solanum melongena* F_1 hybrid cultivars, Orient Express, Ghost Buster, Epic, Classic and Black Magic; three open-pollinated cultivars, Black Beauty, LF3-24 and Lista de Gandia; a Spanish land race, ALM1; and an African landrace, BBS175. Two cultivated relatives of *S. melongena* included the *S. macrocarpon* accession BBS196 and the *S. aethiopicum* accession BBS157.

Plant Culture. Plants of individual accessions for greenhouse and field production were grown from seedlings in the greenhouse using standard production practices. In Beltsville, Maryland, plants were grown at the USDA, ARS, Beltsville Agricultural Research Center (BARC). For open field production, six seven-week old plants of each accession were transplanted to field plots (GPS coordinates: lat. 39º 1' 43.95"N, long. 76º 56' 2.81"W) in June 2011 using a completely randomized design into Keyport fine loam soil using standard horticultural practices for eggplant production in Maryland (University of Maryland, 2007). Field grown plants were spaced at 0.45 m intervals in single rows on polyethylene covered raised beds, with beds positioned on 1.5 m centers. Fertilizer and supplemental water was supplied using trickle irrigation. Soluble fertilizers at a rate of 18.1 kg of N, P_2O_5 and K_2O were applied per mulched acre at each application via trickle irrigation beginning one week after transplanting and every three weeks thereafter for a total of five applications during the production season. In Valencia, Spain, plants were grown at the campus of the Universidad Politécnica de Valencia. For open field production, six seven-week old plants of each accession were transplanted to field plots (GPS coordinates: lat. 39º 28' 55'' N, long. 0º 20' 11'' W) in July 2011 using a completely randomized design into sandy loam soil following standard horticultural practices for eggplant production in the Mediterranean coastal area of Spain (Baixauli 2001). Plants were spaced 1.2 m between rows and 1.0 m apart within the row on black polyethylene covered raised beds, trained with bamboo canes and drip irrigated. Fertilization was applied with drip irrigation throughout the growing cycle on a constant feed basis. Final concentrations of 180 ppm N, 78 ppm P and 150 ppm K, 6 ppm Mg, and 8 ppm S in the dilute fertilizer solution were

supplemented with micronutrients applied in final concentrations of 0.50 ppm Fe, 0.10 ppm B, 0.19 ppm Cu, 0.50 ppm Mn, 0.19 ppm Zn and 0.01 ppm Mo. For respective production locations, three commercially mature fruits (as assessed by the size, and color and glossiness of the skin) were harvested from each of four plants from individual accessions during August (Beltsville) and September or early October (Valencia).

For greenhouse production at BARC, seven-week old transplants of each accession were transplanted in July 2011 to in 5.7 l pots containing Pro-Mix HP Mycorrhizae (Premier Tech Horticulture Ltd.), a 65-75% sphagnum peat moss plus perlite soil-free mix. Pots were distributed in a glasshouse (GPS coordinates: lat. 39º 1' 38.96'' N, long. 76º 55' 35.67'' W) with climate control (heating started at temperatures below 20ºC and cooling at temperatures above 24ºC) using a completely randomized design. Plants were spaced 0.8 m between rows and 0.7 m apart within the row. Plants were trained on bamboo canes and fertilization was applied on a constant feed basis with drip irrigation throughout the growing cycle. Final concentrations of 144 ppm N, 42 ppm P and 221 ppm K, 106 ppm Ca, 50 ppm Mg, and 34 ppm S in the dilute fertilizer solution were supplemented with micronutrients applied in final concentrations of 2.8 ppm Fe, 1.3 ppm B, 0.18 ppm Cu, 0.62 ppm Mn, 0.18 ppm Zn, 0.09 ppm Mo and 8.8 ppm Cl. Pots were periodically flushed with fertilizer-free water in order to avoid salt build up in the potting media. For greenhouse production at the campus of the Universidad Politécnica de Valencia, seven-week old plants of each accession were transplanted in March 2012 to 25 l pots filled with coconut fiber substrate (Horticoco, Valimex, Valencia, Spain). Plants were distributed in a glasshouse (GPS coordinates: lat. 39º 29' 01'' N, long. 0º 20' 27'' W) with climate control (heating started at

temperatures below 15ºC and cooling at temperatures above 30ºC) using a completely randomized design. Plants were spaced 1.7 m between rows and 0.4 m apart within the row, pruned to one shoot, trained with vertical strings and drip irrigated. Fertilization was applied on a constant feed basis throughout the growing cycle. Final concentrations of 175 ppm N, 47 ppm P and 263 ppm K, 130 ppm Ca, 61 ppm Mg, and 90 ppm S in the dilute fertilizer solution were supplemented with micronutrients applied in final concentrations of 0.56 ppm Fe, 0.54 ppm B, 0.02 ppm Cu, 0.25 ppm Mn, 0.25 ppm Zn, 0.01 ppm Mo and 0.16 ppm Cl. Excess water was applied in order to avoid salt build up in the potting substrate. Three commercially mature fruits (as assessed by the size, and color and glossiness of the skin) were harvested from each of four plants from respective accessions during October 2011 (Beltsville) and June or early July 2012 (Valencia).

Sample Preparation. Harvested fruit of individual plants were washed, peeled and a 2-cm wide longitudinal section from stem to blossom end was cut from the middle of the fruit. Excised tissue sections from individual fruit were frozen in liquid N_2, lyophilized and powdered, and stored at −80ºC until analyzed. Subsamples of 0.2 g of the lyophilized and powdered fruit tissue were extracted by vigorous stirring for 15 min at room temperature in 10 ml of methanol–water, 4:1, in a 15-ml plastic centrifuge tube that was sealed after flushing with N_2. The samples were then centrifuged at 4000 *g* for 5 min, the first extract was decanted, and the process was repeated. The first and second extracts were combined and 4 ml of the extract was passed through a Whatman polytetrafluoroethylene (PTFE) syringe filter (0.2 µm pore size). One milliliter aliquots of filtered extracts were transferred to amber glass vials and the solvent evaporated under

a stream of N_2 at 40ºC. The residue was dissolved in 1.0 ml of water–methanol, 4:1, plus 0.02% phosphoric acid. Vials were flushed with N_2, sealed with a Teflon-lined septum cap and stored at −80ºC until analyzed by HPLC.

HPLC Analysis. Phenolic acid conjugates in the fruit tissue extracts were separated and quantified by reverse phase high performance liquid chromatography (RP-HPLC) in 50 µl injections onto a Luna C18(2) column (5 µm particle size, 250 mm long, 4.6 mm i.d.) (Phenomenex; Torrance, CA, USA) using an HP 1100 Series instrument with a quaternary pump, autosampler and photodiode array detector (Agilent Technologies, Palo Alto, CA). Data were analyzed with Agilent ChemStation software (Revision B.03.01). The method used was a modification of that described by Whitaker & Stommel (2003). The binary gradient consisted of 0.02% H_3PO_4 in water (A) and methanol (B) as follows: 0 min, 90A:10B at 1.0 ml min^{-1}; 0–15 min, linear increase to 25% B at 1.0 ml min^{-1}; 15–25 min, linear increase to 50% B at 1.0 ml min^{-1}; 25–28 min, linear increases to 80% B and 1.2 ml min^{-1}; 28–30 min, linear increase to 100% B at 1.2 ml min^{-1}; 30–32 min, 100% B at 1.2 ml min^{-1}; 32–35 min, decrease to 10% B at 1.2 ml min^{-1} and 35–38 min, 10% B with linear decrease to 1.0 ml min^{-1}. Relative quantification was based on absorbance at 325 nm (caffeoyl and feruloyl conjugates) and 280 nm (dihydrocaffeoyl conjugates).

Statistical Analyses. Phenolic acid conjugates were numbered in the order of their HPLC elution time and distributed in six groups (Table 1) on the basis of their chemical structures. Data were transformed with the square root transformation to more closely conform to normality. However, peak 13 and peak 18 had to be transformed with the fourth root transformation (= square root of the square root) to

conform to normality. Transformed data were analyzed using the mixed models procedure in SAS (Version 9.2; SAS Institute, Cary, NC) where all factors were considered random. Residuals were examined and used to identify outliers. The most extreme outlier was removed from the data set and the model was rerun. This was done until the residuals approximated a normal distribution. Estimates of the variance components from the mixed models procedure were used to calculate broad-sense heritability as:

$$H = \sigma^2_G / [\sigma^2_G + (\sigma^2_{GE}/e) + (\sigma^2_e/re)]$$

Where σ^2_G is the genetic variance, σ^2_{GE} is the genotype x environment variance, σ^2_e is the error variance, and re=total number of fruits analyzed per genotype. The transformed data were also analyzed by the SAS general linear models procedure and type III mean squares were used to calculate the upper and lower confidence interval about the estimate of H (Knapp et al. 1985) as:

$$\text{Upper CI} = 1-[(MS_1/MS_2)F_{(1-\alpha/2;df2,df1)}]^{-1}$$

$$\text{Lower CI} = 1-[(MS_1/MS_2)F_{(\alpha/2;df2,df1)}]^{-1}$$

Where MS_1 = mean squares for cultivar, MS_2 = mean squares for environment x cultivar, $\alpha = 0.05$, df2 = degrees of freedom associated with environment x cultivar, and df1 = degrees of freedom associated with cultivar.

For stability analyses, transformed data were analyzed using the mixed models

procedure with environment, cultivar, and the environment x cultivar interaction considered fixed effects. Least squares means were calculated and used in the stability analyses. The environment x cultivar interaction was partitioned into stability variance components (σ^2_i) assignable to each cultivar (Shukla 1972), using the IML procedure in SAS (Kang 1989). An environmental index for each environment was calculated by subtracting the grand mean over all environments from the mean for each environment. Heterogeneity due to this index was removed from the cultivar x environment interaction and the remainder was partitioned into s^2_i assignable to each cultivar, and constitutes variance not explainable by environment x cultivar.

Results

Twenty phenolic acid conjugate compounds were identified in fruit of the 12 eggplant genotypes evaluated and included esters and/or amides of caffeic, dihydrocaffeic and ferulic acid. The phenolic acids have been identified by a combination of LC–MS and NMR analyses as described in our prior studies (Whitaker & Stommel, 2003; Ma et al., 2011; Wu et al., 2013) and by Garcia-Salas et al. (2014). The phenolic acid conjugates were distributed in six groups based on their chemical structures (Table 1). These compounds included six hydroxycinnamic acid amides of polyamines (HCAA; Group 1) and additional minor dihydrocaffeoyl polyamines and hydroxycinnamoyl polyamines that were grouped with this class. Four caffeoylquinic acid esters (CQAE; Group 2) and three hydroxycinnamoylquinic acid esters (HCQAE; Group 3) were identified in the accessions evaluated. Minor hydroxycinnamic acid conjugates exclusive to *S. aethiopicum*, plus 3-*O*-sinapoylquinic acid, 5-*O*-

caffeoylshikimic acid and four incompletely annotated hydroxycinnamic acid conjugates were grouped together as hydroxycinnamic acid conjugates (HCAC; Group 4). Two malonyl caffeoylquinic acid esters (MCQAE; Group 5) and three di-hydroxycinnamoylquinic acid esters (DHCQAE; Group 6) were identified. Two incompletely annotated di-hydroxycinnamoylquinic acid isomers were assigned to the DHCQAE group.

Variance parameter estimates were not significant across environments for total phenolic acid conjugates (Table 2). In contrast, there were significant differences among cultivars and the environment x cultivar interaction was highly significant for total phenolic acid conjugates. Overall, total fruit phenolic acid values for hybrid and open pollinated cultivars were approximately two- to four-fold greater when grown in greenhouse and open field environments in Beltsville, Maryland than in Valencia, Spain (Table 3). Within respective locations, total phenolic acid values for greenhouse and open field conditions were comparable. With the exception of ALM 1, differences between locations were reduced for landraces and the cultivated relatives of *S. melongena,* namely *S. aethiopicum* and *S. macrocarpon*. The hybrid cultivar, Orient Express, and the *S. aethiopicum* cultivar, BBS157, exhibited the lowest total phenolic acid values, particularly under open field locations in the U.S. and Spain. The *S. macrocarpon* cultivar, BBS 196, exhibited some of the highest phenolic acid values under greenhouse and open field conditions at both locations. Consistent with significant environment x cultivar effects for all cultivars, considerable variability in cultivar ranking for total phenolic acid values was evident for most other hybrids and open pollinated cultivars. Only three of the 12 cultivars, Epic, Black Beauty and BBS

196, were stable for total phenolic acid values before and after removal of environmental heterogeneity (Table 3). Only three of the nine cultivars, Black Magic, Ghostbuster and ALM 1, that exhibited instability for total phenolic acid values before removal of environmental heterogeneity, displayed stability after removal of environmental variance. The remaining six cultivars continued to have instability after removing environmental heterogeneity.

Similar to total phenolic acid conjugates, variance parameter estimates were not significant across environments for any of the six phenolic acid conjugate classes evaluated (Table 2). However, there were significant differences among cultivars for all classes. The environment x cultivar interaction was highly significant for all six phenolic acid conjugate classes. A highly significant environment x plant(cultivar) interaction for all six classes of compounds validated a high level of variability observed for phenolic acid conjugate content.

The CQAE class of phenolic acid conjugates represented, on average, 82.0% - 85.7% of phenolic acid conjugates in greenhouse and open field environments (Table 4). The most abundant compound in this class was 5-*O*-caffeoylquinic acid. Only one of the five hybrid cultivars evaluated exhibited stability across environments for this predominant class of phenolic acid conjugates. Similar to total phenolic acid conjugates, CQAE values were substantially greater in fruit produced in Beltsville, Maryland in comparison to Valencia, Spain and comparable in greenhouse and open field conditions within a location.

Similar to total phenolic acid conjugate and CQAE values, HCAA, DHCQAE, MCQAE and HCQAE values from Beltsville grown fruit were generally greater than

those found in fruit produced in Valencia (Table 4). In contrast, HCAC values were typically comparable across locations or greater for fruit produced in Valencia relative to those produced in Beltsville. HCAA comprised 8.6% - 13.6% of the total phenolic acid conjugates within respective environments. The remaining classes, DHCQAE, HCAC, MCQAE and HCQAE, represented only 0.5% - 3.9% of total phenolic acid conjugates. MCQAE conjugate values were notably higher, at least four-fold within an environment, in the *S. macrocarpon* cultivar, BBS 196, in comparison to *S. melongena* and *S. aethiopicum* cultivars. MCQAE values were approximately two-fold higher in BBS 196 fruit produced under greenhouse conditions in comparison to open field-grown fruit. With the exception of the open field environment in Maryland, fruit of the *S. aethiopicum* cultivar, BBS 157, were distinguished by higher levels of HCAC conjugates in comparison to fruit from cultivars of other eggplant species. HCQAE conjugates exhibited stability for all open pollinated cultivars evaluated. DHCQAE phenolic acid conjugates exhibited the least stability across environments with only Ghostbuster and LF3-24 showing stability after removal of environmental heterogeneity. For Classic and BBS 157, all six classes of compounds were unstable before and after removal of environmental heterogeneity.

Overall, most of the cultivars were unstable both before and after removal of environmental heterogeneity. Seven to 10 of the 12 cultivars exhibited instability within individual classes of phenolic acid conjugates after removal of environmental heterogeneity (Table 4). Among 12 cultivars and six classes of phenolic acid conjugates, stability across environments was observed in 24 of the 72 cases evaluated. In five of the 24 cases, removal of environmental heterogeneity provided

stability within a cultivar for an individual compound. In the remaining 19 of the 24 cases of stability across environments, stability was observed both before and after removal of environmental heterogeneity.

Despite variability for phenolic acid conjugates observed within and across environments, broad-sense heritability values and their 95% confidence intervals were high. Broad-sense heritability estimates for the six individual classes of compounds ranged from 0.70 for HCQAE to 0.96 for MCQAE (Table 2). For the predominant class of compounds, CQAE, broad-sense heritability was 0.84. Heritability for total phenolic acid conjugates was 0.87, similar to that observed for the predominant CQAE class of compounds.

Significant correlations between the six phenolic acid conjugate classes were evident for both greenhouse and field conditions at Beltsville and Valencia production locations (Table 5). These correlations were greatest between the predominant class of compounds, CQAE, and the second most abundant class of compounds, HCAA. Moderate, but significant correlations were also evident between the CQAE class of compounds and the MCQAE and HCQAE classes. When significant, correlations were often similar in magnitude for greenhouse and open field conditions and Beltsville and Valencia locations. Non-significant exceptions were small and occurred most frequently between HCQAE and DHCQAE and the five other classes of phenolic acid conjugates.

Discussion

The performance of crop cultivars across environments is a critical determinant in developing new crop cultivars. Our studies utilizing diverse eggplant cultivars were

conducted across greenhouse and open field locations in Beltsville, Maryland and Valencia, Spain. Environmental stimuli including light, temperature stress and pathogens influence the flux of metabolites into the phenylpropanoid pathway responsible for synthesis of phenolic acid conjugates (Dixon and Pavia, 1995). Our results demonstrated that environments were not significant for individual classes or total phenolic acid conjugate content in eggplant fruit. The lack of significant environmental effects in our studies may reflect the optimal cultural conditions that minimize stress and maximize yield and similar geographic latitudes utilized for production. Water and nutrients were not lacking in any environment due to supplemental irrigation and fertilization. Reduced solar irradiation experienced by plants under greenhouse versus open field conditions due to ultraviolet filtering properties of greenhouse glazing, did not have a significant effect on phenolic acid conjugate values. Likewise, controlled environments afforded under greenhouse conditions versus those experienced in the open field, did not have a marked overall effect on phenolic acid conjugate constituents. Significant differences between cultivars and differential response of cultivars across environments were greater sources of variation relative to environment alone. This variation was evident in lack of stability in individual classes and total phenolic acid conjugates over environments.

In related studies, comparisons of organic and conventional cultivation methods for eggplant found that year effects were of greater significance than were production method on total eggplant fruit phenolics and that cultivars were the greatest source of variation for these fruit constituents (Luthria et al., 2010; Raigon et al., 2010). Similarly, Hanson et al. (2006) reported large and significant differences in total eggplant fruit

phenolics content with mean differences of 50% between two years. Recent results reported by Garcia-Salas et al. (2014) demonstrated that variation in total fruit phenolic content varied by eggplant cultivar with non-significant to nearly eight-fold variation in total phenolic content produced during spring versus summer seasons. Similar to eggplant, 5-*O*-caffeoylquinic acid is the major phenolic acid conjugate present in potato tubers and varied almost two-fold among production locations (Payyavula et al., 2012).

In comparison to open pollinated cultivars, hybrids are typically bred to be more widely adapted to varying environmental conditions and have more uniform characteristics than non-hybrids grown under modern production practices. Hence, they can be more predictable in crop performance. Open pollinated cultivars may, however, provide greater stability under highly variable environments with sub-optimal conditions (Setimela et al., 2007). In contrast to hybrids and open pollinated cultivars, landraces are best adapted to specific locales and may perform poorly outside that environment. However, the stability of landraces under adverse conditions is typically high. Clear advantages of eggplant hybrid or open pollinated cultivars, land races or cultivated *S. melongena* relatives for total or individual phenolic acid conjugates, were not evident under our production conditions.

Allard and Bradshaw (1964), originally suggested that heterozygous and heterogeneous populations offered the best opportunity to produce cultivars with small genotype x environment interactions. Relevant to our study, heterozygous genotypes would be expected to possess greater individual buffering against varied environmental conditions. Although a greater proportion of hybrid or open pollinated cultivars exhibited stability for a specific class or total phenolic acid conjugates, greater representation

across cultivar groups is required to better address this question. Phenolic acid conjugates in eggplant fruit were influenced by genetic factors and the interaction of genetic factors with locations and production conditions.

Despite widespread instability across environments for phenolic acid conjugates, abundance of CQAE and HCAA classes relative to other classes in *S. melongena* cultivars evaluated in this study is consistent with our previous findings and those of others (Garcia-Salas et al., 2014; Stommel and Whitaker, 2003). Likewise, relative rankings for extremes of the distribution for high (e.g. ALM 1) and low (e.g. Orient Express) total phenolic acid conjugate levels are consistent with our prior findings (Prohens et al., 2007; Whitaker and Stommel, 2003). Expected species distinctions were also evident with higher levels of MCQAE and HCAC conjugates in *S. macrocarpon* and *S. aethiopicum,* respectively, relative to *S. melongena* (Stommel and Whitaker, 2003). Correlations observed between the six classes of phenolic acid conjugates reflect the interconnected biosynthetic pathways for these groups of compounds. Biosynthetic steps in the phenylpropanoid pathway that distinguish the respective groups of compounds have been reviewed (Prohens et al., 2013).

Relatively high broad-sense heritability estimates for individual classes and total phenolic acid conjugates, indicate that selection for these attributes can be effective in a breeding program. Prohens et al. (2007) reported moderate broad sense heritability for total phenolics in a diverse collection of eggplant genotypes. In our study, variance components for cultivars exceeded those estimated for the cultivar x environment interaction, further suggesting that it may be possible to develop cultivars that are uniform and stable for specific phenolic acid conjugate profiles. Nonetheless, since

changes in cultivar rank order across environments can reduce the effectiveness of selection, stability variances can be useful in selection of stable genotypes. CQAE conjugates, the major class of phenolic acid conjugates in eggplant, exhibited stability after removal of environmental heterogeneity for five of the 12 cultivars evaluated. Four of these cultivars exhibited stability for total phenolic acid conjugates, suggesting that stability for CQAE conjugates positively influenced stability for total levels. However, two cultivars that were stable for total phenolic acid levels, exhibited instability for CQAE, suggesting that other phenolic acid classes as well as other unidentified genetic and/or environmental factors influence stability of these fruit constituents. Prohens et al. (2013) reported that a simple additive dominance model was adequate to explain genetic variance for phenolic acid conjugate constituents. However, additive variance was only significant for the CQAE class of compounds, suggesting that other factors contribute to variation observed for other phenolic acid conjugate classes.

In summary, our results demonstrate the importance of genotype and interactions between genotype and environment on eggplant fruit phenolic acid conjugate content. High heritability, coupled with highly significant cultivar x environment interactions suggests that stability estimates may improve the efficiency of breeding new cultivars with predictable performance across environments for individual phenolic acid conjugates or total levels of these compounds.

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Mention of trade names or commercial products is solely for the purpose of providing specific information and does not imply recommendation or endorsement by the U.S. Department of Agriculture.

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Table 1. Phenolic acid conjugates identified in fruit of *Solanum melongena* hybrids, open-pollinated cultivars, land races, and *S. macrocarpon* and *S. aethiopicum*, two cultivated eggplant relatives. Compounds were organized into six groups based upon chemical structure.

Hydroxycinnamic Acid Amides of Polyamines (HCAA)
N-caffeoylputrescine
N-feruloylputrescine
N1,N10-bis(dihydrocaffeoyl)spermidine
N1-caffeoyl-N10-dihydrocaffeoylspermidine
N1-dihydrocaffeoyl-N10-caffeoylspermidine
N1,N10-bis(caffeoyl)spermidine
Minor dihydrocaffeoyl polyamines [e.g. N1,N5,N14-tris(dihydrocaffeoyl)spermine & N1,N14-bis(dihydrocaffeoyl)spermine]
Minor hydroxycinnamoyl polyamines (caffeoyl, feruloyl, p-coumaroyl)
Caffeoylquinic acid esters (CQAE)
5-*O*-caffeoylquinic acid
5-*O*-(*Z*)-caffeoylquinic acid
4-*O*-caffeoylquinic acid
3-*O*-caffeoylquinic acid
Hydroxycinnamoylquinic acid esters (HCQAE)
5-*O*-*p*-coumaroylquinic acid
5-*O*-feruloylquinic acid

3-*O*-feruloylquinic acid

Hydroxycinnamic acid conjugates (HCAC)

3-*O*-sinapoylquinic acid

5-*O*-caffeoylshikimic acid

Minor hydroxycinnamic acid conjugate exclusive to *S. aethiopicum*

Hydroxycinnamic acid conjugates (4)

Malonyl Caffeoylquinic acid esters (MCQAE)

3-*O*-malonyl-5-*O*-caffeoylquinic acid

4-*O*-caffeoyl-5-*O*-malonylquinic acid

Di-hydroxycinnamoylquinic acid esters (DHCQAE)

3,5-di-*O*-caffeoylquinic acid

3,4-di-*O*-caffeoylquinic acid

4,5-di-*O*-caffeoylquinic acid

Di-hydroxycinnamoylquinic acid isomers (2)

Table 2. Variance parameter estimates from the general linear models procedure in SAS, broadsense heritability (H) and the 95% confidence interval (CI) about H for individual classes of phenolic acid conjugates identified in eggplant fruit grown in Beltsville, Maryland and Valencia, Spain under greenhouse and open field conditions.

Variance parameter	HCAA	CQAE	DHCQAE	HCAC	MCQAE	HCQAE	Total phenolic acids
Environment	178.67	784.48	12.14	4.76	0.17	15.12	941.8
Cultivar	99.03*	355.76*	24.50*	12.11*	2.86*	7.62*	469.73*
Plant(cultivar)	1.93	7.51	0.14	0	0	0.30	12.03
Fruit(plant(cultivar))	0.94	10.85	0.33	2.01**	0	0	19.17
Env x Cultivar	54.73**	171.34**	13.59**	10.48**	0.33**	11.57**	169.19**
Env x plant(cultivar)	23.03**	42.82*	3.57**	6.67**	0.20**	1.28**	48.82*
Error	42.86	297.04	8.49	11.08	0.42	4.75	281.68
model R^2	0.95	0.90	0.93	0.88	0.95	0.93	0.92
H	0.85	0.84	0.86	0.77	0.96	0.70	0.87
Upper CI	0.95	0.95	0.96	0.93	0.99	0.91	0.97
Lower CI	0.65	0.70	0.68	0.48	0.92	0.31	0.76

*, ** Significant at $P = 0.05$ or 0.01, respectively.

Phenolic acid conjugate class abbreviations: hydroxycinnamic acid amides of polyamines (HCAA); caffeoylquinic acid esters (CQAE); hycroxycinnamoylquinic acid esters (HCQAE); hydroxycinnamic acid conjugates (HCAC); malonyl caffeoylquinic acid esters (MCQAE); di-hydroxycinnamoylquinic acid esters (DHCQAE).

Table 3. Total eggplant fruit phenolic acid conjugate least square means (high performance liquid chromatography peak area units) for cultivars grown in greenhouse and open field environments in Beltsville, Maryland and Valencia, Spain. Estimates of stability variance for phenolic acids of cultivars across environments were calculated before (σ^2_i) and after (s^2_i) removal of environmental heterogeneity.

	Maryland		Spain			
Cultivar	Greenhouse	Open field	Greenhouse	Open field	σ^2_i	s^2_i
			Hybrids			
Black Magic	28934	23317	8415	7423	**	ns
Classic	23507	25783	7082	8583	**	**
Epic	17849	19949	6290	4367	ns	ns
Ghostbuster	19036	15790	12414	10266	**	ns
Orient Express	14309	9780	5643	2690	*	**
			Open pollinated			
Black Beauty	24364	24687	8470	6990	ns	ns
LF3-24	20017	22641	6246	6903	**	*
Listada de Gandia	13642	18769	6221	5700	*	**
			Landraces			
ALM 1	41181	33981	11139	8433	**	ns
BBS 175	24602	24715	19364	13624	**	*
			Solanum aethiopicum			

BBS 157	10818	6974	7270	5350	**	**
		Solanum macrocarpon				
BBS 196	34711	35235	20822	18501	ns	ns

*, **, ns: Significant at *P* = 0.05 or 0.01 and non-significant, respectively.

Phenolic acid conjugate class abbreviations: hydroxycinnamic acid amides of polyamines (HCAA); caffeoylquinic acid esters (CQAE); hycroxycinnamoylquinic acid esters (HCQAE); hydroxycinnamic acid conjugates (HCAC); malonyl caffeoylquinic acid esters (MCQAE); di-hydroxycinnamoylquinic acid esters (DHCQAE).

Table 4. Eggplant fruit phenolic acid conjugate class least square means (high performance liquid chromatography peak area units) and percent of total phenolic acid values for individual phenolic acid classes of cultivars grown in greenhouse and open field environments at Beltsville, Maryland and Valencia, Spain. Estimates of stability variance for phenolic acids of cultivars across environments were calculated before (σ^2_i) and after (s^2_i) removal of environmental heterogeneity.

HCAA						
	Maryland		Spain			
Cultivar	Greenhouse	Open field	Greenhouse	Open field	σ^2_i	s^2_i
			Hybrids			
Black Magic	4591 (16.5)	5696 (24.4)	1687 (21.5)	927 (12.6)	**	ns
Classic	2424 (10.5)	6908 (23.8)	520 (7.2)	652 (7.2)	**	**
Epic	3302 (19.2)	3715 (18.6)	586 (9.4)	348 (6.9)	**	ns
Ghostbuster	2220 (11.5)	2582 (16.5)	900 (7.3)	884 (8.1)	ns	ns
Orient Express	789 (5.5)	603 (6.2)	304 (5.4)	138 (5.2)	**	*
			Open pollinated			
Black Beauty	4732 (19.5)	4451 (17.7)	448 (5.3)	1026 (14.7)	**	**
LF3-24	2206 (11.0)	2508 (11.3)	522 (8.3)	569 (7.4)	ns	ns
Listada de Gandia	1202 (8.1)	2418 (13.2)	316 (5.0)	420 (7.4)	**	**
			Landraces			
ALM 1	2932 (6.5)	3012 (7.9)	1132 (9.3)	608 (7.0)	ns	*

BBS 175	2157 (9.4)	3115 (12.7)	2017 (10.2)	1336 (10.1)	**	**
			Solanum aethiopicum			
BBS 157	590 (5.1)	392 (5.6)	519 (7.2)	225 (4.3)	**	**
			Solanum macrocarpon			
BBS 196	2458 (7.2)	4527 (12.9)	2457 (12.1)	1678 (9.7)	**	**
Mean	2292 (10.7)	2827 (13.6)	842 (9.3)	665 (8.6)		
			CQAE			
	Maryland		Spain			
Cultivar	Greenhouse	Open field	Greenhouse	Open field	σ^2_i	s^2_i
			Hybrids			
Black Magic	22464 (80.5)	16600 (71.3)	5690 (72.5)	5856 (79.4)	**	*
Classic	19718 (85.7)	20874 (71.9)	6376 (88.0)	7779 (85.9)	*	*
Epic	13303 (77.5)	15438 (77.4)	5333 (85.4)	4158 (83.0)	ns	ns
Ghostbuster	16261 (84.3)	11800 (75.3)	10845 (87.9)	9286 (85.6)	**	*
Orient Express	13053 (91.5)	8810 (90.5)	4847 (86.8)	2255 (84.6)	*	**
			Open pollinated			
Black Beauty	18805 (77.7)	19690 (78.4)	7629 (90.9)	5492 (78.8)	ns	ns
LF3-24	17080 (85.5)	18942 (85.4)	5214 (83.3)	6612 (85.6)	**	**
Listada de Gandia	13035 (88.4)	15369 (83.7)	5647 (89.1)	5005 (88.2)	ns	ns
			Landraces			
ALM 1	39303 (87.7)	33160 (87.1)	10233 (84.0)	7528 (86.9)	**	ns

BBS 175	19547 (85.1)	19432 (78.9)	16582 (84.2)	11054 (83.3)	**	*
			Solanum aethiopicum			
BBS 157	9537 (82.7)	5846 (84.1)	5532 (76.8)	3922 (74.5)	**	**
			Solanum macrocarpon			
BBS 196	26008 (76.5)	27387 (78.0)	12955 (63.6)	13296 (76.9)	ns	ns
Mean	18368 (85.7)	17017 (82.0)	7728 (85.0)	6521 (84.6)		

DHCQAE

	Maryland		Spain			
Cultivar	Greenhouse	Open field	Greenhouse	Open field	σ^2_i	s^2_i
			Hybrids			
Black Magic	205 (0.7)	294 (1.3)	16 (0.2)	51 (0.7)	**	**
Classic	167 (0.7)	374 (1.3)	30 (0.4)	54 (0.6)	**	**
Epic	112 (0.7)	223 (1.1)	7 (0.1)	66 (1.3)	**	**
Ghostbuster	86 (0.4)	173 (1.1)	46 (0.4)	30 (0.3)	ns	ns
Orient Express	29 (0.2)	15 (0.2)	9 (0.2)	0 (0)	**	**
			Open pollinated			
Black Beauty	205 (0.7)	294 (1.0)	16 (0.2)	51 (1.0)	**	**
LF3-24	0 (0)	0.4 (0.01)	2 (0.01)	12 (0.2)	**	ns
Listada de Gandia	63 (0.4)	55 (0.3)	14 (0.2)	2 (0.01)	ns	*
			Landraces			
ALM 1	343 (0.8)	494 (1.3)	83 (0.7)	23 (0.3)	**	*
BBS 175	470 (2.0)	682 (2.8)	160 (0.8)	67 (0.5)	**	**

			Solanum aethiopicum			
BBS 157	583 (5.1)	341 (4.9)	436 (6.1)	163 (3.1)	**	**
			Solanum macrocarpon			
BBS 196	0 (0)	53 (0.2)	72 (0.4)	66 (0.4)	**	**
Mean	132 (0.6)	192 (0.9)	47 (0.5)	39 (0.5)		

HCAC

	Maryland		Spain			
Cultivar	Greenhouse	Open field	Greenhouse	Open field	σ^2	s^2
			Hybrids			
Black Magic	126 (0.5)	189 (0.8)	262 (3.3)	298 (4.0)	ns	ns
Classic	111 (0.5)	268 (0.9)	141 (1.9)	283 (3.1)	**	**
Epic	67 (0.4)	169 (0.8)	142 (2.3)	268 (5.3)	ns	*
Ghostbuster	129 (0.7)	307 (2.0)	154 (1.3)	348 (3.2)	**	**
Orient Express	70 (0.5)	99 (1.0)	147 (2.6)	113 (4.2)	ns	ns
			Open pollinated			
Black Beauty	88 (0.5)	187 (0.8)	148 (3.3)	198 (4.0)	ns	ns
LF3-24	129 (0.6)	257 (1.2)	397 (6.3)	319 (4.1)	ns	ns
Listada de Gandia	119 (0.8)	242 (1.3)	215 (3.4)	109 (1.9)	**	**
			Landraces			
ALM 1	365 (0.8)	374 (1.0)	411 (3.4)	215 (2.5)	**	**
BBS 175	224 (1.0)	436 (1.8)	424 (2.2)	444 (3.3)	ns	ns

			Solanum aethiopicum			
BBS 157	720 (6.2)	260 (3.7)	698 (9.7)	933 (17.7)	**	**
			Solanum macrocarpon			
BBS 196	1 (0.01)	404 (1.1)	457 (2.2)	376 (2.2)	**	**
Mean	143 (0.7)	257 (1.2)	278 (3.1)	300 (3.9)		

MCQAE

	Maryland		Spain			
Cultivar	Greenhouse	Open field	Greenhouse	Open field	σ^2_i	s^2_1
			Hybrids			
Black Magic	210 (0.8)	298 (1.3)	150 (1.9)	104 (1.4)	ns	ns
Classic	354 (1.5)	458 (1.6)	181 (2.5)	149 (1.6)	ns	ns
Epic	144 (0.8)	268 (1.3)	89 (1.4)	18 (0.4)	**	**
Ghostbuster	361 (1.9)	632 (4.0)	180 (1.5)	106 (1.0)	**	**
Orient Express	84 (0.6)	5 (0.01)	3 (0.1)	22 (0.8)	**	**
			Open pollinated			
Black Beauty	190 (0.8)	293 (1.2)	106 (1.3)	72 (1.0)	ns	ns
LF3-24	280 (1.4)	180 (0.8)	65 (1.0)	90 (1.2)	ns	*
Listada de Gandia	36 (0.2)	59 (0.3)	87 (1.4)	0 (0)	**	**
			Landraces			
ALM 1	1013 (2.3)	456 (1.2)	283 (2.3)	94 (1.1)	**	*
BBS 175	441 (1.9)	486 (2.0)	424 (2.2)	245 (1.9)	ns	ns
			Solanum aethiopicum			

BBS 157	0 (0)	0 (0)	0	8 (0.2)	**	**
			Solanum macrocarpon			
BBS 196	5363 (15.8)	2639 (7.5)	4428 (21.7)	1872 (10.8)	**	**
Mean	257 (1.2)	223 (1.1)	138 (1.5)	81 (1.1)		

HCQAE

	Maryland		Spain			
Cultivar	Greenhouse	Open field	Greenhouse	Open field	σ^2_i	s^2_1
			Hybrids			
Black Magic	296 (1.1)	221 (0.9)	41 (0.5)	135 (1.8)	ns	*
Classic	241 (1.0)	151 (0.5)	0 (0)	135 (1.5)	**	**
Epic	236 (1.4)	129 (0.6)	90 (1.4)	150 (3.0)	**	**
Ghostbuster	230 (1.2)	182 (1.2)	217 (1.8)	199 (1.8)	**	ns
Orient Express	238 (1.7)	203 (2.1)	277 (5.0)	137 (5.2)	**	**
			Open pollinated			
Black Beauty	233 (1.0)	257 (1.0)	46 (0.5)	117 (1.7)	ns	ns
LF3-24	287 (1.4)	300 (1.4)	611 (1.0)	117 (1.5)	ns	ns
Listada de Gandia	294 (2.0)	211 (1.1)	59 (0.9)	136 (2.4)	ns	ns
			Landraces			
ALM 1	842 (1.9)	569 (1.5)	37 (0.3)	190 (2.2)	**	**
BBS 175	137 (0.6)	472 (1.9)	77 (0.4)	118 (0.9)	**	**
			Solanum aethiopicum			

BBS 157	98 (0.8)	110 (1.6)	22 (0.3)	15 (0.3)	**	**
		Solanum macrocarpon				
BBS 196	151 (0.4)	119 (0.3)	0 (0)	0 (0)	**	**
Mean	253 (1.2)	228 (1.1)	55 (0.6)	105 (1.4)		

*, **, ns: Significant at *P* = 0.05 or 0.01 and non-significant, respectively.

Phenolic acid conjugate class abbreviations: hydroxycinnamic acid amides of polyamines (HCAA); caffeoylquinic acid esters (CQAE); hycroxycinnamoylquinic acid esters (HCQAE); hydroxycinnamic acid conjugates (HCAC); malonyl caffeoylquinic acid esters (MCQAE); di-hydroxycinnamoylquinic acid esters (DHCQAE).

Table 5. Pearson correlation coefficients for phenolic acid conjugate classes in eggplant fruit grown in Beltsville, Maryland and Valencia, Spain under greenhouse and open field conditions.

			CQAE	DHCQAE	HCAC	MCQAE	HCQAE
HCAA	Maryland	Greenhouse	0.62	-0.03	-0.17	0.40	0.37
		Open field	0.72	0.23	0.27	0.70	0.16
	Spain	Greenhouse	0.71	0.32	0.43	0.60	-0.16
		Open field	0.86	0.30	0.18	0.62	-0.02
CQAE	Maryland	Greenhouse		0.11	0.02	0.61	0.58
		Open field		0.17	0.43	0.67	0.51
	Spain	Greenhouse		0.41	0.37	0.56	-0.03
		Open field		0.32	0.32	0.60	0.03
DHCQAE	Maryland	Greenhouse			0.63	-0.38	-0.04
		Open field			0.37	0.10	0.26
	Spain	Greenhouse			0.59	-0.10	-0.16
		Open field			0.51	0.27	-0.27
HCAC	Maryland	Greenhouse				-0.49	-0.09
		Open field				0.37	0.28
	Spain	Greenhouse				0.07	-0.18
		Open field				0.27	-0.23

MCQAE	Maryland	Greenhouse	0.13
		Open field	0.14
	Spain	Greenhouse	-0.39
		Open field	-0.29

Shaded cells, significant at $P \leq 0.05$.

Phenolic acid conjugate class abbreviations: hydroxycinnamic acid amides of polyamines (HCAA); caffeoylquinic acid esters (CQAE); hycroxycinnamoylquinic acid esters (HCQAE); hydroxycinnamic acid conjugates (HCAC); malonyl caffeoylquinic acid esters (MCQAE); di-hydroxycinnamoylquinic acid esters (DHCQAE).