Identification of QTL affecting Vitamin C in Melon

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ABSTRACT

Vitamin C, also known as ascorbic acid, is an important fruit quality trait in melon (*Cucumis melo* L.). The purpose of this study was to identify randomly amplified polymorphic DNA (RAPD) markers associated with quantitative trait loci (QTL) for ascorbic acid content using bulked segregant analysis in an F_2 population from the melon cross of 'TAM Dulce' (high ascorbic acid) x TGR1551 (low ascorbic acid). A continuous distribution for ascorbic acid content was observed in the F_2 population indicating quantitative inheritance for the trait. Ascorbic acid was positively correlated with sucrose % composition (r=0.23) and negatively correlated with glucose % composition (r= -0.39). A total of 500 random primers were used to simultaneously screen between low and high ascorbic acid bulks, and between the parents 'TAM Dulce' and TGR1551. Nine RAPD markers, four amplified from 'TAM Dulce' and five amplified from TGR1551, were significantly associated with QTL for ascorbic acid content. Three and two QTL affecting ascorbic acid content accounted for 14% and 12% of the phenotypic variation, respectively. Of the nine markers identified, four were consistently associated with mature melon fruit sweetness. Marker OAW06.600 obtained from TGR1551 was associated with sucrose, sucrose % composition, and glucose % composition as well as ascorbic acid. These RAPD markers associated with ascorbic acid content could be applied in selection for enhanced ascorbic acid levels in melon.

RESUMEN

La vitamina C, también conocida como ácido ascórbico, es una carácter importante de la calidad del fruto del melón (*Cucumis melo* L.). El propósito de este estudio fue identificar marcadores RAPD (ADN polimórfico amplificado al azar) asociados con loci de caracteres cuantitativos (QTL) en lo referente a su contenido de ácido ascórbico usando el análisis de segregación en grupo de una población F_2 de la cruza de melón 'TAM Dulce' (alto contenido de ácido ascórbico) x TGR1551 (bajo contenido de ácido ascórbico). Se observó una distribución continua del contenido de ácido ascórbico en la población F_2 indicando una herencia cuantitativa para este carácter. El contenido de ácido ascórbico se correlacionó positivamente con el porcentaje de composición de sacarosa (R = 0.23) y negativamente con el porcentaje de composición de glucosa (R= -0.39). Un total de 500 primers aleatorios se usaron simultáneamente para distinguir entre grupos de alto y bajo contenido de ácido ascórbico, y entre los padres 'TAM Dulce' y TGR1551. Nueve marcadores RAPD, cuatro amplificados de 'Tam Dulce' y cinco amplificados de TGR1551, estuvieron asociados significativamente con el QTL para el contenido de ácido ascórbico. Tres y dos QTL que afectaron el contenido de ácido ascórbico explicaron el 14 y el 12% de la variación fenotípica, respectivamente. De los nueve marcadores identificados, cuatro estuvieron consistentemente asociados con la dulzura del fruto maduro de melón. El marcador OAW06.600 obtenido de TGR1551 se asoció con la sacarosa, el porcentaje de composición de sacarosa, y el porcentaje de composición de glucosa, así como con el ácido ascórbico. Estos marcadores RAPD asociados con el contenido de ácido ascórbico podrían ser utilizados para la selección de melón con mayor contenido de ácido ascórbico.

Additional Index Words: ascorbic acid, randomly amplified polymorphic DNA (RAPD) markers, quantitative trait loci

All melon (*Cucumis melo* L.) fruit flesh is a significant source of ascorbic acid, folic acid, and potassium (Richter, 2000) as well as free sugars and water (Martyn and Miller, 1996). Vitamin C, also known as ascorbic acid derived from glucose (Hopkins, 1963), is an important nutrient for human health (Lester and Crosby, 2002). It functions as a water soluble antioxidant in the human body (Lavine, 1986). It also plays a crucial role in keeping the immune system healthy (Eichholzer et al., 2001; Larsen, 1997). Due to consumer preference for healthy food, ascorbic acid is a highly important fruit quality trait in melon. The improvement of ascorbic acid content is a goal of the Texas melon breeding program.

Bulked segregant analysis (BSA) (Michelmore et al., 1991) is an efficient method to rapidly identify molecular markers linked to a specific gene using DNA bulks from F_2 plants. This technique, along with RAPDs, has been used to tag

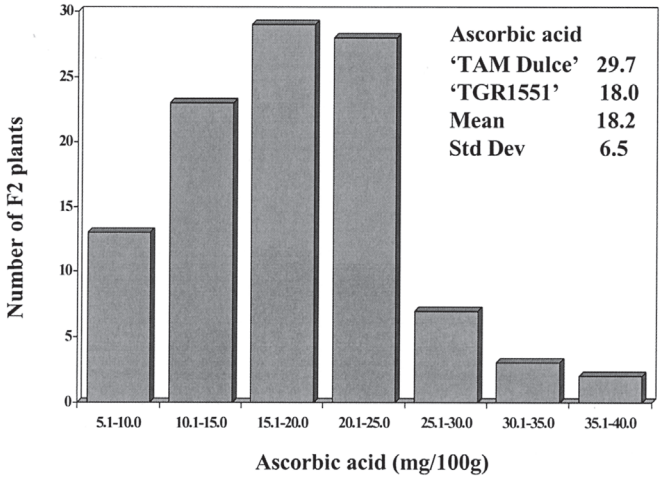

Fig. 1. A frequency distribution for ascorbic acid of F_2 plants derived from the melon cross of 'TAM Dulce' (high ascorbic acid) x TGR1551 (low ascorbic acid).

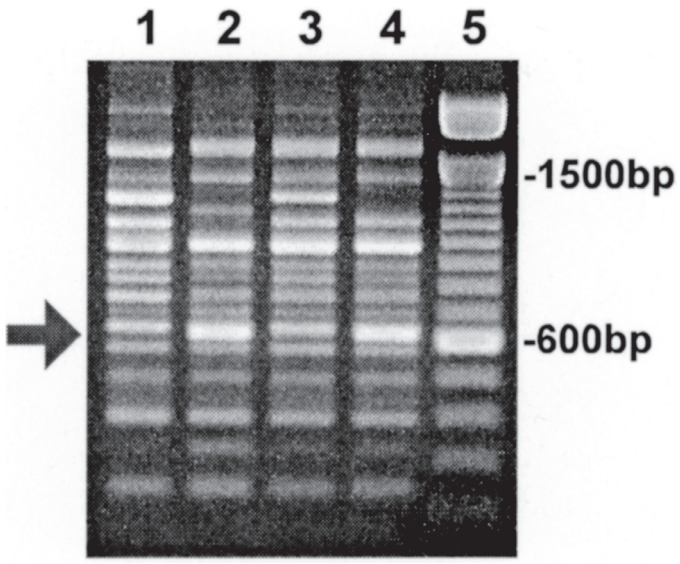

Fig. 2. RAPD marker OAW06.600 expressing polymorphism between two DNA bulks from high and low ascorbic acid F_2 plants, and between the high ascorbic acid parent 'TAM Dulce' and the low ascorbic acid parent TGR1551. 1='TAM Dulce', 2=TGR1551, 3=DNA bulk from eight high ascorbic acid F_2 plants, 4=DNA bulk from eight low ascorbic acid F_2 plants, and 5=a 100-bp DNA marker ladder.

the single recessive *ms-3* gene controlling male sterility (Park et al., 2004c) as well as single genes for disease and pest resistance such as the dominant *Fom 2* gene for resistance to Fusarium wilt (Wechter et al., 1995), the dominant *Vat* gene for resistance to melon aphid (Klingler et al., 2001), and the recessive *nsv* gene for resistance to the *Carmovirus* melon necrotic spot virus (Morales et al., 2002) in melons. Also, it has been applied in identifying RAPD markers associated with quantitative genes for mature melon fruit sweetness, size, and shape traits (Park and Crosby, 2004a; Park et al., 2004b).

Introducing high ascorbic acid genes into low or moderate ascorbic acid cultivars and breeding lines is a strategy recommended for enhancing melon fruit quality. Molecular markers linked to genes regulating ascorbic acid would be useful in transferring the high ascorbic acid genes into low ascorbic acid melon cultivars and lines. However, DNA markers associated with QTL controlling ascorbic acid present in 'TAM Dulce', a western shipper muskmelon type, have not been reported.

The objective of this study was to identify RAPD markers associated with QTL controlling ascorbic acid by means of BSA in an F_2 population derived from the melon cross of 'TAM Dulce' (high ascorbic acid) x TGR1551 (low ascorbic acid). Pearson correlations of ascorbic acid with seven mature fruit sweetness traits were also calculated in the population.

MATERIALS AND METHODS

Plant Material. One hundred five F_2 plants derived from the melon cross of 'TAM Dulce' x TGR1551 were planted in a greenhouse at the Texas Agricultural Research and Extension Center-Weslaco, Texas A&M University on 15 October 2002. The 'TAM Dulce' parent, a western shipper muskmelon type with high fruit quality, is resistant to powdery mildew (races 1 and 2), downy mildew, and fusarium wilt (race 2). The TGR1551 parent is a wild agrestis type with low fruit quality. Major quality characteristics of the two parents are indicated in Table 1. Data for ascorbic acid content were obtained from the F_2 plants using the procedure of Hodges et al. (2001).

RAPD. Fully expanded leaves of 105 F_2 plants along with their parents were collected at 21 days after planting in the greenhouse. Total genomic DNA was extracted from the leaf tissue using the method of Skroch and Nienhuis (1995). A total of 500 random 10-mer primers (Operon Technologies, Alameda, California) were used for the RAPD analysis (Williams et al., 1990). Polymerase chain reactions (PCR) were performed on 96-well plates in a MJ Research thermalcycler (model PTC-0100; MJ Research, Waltham, Massachusetts). Protocols for PCR and the composition of the final volume of reactants were the same as those described by Skroch and Nienhuis (1995). A 100-base pair (bp) DNA ladder (Life Technologies, Grand Island, New York) was used to estimate the length of RAPD markers. The name of each RAPD marker is derived from an 'O' prefix for Operon primers, the letters identifying the Operon kit, Operon primer

Table 1. A summary of selected fruit quality characteristics of the two melon parents 'TAM Dulce' and TGR1551.

Fruit quality trait	'TAM Dulce'	TGR1551
Ascorbic acid (mg/100g)	High	Low
Total soluble solids (%)	High	Low
Sucrose (mg/g)	High	Low
Glucose (mg/g)	Moderate	Moderate
Fructose (mg/g)	High	Moderate
Sucrose % composition of total sugars	High	Low
Glucose % composition of total sugars	Moderate	High
Fructose % composition of total sugars	Moderate	High
Andromonoecious (a)	Perfect	Mono

number, and the approximate length (bp) of the marker (Park et al., 2004a).

Bulked Segregant Analysis. Two low and high DNA bulks were prepared from eight selected F_2 plants with the highest and lowest values for ascorbic acid, respectively. The 500 primers were used to simultaneously screen between the low and high DNA bulks, and between the parents 'TAM Dulce' and TGR1551. Primers that generated polymorphisms between the low and high DNA bulks for ascorbic acid were tested in the F_2 population derived from the cross between 'TAM Dulce' and TGR1551 for identifying ascorbic acid QTL.

Linkage Analysis. To detect segregation distortion of markers, the F_2 population marker datum was tested for goodness-of-fit to a 3:1 ratio using the chi-square test. Due to the dominant nature of RAPD markers, the linkage analysis of four markers obtained from 'TAM Dulce' or five markers obtained from TGR1551 was separately performed on the data for 105 F_2 plants of the cross 'TAM Dulce' x TGR1551 using MAPMAKER version 3.0 (Lander et al., 1987). Map distances [centimorgan (cM)] between ordered loci of markers were calculated using recombination fractions and the Kosambi mapping function (Kosambi, 1944).

Detection of QTL. Simple linear regression for each pairwise combination of quantitative trait and marker locus was used to analyze the data for detection of QTL affecting ascorbic acid content. Significant differences in trait associations were based on F-tests (P<0.05) (Edwards et al., 1987). Loci with the lowest P value per QTL were chosen and then were added in a stepwise multiple regression to select the best set of markers (P<0.05) for prediction of the total trait phenotypic variation explained by the identified QTL (Paterson et al., 1991). Pearson correlations between ascorbic acid and seven mature fruit sweetness traits including three sugar components were also determined in this genetic population. All statistical analyses were conducted using the Statistical Analysis System (SAS Inst., Cary, N.C.).

RESULTS AND DISCUSSION

Inheritance of Ascorbic Acid. A distinct separation for ascorbic acid content between the parents was observed (Table 1). Fruits of 'TAM Dulce' had high ascorbic acid content. In contrast, TGR1551 plants possessed low ascorbic acid content. All F_1 plants had low ascorbic acid content. We found a skewed distribution for ascorbic acid towards low values. A continuous frequency distribution for ascorbic acid content was noted in the F_2 population from the cross of 'TAM Dulce' x TGR1551 in the greenhouse (Fig. 1) indicating quantitative inheritance for the quality trait. Complex inheritance patterns of three organic acids (Etienne et al., 2002) and two antioxidant compounds (Causse et al., 2002) were also reported in other crops.

Correlations of Ascorbic Acid with Sweetness. A significant positive correlation was observed between ascorbic acid content and sucrose % composition, while a significant negative correlation was detected between ascorbic acid content and glucose % composition (Table 2). It is expected that a significant negative correlation would occur between ascorbic acid and glucose composition, as glucose is the precursor molecule for ascorbic acid (Hopkins, 1963). We found no significant correlations of ascorbic acid content with other important mature fruit sweetness traits such as total soluble solids (TSS), sucrose, and fructose contents in this population. In peach, however, citric acid content was negatively correlated with TSS and sucrose contents and positively correlated with glucose and fructose contents (Etienne et al., 2002). Causse et al. (2002) reported a positive correlation between carotene and TSS contents in tomato.

Identification of QTL for Ascorbic Acid. A total of 500 primers were used for the RAPD analysis of two different bulks for ascorbic acid along with their parents 'TAM Dulce'

Table 2. Pearson correlations of ascorbic acid (AA), total soluble solids (TSS), and sugars in an F_2 population derived from the melon cross of 'TAM Dulce' x TGR1551.

Trait	TSS	Sucrose	Glucose	Fructose	SCTS[1]	GCTS	FCTS
AA	0.06^{NS}	0.15^{NS}	-0.08^{NS}	0.12^{NS}	0.23*	-0.39**	0.17^{NS}

[1]SCTS = sucrose % composition of total sugars, GCTS = glucose % composition of total sugars, FCTS = fructose % composition of total sugars.

^{NS},*,**Nonsignificant or significant at $P \leq 0.05$ or 0.01, respectively.

Table 3. Chi-square analyses for segregation of nine RAPD markers associated with ascorbic acid in an F_2 population derived from the melon cross of 'TAM Dulce' x TGR1551.

		Number of F_2 plants				
Marker	Source	Presence	Absence	Ratio	X^2	P
OAT03.1600	TAM Dulce	79	26	3:1	0.00	0.96
OAU13.1350	TAM Dulce	75	30	3:1	0.53	0.46
OAW06.1100	TAM Dulce	80	25	3:1	0.02	0.87
OAT03.250	TAM Dulce	75	30	3:1	0.53	0.46
OAS14.800	TGR1551	72	33	3:1	1.98	0.16
OAU02.600	TGR1551	72	33	3:1	1.98	0.16
OAU03.700	TGR1551	72	33	3:1	1.98	0.16
OAW10.400	TGR1551	70	35	3:1	3.45	0.06
OAW06.600	TGR1551	80	25	3:1	0.02	0.87

Table 4. Simple linear regression and stepwise multiple regression analyses of marker and data for detection of QTL for ascorbic acid in an F_2 population derived from the cross of 'TAM Dulce' (high ascorbic acid) x TGR1551 (low ascorbic acid).

			Single-factor ANOVA		Average value		Stepwise regression	
RAPD marker	Source	Linkage	*P*	R^2 (%)	Presence	Absence	*P*	R^2 (%)
OAT03.1600	TAM Dulce	Unlinked	0.020	5	19.1[z]	15.7[y]	0.020	5
OAT03.250	TAM Dulce	Unlinked	0.024	5	19.2	16.0	0.025	5
OAW06.1100	TAM Dulce	Unlinked	0.039	4	17.5	20.6	0.033	4
OAU13.1350	TAM Dulce	Unlinked	0.026	5	19.0	14.0		
							Cumulative R^2 = 14	
OAW10.400	TGR1551	Linked[x]	0.002	9	16.9	21.1	0.002	9
OAW06.600	TGR1551	Unlinked	0.027	5	17.5	20.8	0.047	3
OAU03.700	TGR1551	Linked	0.003	8	17.0	21.2		
OAU02.600	TGR1551	Linked	0.007	7	17.1	21.0		
OAS14.800	TGR1551	Linked	0.007	7	17.1	21.0		
							Cumulative R^2 = 12	

[z]An average value of F_2 plants with band presence for the marker.
[y]An average value of F_2 plants with band absence for the marker.
[x]Four RAPD markers, amplified from TGR1551, were linked within a distance of 8.5 cM on one linkage group.

Table 5. Common RAPD markers associated with two to six traits including ascorbic acid (AA), total soluble solids (TSS), and sugars in an F_2 population from the cross 'TAM Dulce' x TGR1551.

Marker	Source	AA	TSS	Sucrose	Glucose	Fructose	SCTS[1]	GCTS	FCTS
OAT03.1600	TAM Dulce	*	NS	NS	NS	NS	NS	*	NS
OAU13.1350	TAM Dulce	*	NS	***	NS	NS	***	***	NS
OAT03.250	TAM Dulce	*	*	*	NS	*	*	**	NS
OAW06.600	TGR1551	*	**	***	NS	*	***	***	NS

[1]SCTS = sucrose % composition of total sugars, GCTS = glucose % composition of total sugars, FCTS = fructose % composition of total sugars.
[NS],*,**,***Nonsignificant or significant at $P \leq 0.05$, 0.01 or 0.001, respectively.

and TGR1551. Nine RAPD markers were polymorphic between the two different DNA bulks. Four displayed an amplified DNA fragment in the high bulk that was absent in the low bulk. Five showed an amplified DNA fragment in the low bulk that was absent in the high bulk. An example of marker OAW06.600 is shown in Fig. 2. These nine marker fragments segregated in the F_2 population of the cross 'TAM Dulce' x TGR1551. A goodness-of-fit to a 3:1 ratio for band presence to band absence for each of the nine markers was observed in 105 F_2 plants (Table 3). Of the five markers that displayed an amplified DNA fragment in the low bulk, four were linked within a distance of 8.5 cM on one linkage group. The four markers that showed an amplified DNA fragment in the high bulk were unlinked based on linkage analysis, suggesting that they are located on different chromosomes.

Nine RAPD markers, four produced from 'TAM Dulce' and five obtained from TGR1551, were associated with QTL regulating ascorbic acid concentration in our population based on simple linear regression (Table 4). For the genetic markers, except OAW06.1100, high ascorbic acid alleles were contributed by the 'TAM Dulce' parent. The four unlinked markers accounted for 4% to 5% of the variation for the ascorbic acid trait. Three markers OAT03.1600, OAT03.250, and OAW06.1100 from 'TAM Dulce' explaining 14% of the total variation for the trait were detected using the stepwise multiple regression analysis. The five markers accounted for 5% to 9% of the variation for the vitamin C trait. Two unlinked markers OAW10.400 and OAW06.600 from TGR1551 were significant in the stepwise multiple regression with a total R^2 of 12%.

RAPD markers linked to quantitative genes for fruit size and shape traits as well as qualitative genes for pest and disease resistance have been detected successfully by means of BSA in melons (Klingler et al., 2001; Morales et al., 2002; Park and Crosby, 2004a; Wechter et al., 1995). Etienne et al. (2002) mapped a single QTL with major effect influencing organic acid contents such as malic acid, citric acid, and quinic acid on a peach linkage map. Causse et al. (2002) tagged QTL affecting antioxidant compounds including lycopene and carotene contents on a tomato linkage map. A major QTL controlling titratable acidity and pH was reported in peach (Etienne et al., 2002), whereas few to many QTL affecting the two traits were found in several tomato populations (Causse et al., 2002; Georgelis et al., 2004; Paterson et al., 1991). However, this is the first report of RAPD markers associated with QTL for the important antioxidant, vitamin C, by means of BSA in melon. Among watermelon and several melon types, muskmelon melons possessed the highest vitamin C content (Pratt, 1971). Therefore, these nine markers identified in the muskmelon type could be at least partially utilized in improving the level of this nutrient in new melon cultivars.

Common Markers Associated with Ascorbic Acid and Sweetness. Of the nine RAPD markers associated with ascorbic acid, four were noted to be consistently associated with one to five mature melon fruit sweetness traits in this

genetic population based on the finding of Park and Crosby (2004b) (Table 5). Particularly, OAU13.1350 produced from 'TAM Dulce' was associated with sucrose, sucrose % composition of total sugars, and glucose % composition of total sugars, and accounted for 10% to 19% of the phenotypic variation for these sweetness traits. OAW06.600 generated from TGR1551 was associated with TSS, sucrose, fructose, sucrose % composition of total sugars, and glucose % composition of total sugars, and explained 5% to 18% of the variation for the traits. OAT03.250 was also associated with the five sugar traits. The andromonoecious (*a*) gene on linkage group 4 of the classical melon map regulating stamen absence or stamen presence in female flowers was reported by Park and Crosby (2004b) to be significantly associated with two sugar traits such as TSS and sucrose in the F_2 population from the cross of 'TAM Dulce' x TGR1551. However, we found no significant association of the a gene with ascorbic acid content. Clusters of QTL in a genomic region controlling several melon fruit sweetness traits (Park et al., 2004b), melon fruit size and shape traits (Park and Crosby, 2004a; Perin et al., 2002), tomato fruit size and quality traits (Causse et al., 2002; Georgelis et al., 2004), and peach fruit sweetness and quality traits (Etienne et al., 2002) have been reported. These RAPD markers associated with the sugar synthesis QTL could be useful to transfer these genes into a low sugar cultivar or breeding line to enhance the mature melon fruit sweetness.

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