J. Amer. Soc. Hort. Sci. 144(5):352–362. 2019. https://doi.org/10.21273/JASHS04729-19

Quantitative Trait Locus Analysis in Avocado: The Challenge of a Slow-maturing Horticultural Tree Crop

Vanessa E.T.M. Ashworth[5]
Department of Botany and Plant Sciences, University of California, Riverside, CA 92521

Haofeng Chen[1] **and Carlos L. Calderón-Vázquez**[2]
Department of Ecology and Evolutionary Biology, University of California, Irvine, CA 92697

Mary Lu Arpaia
Department of Botany and Plant Sciences, University of California, Riverside, CA 92521

David N. Kuhn[3]
USDA-ARS Subtropical Horticulture Research Station, Miami, FL 33158

Mary L. Durbin[3] **and Livia Tommasini**[4]
Department of Ecology and Evolutionary Biology, University of California, Irvine, CA 92697

Elizabeth Deyett and Zhenyu Jia
Department of Botany and Plant Sciences, University of California, Riverside, CA 92521

Michael T. Clegg[3]
Department of Ecology and Evolutionary Biology, University of California, Irvine, CA 92697

Philippe E. Rolshausen[5]
Department of Botany and Plant Sciences, University of California, Riverside, CA 92521

Additional index words. *Persea americana*, β-sitosterol, candidate gene, linkage map, marker-assisted selection, vitamin E

Abstract. The glossy, green-fleshed fruit of the avocado (*Persea americana*) has been the object of human selection for thousands of years. Recent interest in healthy nutrition has singled out the avocado as an excellent source of several phytonutrients. Yet as a sizeable, slow-maturing tree crop, it has been largely neglected by genetic studies, owing to a long breeding cycle and costly field trials. We use a small, replicated experimental population of 50 progeny, grown at two locations in two successive years, to explore the feasibility of developing a dense genetic linkage map and to implement quantitative trait locus (QTL) analysis for seven phenotypic traits. Additionally, we test the utility of candidate-gene single-nucleotide polymorphisms developed to genes from biosynthetic pathways of phytonutrients beneficial to human health. The resulting linkage map consisted of 1346 markers (1044.7 cM) distributed across 12 linkage groups. Numerous markers on Linkage Group 10 were associated with a QTL for flowering type. One marker on Linkage Group 1 tracked a QTL for β-sitosterol content of the fruit. A region on Linkage Group 3 tracked vitamin E (α-tocopherol) content of the fruit, and several markers were stable across both locations and study years. We argue that the pursuit of linkage mapping and QTL analysis is worthwhile, even when population size is small.

Avocado is a long-lived tree crop grown worldwide for its tasty and nutritionally valuable fruit. Cultivar Hass dominates the United States market, where production in 2017 ran to 146,000 tons valued at $392 million (U.S. Department of Agriculture, 2018). Mexico generated over half of the global output of primarily 'Hass' in 2017, with Peru, Chile, South Africa, Dominican Republic, New Zealand, Israel, and others contributing a substantial market share.

'Hass' has attained its current popularity owing to its excellent flavor, but the cultivar does not excel in all aspects of its growth and productivity, and there is a need to develop new cultivars with improved characteristics. Breeders, therefore, need to consider a wide range of yield- and growth-related attributes that, collectively, ensure efficient and reliable fruit production into the future (Lahav and Lavi, 2009), including tree size and shape, flowering season, and early onset of fruit production, as well as factors contributing to a high fruit set, such as flowering type. Fruit nutritional composition is a further aspect that has seen a recent surge in interest. Among the health benefits attributed to avocado are its heart-healthy properties, reduction of blood lipids, and anticarcinogenic properties (D'Ambrosio, 2007; Ding et al., 2009; Lopez-Ledesma et al.,

Received for publication 29 Apr. 2019. Accepted for publication 4 July 2019. This research was supported in part by a University of California Discovery Grant and the California Avocado Commission (CAC) to M.C., V.A., C.C., H.C., M.D., and L.T.; by the CAC to M.A.; and USDA-ARS (CRIS 6631-21000-022) to D.K.

[1]Current address: National Institute for Health and Family Planning, No. 12 Dahuisi Road, Beijing 100081, China.
[2]Current address: Instituto Politécnico Nacional, CIIDIR Unidad Sinaloa, San Joachín, Guasave, Sinaloa, Mexico.
[3]Retired.
[4]Independent researcher.
[5]Corresponding authors. E-mail: vanessa.ashworth@ucr.edu or philippe.rolshausen@ucr.edu.

1996) conferred by three main groups of compounds: β-sitosterol, carotenoids, and vitamin E.

Most of these phenotypic traits are inherited in a quantitative fashion; i.e., they are controlled by many genes of small effect and are typically under strong environmental influence. Yet only the genetic component of a phenotype will respond to breeding. Two studies in avocado (Calderón-Vázquez et al., 2013; Chen et al., 2007) used quantitative genetics to tease apart the genetic and the environmental components of the phenotypic value of a suite of quantitative traits. Chen et al. (2007) demonstrated for the progeny of cultivar Gwen that major growth-related traits, such as plant height and trunk- and canopy diameter, were under genetic control and showed sufficient heritability to respond to selection. Similarly, Calderón-Vázquez et al. (2013) showed for a 'Gwen' × 'Fuerte' experimental population—a subset of the population studied by Chen et al. (2007)—that β-sitosterol, carotenoids, and vitamin E of the fruit are likely to respond to breeding.

On theoretical grounds, therefore, breeding avocado for growth-related traits and enhanced levels of fruit nutrients is feasible. However, breeding in this long-lived tree crop is frustrated by an outcrossing breeding system, high heterozygosity, long generation times [up to 15 years (Bergh and Lahav, 1996)], and the need for costly field trials to accommodate tree size and a protracted maturation (Van Nocker and Gardiner, 2014). Moreover, controlled pollination is impracticable (Degani et al., 2003; Lammerts, 1942) owing to a profusion of tiny flowers and immature fruitlets—most of which are shed prematurely, and conventional breeding populations (e.g., doubled haploids, recombinant inbred lines) do not exist. At this time, avocado breeders have no option but to use phenotypic selection, which is associated with slow breeding advance. A move toward molecular breeding is a promising alternative to accelerate selection progress and to reduce costs associated with the maintenance of breeding populations.

When designing large-scale experiments leading to molecular breeding, the problem of high land and labor costs loom large, so genetic mapping populations tend to be small and poorly replicated, predisposing data to low statistical power. Yet many horticultural tree crops produce high-value fruit for which the genetic dissection of phenotypic traits is of considerable interest, raising the question whether mapping and quantitative trait locus studies may nonetheless be worthwhile, given adequate precautions. With the advent of next-generation technologies, the costs associated with developing abundant genetic markers have declined significantly, and a shortage of markers no longer represents a constraint. We explore the possibility of generating a linkage map and of estimating QTLs for seven phenotypic traits collected in a mapping population of 50 trees using over 5000 molecular markers. We ask whether a modestly sized mapping population can be used to estimate significant QTL loci and whether these loci are likely to be sufficiently robust.

Materials and Methods

Mapping population. The experimental population of avocado trees consisted of the full-sib progeny of a 'Gwen' (G) × 'Fuerte' (F) cross. The G × F progeny is a subset of a larger population of open-pollinated trees raised from the fruit of a 'Gwen' maternal tree. Each progeny tree was screened using 10 simple sequence repeat (SSR) markers (Ashworth et al., 2004) to verify the origin of the pollen source. Of more than 200 progeny genotypes analyzed, 50 were the result of the cross G × F and were set aside for the mapping project. The remainder consisted of about 50 individuals each of G × 'Bacon', G × 'Zutano', and a miscellaneous group of largely unidentified pollen origin (Chen et al., 2007) that are not considered further here.

Four clonal replicates of each G × F progeny tree were grafted on 'Duke 7' rootstock and planted at two sites in southern California: two of the four replicate trees were grown in a randomized block design at a coastal location [University of California (UC) South Coast Research and Extension Center, Irvine, CA] and the other two replicate trees at an inland location (Agricultural Operations, UC Riverside campus, Riverside, CA), also in a randomized block layout. Each location, therefore, contained two replicates of 50 tree genotypes (100 trees). All trees were planted in the ground between Fall 2001 and Spring 2003.

Trees were spaced at 6.1 m between rows and at 4.6 m between trees within the same row. At the coastal site, fertilizer was applied at 0.45 kg/tree as a granular formulation of 15N–6.5P–12.5K in late March/early April. At the inland site, a 32N–0P–0K fertilizer solution was introduced into the irrigation water at 284.24 $L \cdot ha^{-1}$ in January. At both locations, the fertilizer regime was managed to industry standard. Irrigation water was dispensed from two microsprinklers per tree following guidelines established by California Irrigation Management Information System (CIMIS, 2003). The coastal location (Irvine) differed from the inland location (Riverside) by higher average rainfall, cooler average summer temperatures, and warmer average winter temperatures (Table 1). Soils at both locations were sandy loams. The Riverside site followed a gentle hillside contour that consisted of three different sandy loam subtypes (Table 1).

Phenotypic traits. Seven datasets were collected from the experimental trees, including one qualitative (flowering type) and six quantitative (three measures of tree dimension, and three nutrients assayed in the avocado fruit flesh). Descriptive statistics for each quantitative trait are provided in Fig. 1.

Flowering type was recorded in Apr. 2013 at the coastal location in 100 trees. Avocado flowers exhibit protogynous dichogamy, a mechanism designed to prevent self-pollination by temporally separating stigma receptivity and pollen release (Sedgley, 1985). A tree was recorded as having B-type flowering if its flowers were in the male phase in the morning and as having A-type flowering if flowers were in the female phase in the morning. In commercial orchards, optimal pollination and fruit set in cultivars with A-type flowering (e.g., 'Hass' and 'Gwen') is achieved by interplanting with B-type pollinizer cultivars (e.g., 'Fuerte' and 'Bacon') (Alcaraz and Hormaza, 2009). This trait was scored as a discrete character (presence or absence), with A-type flowering recorded as "1" and B-type flowering as "2."

Measures of tree growth were collected at both locations each year from 2003 to 2005, but only the final year's data were used in this study because the later-planted trees were still very immature during the first two years. Three measurements of tree dimension—trunk diameter, tree height, and canopy diameter—were recorded as a way of characterizing the three-dimensional aspect of early tree growth (Chen et al., 2007). Trunk diameter was determined at ≈10 cm aboveground in two perpendicular orientations, with values averaged. Plant height

Table 1. Climatic characteristics at Irvine and Riverside, CA, the two locations of the avocado mapping populations. Data are averages for 1981–2010 (U.S. Climate Data, 2018).

Climate	Irvine	Riverside
Annual high temperature (°C)	22.6	26.4
Highest monthly average temperature—August (°C)	28.3	35.0
Annual low temperature (°C)	12.4	10.8
Lowest monthly average temperature—December (°C)	8.3	5.6
Average temperature (°C)	17.5	18.6
Average annual precipitation (mm)	366.7	262.1
Soil type	San Emigdio fine sandy loam	Arlington fine sandy loam; Hanford coarse sandy loam; Ramona sandy loam

was measured from ground level to the tip of the tree. Canopy diameter was determined at the widest part of the canopy in two orientations: parallel to the orchard row and perpendicular to the row, with the two values averaged.

Fruit nutrient composition [α-tocopherol (the most biologically active form of vitamin E in humans), β-sitosterol, and carotenoids] was assayed in fruit collected at both locations in 2009 and 2010. Fruit preparation and chemical assays for determination of the contents of α-tocopherol, β-sitosterol, and carotenoids in fruit tissue were adapted from Jeong and Lachance (2001), Mäeorg et al. (2007), and Ryan et al. (2007) and are detailed in Calderón-Vázquez et al. (2013). For any given tree, five fruit were picked at an optimum dry weight of 20% and then allowed to ripen in the laboratory. At ripeness, the flesh from the five fruit was pooled and homogenized, and aliquots were frozen and set aside for further analyses. Total carotenoids, which include α-carotene, β-carotene, β-cryptoxanthin, lutein, and zeaxanthin, were isolated using two extractions in hexane/petroleum ether (1:1). An aliquot of the resulting aqueous phase was analyzed by taking a spectrophotometric reading at 456 nm and comparing it to a standard curve for β-carotene (C4582; Sigma-Aldrich, St. Louis, MO) according to Luterotti et al. (2006). Beta-sitosterol and α-tocopherol contents were determined by application of the organic phase fraction to thin-layer chromatographic plates. Bands were visualized by dipping in phosphomolybdic acid (02553, Sigma-Aldrich) and quantified on an AlphaImager HP System (ProteinSimple, Santa Clara, CA) using standard curves generated from reference samples [β-sitosterol (S1270, Sigma-Aldrich), α-tocopherol (T3251, Sigma-Aldrich)]. Values for the parental cultivars Gwen and Fuerte were determined in trees growing at the coastal location using the same preparation and assay conditions as for the progeny (Calderón-Vázquez et al., 2013).

Statistical analyses of the phenotypic data were performed in R version 3.4.4 (R Core Team, 2019) using a nonparametric Kruskal–Wallis test to compare datasets, followed by a Wilcox test for pairwise comparisons and calculation of probability values.

Genetic markers. The genetic markers implemented in this study consisted of SSRs and single-nucleotide polymorphisms (SNPs) from several sources; the bulk of markers were SNPs developed by Kuhn et al. (2019). In our map, these SNPs were used to augment the total number of markers to ensure adequate map density. The second set of SNP markers was developed in a gene discovery effort targeting candidate genes from several biosynthetic pathways involved in fruit nutrient composition. These candidate-gene SNPs (CG-SNPs) have not previously been published and their development is described in the following two paragraphs. In addition, we used published SSR markers developed by Sharon et al. (1997), Borrone et al. (2007), and Ashworth et al. (2004), as well as 28 SSR markers available from GenBank (V.E. Ashworth, C. Calderón-Vázquez, M.L. Durbin, L. Tommasini, and M.T. Clegg, unpublished data).

SNPs by Kuhn et al. [2019 (FL-SNPs)] originated by Illumina GAII sequencing (Illumina, San Diego, CA), and the individuals of our 'Gwen' × 'Fuerte' mapping population were included on the Illumina Infinium oligonucleotide array chip that assayed each tree genotype for 5050 FL-SNP markers. Details of marker development are provided in Kuhn et al. (2019).

Nutrient-related candidate genes were identified by aligning avocado expressed sequence tag (EST)/cDNA (complementary DNA) sequences from fruit-, flower-, and other organ-specific libraries developed by Cornell University [Ithaca, NY (Floral Genome Project, 2005)], HortResearch (Mt Albert, New Zealand), and CINVESTAV (Irapuato, Mexico) to sequences of functionally characterized gene sequences deposited in TAIR (2005) or NCBI (2005). Avocado mRNA sequences showing high similarity to core enzymes in the flavonoid, carotenoid, fatty acid, and B-, C-, and E-vitamin biosynthesis pathways were retained. Their relevance in determining fruit nutritional composition was further verified by comparison with sequences from an avocado cDNA library developed from the fruit of cultivar Hass. Sequence alignment allowed design of amplification primers in conserved regions. Nested sequencing primers provided about 500 base pairs of high-quality DNA sequence.

SNP discovery was performed in sequences from a panel of 10 randomly chosen 'Gwen'×'Fuerte' progeny genotypes. SNPs were identified by standard resequencing using the Sanger method. Sequence reads were assembled using Phred/Phrap/Consed (Ewing and Green, 1998; Gordon et al., 1998), and PolyPhred was used to detect the SNP sites (Nickerson et al., 1997). A total of 83 SNPs was developed from 28 candidate genes. Avocado genomic DNA of the 10 'Gwen' × 'Fuerte' progeny was extracted from frozen young (flushing) leaves using the DNeasy Plant Mini Kit (Qiagen, Valencia, CA). Forward and reverse reads were generated during the sequencing phase. Sequences from the SNP phase were

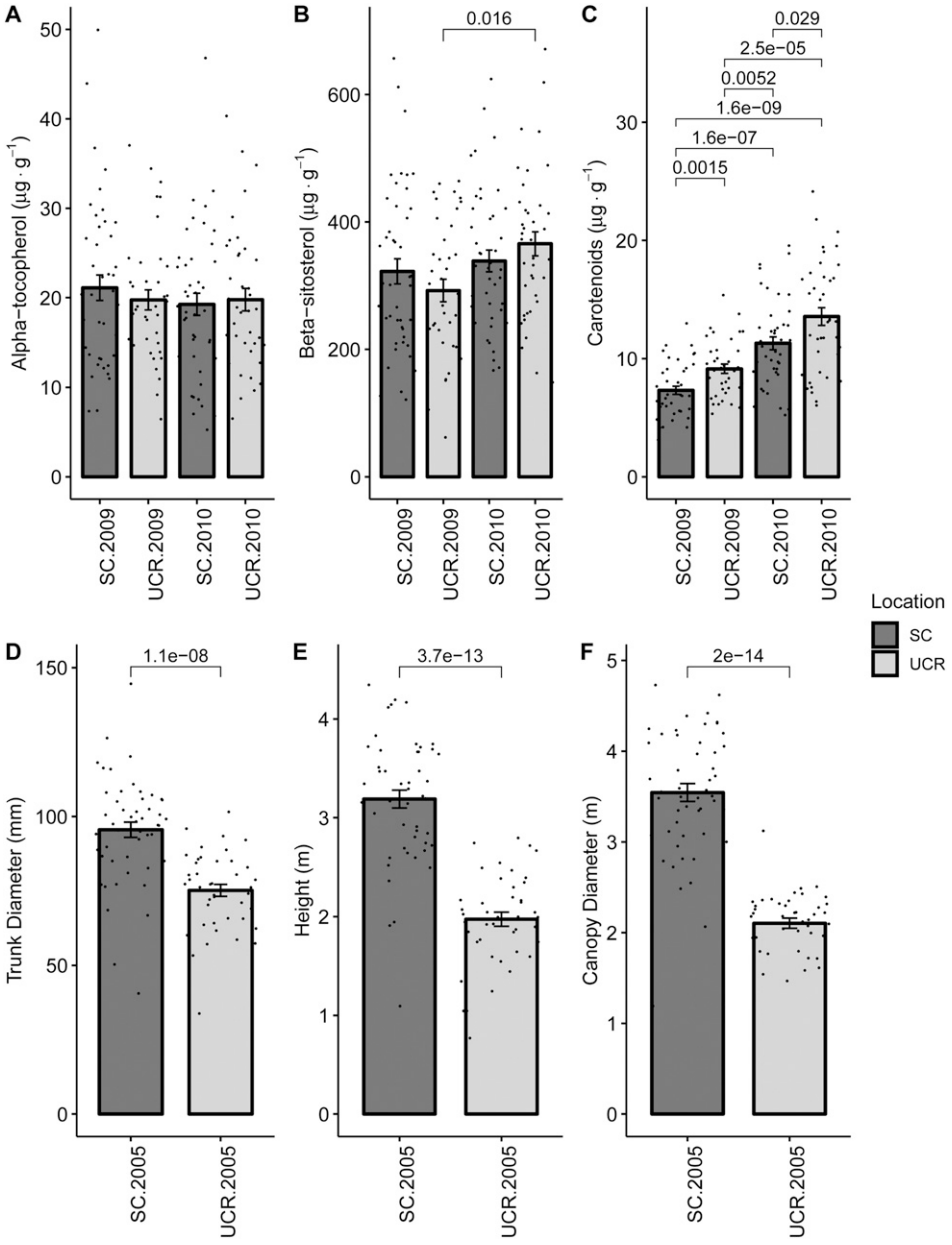


Fig. 1. Variance statistics for six quantitative traits determined in an avocado mapping population growing at two locations in southern California [South Coast Research & Extension Center in Irvine, CA (SC) and Agricultural Operations of the University of California at Riverside (UCR)]. Dots represent samples, bars show means and SE. Numbers above brackets are probability values (no brackets are shown for $P > 0.05$).

sequenced only in one direction (either 5′ to 3′ or 3′ to 5′), either using polymerase chain reaction (PCR) amplification primers or nested primers (Supplemental Table 1). PCR amplification conditions were as follows: preheating at 94 °C for 2 min, then 35 cycles of 94 °C for 30 s, annealing at primer-specific temperatures (47 to 58 °C) for 30 s and extension at 72 °C for between 30 s and 1 min 45 s, ending with a final extension of 72 °C for 5 min. PCR products were purified using the QIAquick PCR purification kit (Qiagen) or ExoSAP-IT (USB-Affymetrix, Cleveland, OH). Sequencing products were run on a DNA sequencer (Applied Biosystems 3730xl DNA Analyzer; Thermo Fisher Scientific, Waltham, MA).

SSR markers included 53 published markers. They were sourced from Sharon et al. (1997; 1 marker), Borrone et al. (2007; 13 markers), and Ashworth et al. (2004; 39 markers). Twenty-eight new SSR markers are detailed in Supplemental Table 2; their development and assay conditions are identical to those given in Ashworth et al. (2004). SSR markers of Borrone et al. (2007) were developed from ESTs.

SSR markers originating at UC (CA-SSRs) were prefixed with AVO, AUCR, or AVD if developed from a genomic library enriched for dinucleotide repeats; a prefix of AVT denotes development from a trinucleotide-enriched genomic library (Ashworth et al., 2004). SSR markers developed by Borrone et al. (2007; FL-SSRs) are prefixed with SHRSPa (Subtropical Horticulture Research Station—*Persea americana*) followed by a three-digit number. AVMIX3 originated from Sharon et al. (1997). CG-SNPs are abbreviated in relation to the candidate gene name and numbered sequentially based on the SNP position within the gene sequence. The FL-SNPs (Kuhn et al., 2019) are prefixed by SHRSPaS00, followed by SNP numbers in the range 1000 to 6999. All CG-SNPs from the same candidate gene were retained unless a SNP showed strong segregation distortion or many missing data.

Linkage map construction. Our linkage map [henceforth "California (CA)"-map] was generated using the regression mapping algorithm implemented in JoinMap version 4 (Van Ooijen, 2006) that allows analysis of a mixed set of marker types and segregation patterns. Population type was set to cross pollination (CP). We used regression mapping combined with the Kosambi function of transforming recombination frequencies into map units (centiMorgans). A log-of-odds (LOD) value of 5.0 was used for linkage group selection. MapChart version 2 (Voorrips, 2002) enabled markers to be graphically represented on their corresponding linkage group (LGs) based on the map distances determined via linkage analysis.

The chi-squared test implemented in Joinmap (Van Ooijen, 2006) was used to examine each marker for segregation distortion. Although distorted markers can be the cause of Type 1 Error (detecting false linkage), only markers with values of 8 or higher were pruned from the dataset, as modest amounts of segregation distortion are thought to contribute pertinent information (Hackett and Broadfoot, 2003; Wang et al., 2005).

To explore whether missing data may be affecting marker distribution and distances when working with small mapping populations, we developed a second map from which all markers with missing data had been removed. Additionally, we compared the CA-map to a high-density map integrated from four reciprocal mapping populations [514 progeny of 'Tonnage' × 'Simmonds', 249 of 'Simmonds' × 'Tonnage', 346 of 'Hass' × 'Bacon', and 230 of 'Bacon' × 'Hass'; henceforth "FL-map" (Rendón-Anaya et al., 2019)] that included the same set of 5050 next-generation SNPs (Kuhn et al., 2019). The comparison was made using the VLOOKUP function in Excel (version 16.16.1; Microsoft, Redmond, WA) to check for marker distribution across and within linkage groups for markers common to both maps.

QTL analysis. QTL analysis was performed using both interval mapping [IM (Lander and Botstein, 1989)] and non-parametric mapping [Kruskal–Wallis (KW) test; Kruskal and Wallis (1952)] implemented in MapQTL version 5 (Van Ooijen, 2004). Under IM, QTL significance was assigned to a marker locus in relation to the LOD likelihood scores determined using 1000 permutations of the data at a significance level of $P = 0.05$. In the maximum likelihood mixture model of IM, where LOD scores are calculated using an iterative algorithm, an iteration number of 20 was used as a cut-off to declare a significant QTL, with values above 20 representing a poor fit of the data to the model (Van Ooijen, 2004). Markers exceeding the cutoff of 20 for iteration number were disregarded. The KW test evaluates each marker independently regardless of its location on the linkage map. It is recommended for data that are not normally distributed, such as qualitative data, counts, data with outliers, and truncated data probabilities (Kruglyak and Lander, 1995), and it assigns significance in relation to the test statistic K*, with a value of $P \geq 0.005$ (denoted as **** in MapQTL) considered sufficiently stringent to declare a marker as being significantly associated with a QTL.

To verify significant QTLs, we performed an approximation of the multiple-QTL model (MQM) by manually selecting markers located close to a QTL as cofactors. The MQM model is more accurate and efficient at detecting QTLs than IM because the latter ignores the effects of other QTLs, but MQM suffers from being computationally intensive. A work-around was developed by Jansen (1993) and is implemented in MapQTL in the "rMQM" module. However, owing to the small population size and heterogeneously heterozygous population type ("CP" in MapQTL) of this dataset, we were not able to take advantage of the Automatic Cofactor Selection analysis available in MapQTL to perform backward elimination because it uses many degrees of freedom (df) and is computationally too demanding. Instead, we manually chose cofactors guided by the output from IM, sequentially selecting markers closest to a significant QTL and running rMQM. QTLs were retained if successive exclusion of cofactors did not alter the LOD values associated with the QTL.

Where multiple datasets were available, MapQTL analyses were performed for each location (coastal or inland) separately in the case of the growth-related traits (trunk diameter, plant height, and canopy diameter), as previous studies had shown significant location effects (Chen et al., 2007). For fruit nutrient content, analyses were also run on separate datasets (2 years and two locations) because Calderón-Vázquez et al. (2013) had demonstrated significant effects of harvest year on the contents of two of the three nutrients and a significant location effect on carotenoid contents, as well as interaction effects for genotype × environment (β-sitosterol and carotenoids) and genotype × year (β-sitosterol). Flowering was analyzed for a single year at the coastal location.

In all cases, we examined the output from both IM and the non-parametric KW test to declare significant QTLs, emphasizing those markers that were endorsed by both algorithms. Consideration of both the IM and KW output was deemed prudent (Kruglyak and Lander, 1995), given that the small population size (n = 50) may have affected the accuracy or power of the algorithms.

Results

Phenotypic traits. Plots showing the distribution of tree measurements at both locations and of the fruit nutrient data at all four location/year combinations are presented in Fig. 1. Trees were consistently somewhat shorter at Riverside than at Irvine, averaging 1.97 ± 0.466 and 3.19 ± 0.639 m, respectively. Trees at Riverside also developed smaller canopies (2.1 ± 0.368 and 3.55 ± 0.691 m, respectively) and trunk diameters (75.13 ± 13.1 and 95.53 ± 18.0 mm, respectively).

Values of the three fruit nutrients responded differently depending on environment and year; α-tocopherol values were not significantly different for either year or location. Beta-sitosterol values were significantly different between years at the Riverside location, with higher values occurring in 2010. Differences between years at the Irvine location were not significant. Carotenoid contents were significantly different for all location/year comparisons, with values significantly higher at Riverside than at Irvine and significantly higher in 2010 than in 2009.

One genotype consistently produced fruit with the highest α-tocopherol concentrations at Irvine in both years and at Riverside in 2010 but failed to produce any fruit at Riverside in 2009, leading to a missing data point. The same genotype was also responsible for the highest β-sitosterol values at Irvine and Riverside in 2010 and the second-highest value in Irvine in 2009. In both years, almost half the progeny in Irvine exceeded α-tocopherol contents measured in the parental cultivars [19.5 and 19.0 $\mu g \cdot g^{-1}$ fresh weight (FW) in 'Gwen' and 'Fuerte', respectively]. Two genotypes exceeded the value of their maternal parent more than 2-fold. Progeny values varied more than 6-fold (2009) and 8-fold (2010) at Irvine and more than 5-fold (2009) and 6-fold (2010) at UCR.

For β-sitosterol, values of the male parent (672 $\mu g \cdot g^{-1}$ FW) consistently exceeded values in the progeny; but seven and five progeny genotypes, respectively, exceeded the value in 'Gwen' (469 $\mu g \cdot g^{-1}$ FW) in 2009 and 2010. Progeny values varied more than 5-fold (2009) and 4-fold (2010) at Irvine and more than 7-fold (2009) and 4-fold (2010) at UCR.

Carotenoid contents were higher in 'Fuerte' (9.8 $\mu g \cdot g^{-1}$ FW) than in 'Gwen' (8.37 $\mu g \cdot g^{-1}$ FW). In 2009 and 2010, eight and 27 progeny genotypes, respectively, exceeded 'Fuerte' values. Values in the progeny varied 4-fold (2009) and 3-fold (2010) in Irvine and 3-fold (2009) and almost 4-fold (2010) at UCR.

Flowering type was determined at Irvine for 47 genotypes for which two replicate trees were available, 31 genotypes showing B-type flowering (as in 'Fuerte'), and 16 showing A-type flowering (as in 'Gwen'). All replicate pairs showed the same flowering type.

Linkage mapping. We pre-screened 5050 FL-SNPs developed by Kuhn et al. (2019) to eliminate markers that were invariant or uninformative in the parental genotypes 'Gwen' and 'Fuerte'. The remaining FL-SNP markers (2608) were then combined with 146 informative SNP and SSR markers; 83 SNPs developed to eight candidate genes of nutritional pathways and 63 SSR markers. In total, 2754 markers were imported into a JoinMap version 4.0 (Van Ooijen, 2006) data matrix for linkage mapping, of which 1346 markers (49%) placed on 12 linkage groups at a LOD value of 5.0, constituting the CA-map (Supplemental Fig. 1).

A total of 1399 markers were eliminated because of identical segregation or because of strong segregation distortion (38 markers with $\chi^2 = 8.00–31.04$, $P = 0.01–0.0000001$, df = 1–3). The placed markers consisted of 1235 FL-SNPs (91.8%), 58 CG-SNPs (4.3%), and 53 SSR markers [AVMIX3, 13 FL-SSRs, and 39 CA-SSRs (3.9%)]. Of the 1346 markers on the map, 616 (45.8%) were heterozygous in both parents, of which six segregated with four alleles (SSRs), 20 with three alleles (SSRs), and 590 with two alleles (SNPs and SSRs). Markers segregating in only one of the parents (730; 54.2%) numbered 309 in 'Gwen' and 421 in 'Fuerte'.

Marker number per linkage group averaged 112, ranging from 56 loci (LG12) to 207 loci (LG2). Combined linkage group length was 1044.7 cM, ranging from 61.483 cM on LG2 to 121.125 cM on LG3, and averaging 87.06 ± 19.77 cM/linkage group. The mean number of loci/cM was 1.32. Gaps larger than 5 cM occurred on four linkage groups. The densest linkage group was LG2 (3.37 loci/cM). Sparse coverage characterized distal portions of LG7 (Supplemental Fig. 2). Supplemental Table 3 shows marker order on the 12 avocado linkage groups obtained in this study.

An exploratory map made up exclusively of markers containing no missing data closely resembled the CA-map. Also using a LOD value of 5.0 to assign markers to linkage groups, this map contained 1238 markers on 12 linkage groups with a combined length of 1036.3 cM. Linkage groups averaged 103 loci and 86.35 ± 27.44 cM. Of the 1238 placed markers, one SSR marker segregated with four alleles, four SSRs segregated with three alleles, 555 were of JoinMap segregation type hk×hk, 289 of type lm×ll, and 389 of type nn×np.

Comparison of the CA-map with the highly saturated FL-map (Rendón-Anaya et al., 2019) showed excellent agreement between the two maps, as markers common to both maps were assigned to the same linkage group and marker order was comparable (Supplemental Fig. 2). Although a few linkage groups showed inverted segments (Supplemental Fig. 2), we did not adopt the FL-map marker order. FL-map linkage groups contained ≈2.0 to 3.3 times as many marker loci as their CA-map counterparts. Overall, the number of loci on the FL-map was about 2.6 times greater than that on the CA-map, and total linkage group length (cM) of the FL-map was 1.73 times greater. The average marker density for the FL- and CA-maps was 1.97 and 1.32 markers/cM, respectively.

Of the 58 CG-SNPs assigned to a linkage group, the greatest number (13 SNPs; 22.4%) mapped to LG2. SNPs of the same candidate gene always mapped to the same linkage group. In most cases SNPs from the same candidate gene mapped in close proximity. Exceptions were the SNPs of CUT1 (12.569 cM apart), MEP (8.119 cM apart), PSY (6.731 cM apart), and VTE1_687 (6.015 cM from the nearest SNP, VTE1_573).

QTL analysis. The number of markers showing a significant association (based on KW and IM) with each of the seven phenotypic traits is summarized in Table 2. IM failed to identify any markers associated significantly with canopy diameter, tree height, or trunk diameter at either location. KW identified five significant markers for trunk diameter and three for canopy diameter at Irvine and a single significant marker for canopy diameter and tree height at Riverside.

The content of total carotenoids in the fruit did not show significant association with any marker based on IM (Table 2). Based on KW, significant QTLs were located on LG1, 3, and 6.

QTL analysis of fruit β-sitosterol content at Riverside in 2010 revealed one marker (SHRSPaS006673) at 61.087 cM on LG1 to be significantly associated using IM at a LOD of 3.72 (Fig. 2), explaining 35.6% of the variance (Table 2). This marker also achieved significance in the KW analysis in the same location and year, and at Irvine in 2009 (Table 2). Marker SHRSPaS001205 (LG1), less than 2 cM away from SHRSPaS006673, was also significantly associated with β-sitosterol content at Irvine in 2009 and Riverside in 2010, based on KW analysis. Figure 2 compares the IM LOD profiles of markers on LG1 for β-sitosterol in all four datasets (Irvine and Riverside in 2009 and 2010).

In IM analyses, markers on LG3 were significantly associated with α-tocopherol content at Irvine in both years—12 in 2009 and 15 in 2010—achieving LOD values of up to 4.52 and 4.61, respectively, and explaining up to 37.7% and 38.3% of the variance, respectively (Table 2). No marker attained significance based on IM at Riverside in 2009. Two markers, SHRSPa001282 and SHRSPa003314, were declared significant at both locations and in both years, based on IM and/or KW. Significant QTLs resided on the proximal end of LG3 at 7.968 to 18.601 cM (IM) and at 0 to 27.638 cM (KW; Fig. 2). Three HPT1 CG-SNPs were declared significant based on KW only (Supplemental Table 3).

Flowering type showed significant association with many markers under IM, with LOD values far exceeding the permutation-based thresholds for significance. IM showed a significant association with 45 markers, all of which resided on LG10 (Table 2; Supplemental Table 3; Fig. 2). Twenty-four markers on LG10 exceeded the genome-wide LOD threshold of 7.1 and explained 50.4% to 100% of the variance in flowering type. Six of these markers achieved LOD scores of 99.99 in IM and explained 100% of the variance—but were disregarded because they did not track phenotypic values and represented an artifact of the IM maximum likelihood algorithm applied to non-normal (discrete) data (Van Ooijen, 2009). A further 21 markers on LG10 exceeded the LG-specific LOD threshold, including the CG-SNP DXPS1_1593. All markers on LG10 declared significant at the genome-wide cutoff were located between 26.808 to 53.308 cM (Supplemental Table 3; Fig. 2). Eight of the 24 markers exceeding the genome-wide threshold under IM received no support in the KW test, including the six markers with a 99.99 LOD score. KW analysis identified 22 markers associated significantly with flowering type (Table 2), all but one also residing on LG10: a single QTL-associated marker, SHRSPaS003811, located to LG6 (Supplemental Table 3). The two highest-scoring markers in the KW test had K* values of 38.251 (SHRSPaS001390 and SHRSPaS004380) and were declared significant at $P = 0.00001$. Their validity as QTLs was endorsed by IM, which assigned LOD values of 18.66 and 18.34, respectively. Among the markers associated significantly

Table 2. Evaluation of quantitative trait loci (QTLs) identified by interval mapping (IM) or Kruskal–Wallis analysis (KW) implemented in MapQTL version 5 (Van Ooijen, 2004) for avocado mapping populations growing at two locations in southern California (Irvine and Riverside). Comparisons are made for all markers declared to be significant under the interval mapping (IM) or Kruskal–Wallis (KW) algorithms. Column headings details are as follows. IM = the number of significant loci declared by IM; in parentheses is the percentage of the variance explained by the locus with the highest log-of-odds (LOD) score. KW = the number of significant loci with a significance of **** or higher, based on KW. LGs-IM = the number of different linkage groups (LGs) from which significant markers were drawn, based on IM. LGs-KW = the number of different LGs from which significant markers were drawn, based on KW. QTL ≥ two environments = the number of QTLs present in at least two environments (two locations and 2 years for nutrients; two locations for tree measurements).

Nutrient	Location, yr	IM [no. (%)]	KW (no.)	LGs-IM (no.)	LGs-KW (no.)	QTL ≥ two environments
Alpha-tocopherol	Irvine, 2009	12 (37.7)	21	1	3	21 (5, 2)[z]
	Irvine, 2010	15 (38.3)	24	1	4	
	Riverside, 2009	0 (39.5)	11	n/a	3	
	Riverside, 2010	0 (37.4)	14	n/a	1	
Beta-sitosterol	Irvine, 2009	0 (34.8)	17	n/a	1	11
	Irvine, 2010	0 (33.9)	6	n/a	1	
	Riverside, 2009	0 (35.0)	5	n/a	2	
	Riverside, 2010	1 (35.6)	12	1	3	
Carotenoids	Irvine, 2009	0 (28.5)	1	n/a	1	1
	Irvine, 2010	0 (31.4)	3	n/a	2	
	Riverside, 2009	0 (35.8)	8	n/a	1	
	Riverside, 2010	0 (35.4)	3	n/a	2	
Trunk diameter	Irvine, 2005	0 (26.6)	5	n/a	3	0
	Riverside, 2005	0 (25.3)	0	n/a	n/a	
Canopy diameter	Irvine, 2005	0 (26.3)	3	n/a	2	0
	Riverside, 2005	0 (34.1)	1	n/a	1	
Height	Irvine, 2005	0 (33.9)	0	n/a	n/a	0
	Riverside, 2005	0 (31.8)	1	0	1	
Flowering type	Irvine, 2013	45 (24)[y] (100.0)	22	1	2	n/a

[z]In parentheses: number of QTLs shared by three and four environments, respectively.
[y]24 QTLs for flowering type were declared significant using the genome-wide permutation threshold [18 after elimination of 6 QTLs with artifactually high LOD values (Van Ooijen, 2009)] and 45 using the linkage-group specific threshold (39 after adjusting for artifactual LOD values).

with flowering type was one SSR marker (AVD010; Supplemental Table 3).

Discussion

Despite the limited statistical power associated with small sample sizes, this study provided useful mapping information on two important phenotypic traits: flowering type and vitamin E (α-tocopherol) content of the fruit.

Flowering type is not a quantitative trait, and Lavi et al. (1993) suggested control by several loci with several alleles at each locus. A closer look at our data for flowering type uncovered a one-gene Mendelian model that likely governs this important trait in avocado. Using the 13 top-scoring loci on LG10 endorsed by both IM and KW, pairwise analysis showed that they were highly correlated with one another, suggesting a single causal locus with flanking loci linked through linkage disequilibrium (LD). Moreover, 29 (100%) individuals with genotype ''ll'' had B-type flowering, whereas—among individuals with genotype ''lm''—16 (89%) individuals had A-type flowering and 2 (11%) individuals had B-type flowering. These results indicate that ''m'' is the dominant allele while ''l'' is the recessive allele. The two individuals with genotype ''lm'' showing the unexpected phenotype likely reflect the effect caused by a gene × environment interaction, which may reduce the penetrance of the dominant trait. This assumption is well supported by Sedgley and Annells' findings (1981), which indicated that avocado flowering was affected by cold temperature, allowing the male and female phases of the flower to overlap. Elucidation of the genes determining flowering type would provide greater flexibility to growers in their choice of pollinizer cultivars.

Alpha-tocopherol content exhibited moderate to high heritability in quantitative genetic analyses (Calderón-Vázquez et al., 2013; Chen et al., 2007) and might be expected to yield some success in breeding programs. The current mapping studies suggest that the variation underlying flowering type and α-tocopherol may be the result of mutations at a single genetic locus. A third trait (β-sitosterol content of the fruit), also with a substantial heritability (Calderón-Vázquez et al., 2013), provided promising, although not entirely consistent, evidence for a particular chromosomal location.

Not surprisingly, traits of low to moderate heritability do not give consistent results in the QTL analyses, as is the case for plant height, canopy diameter, and trunk diameter [broad-sense heritability estimates in the low- to medium range (0.266 to 0.366; Chen et al., 2007)]. Variation underlying these morphological traits is likely to be controlled by many loci throughout the genome and to be subject to substantial environmental variation. So, the failure to map variants associated with these traits is to be expected. Moreover, the high positive correlations between these three measurement traits (Chen et al., 2007) suggest that breeding for tree architecture may not be straightforward. The fact that QTL analysis for these three growth traits

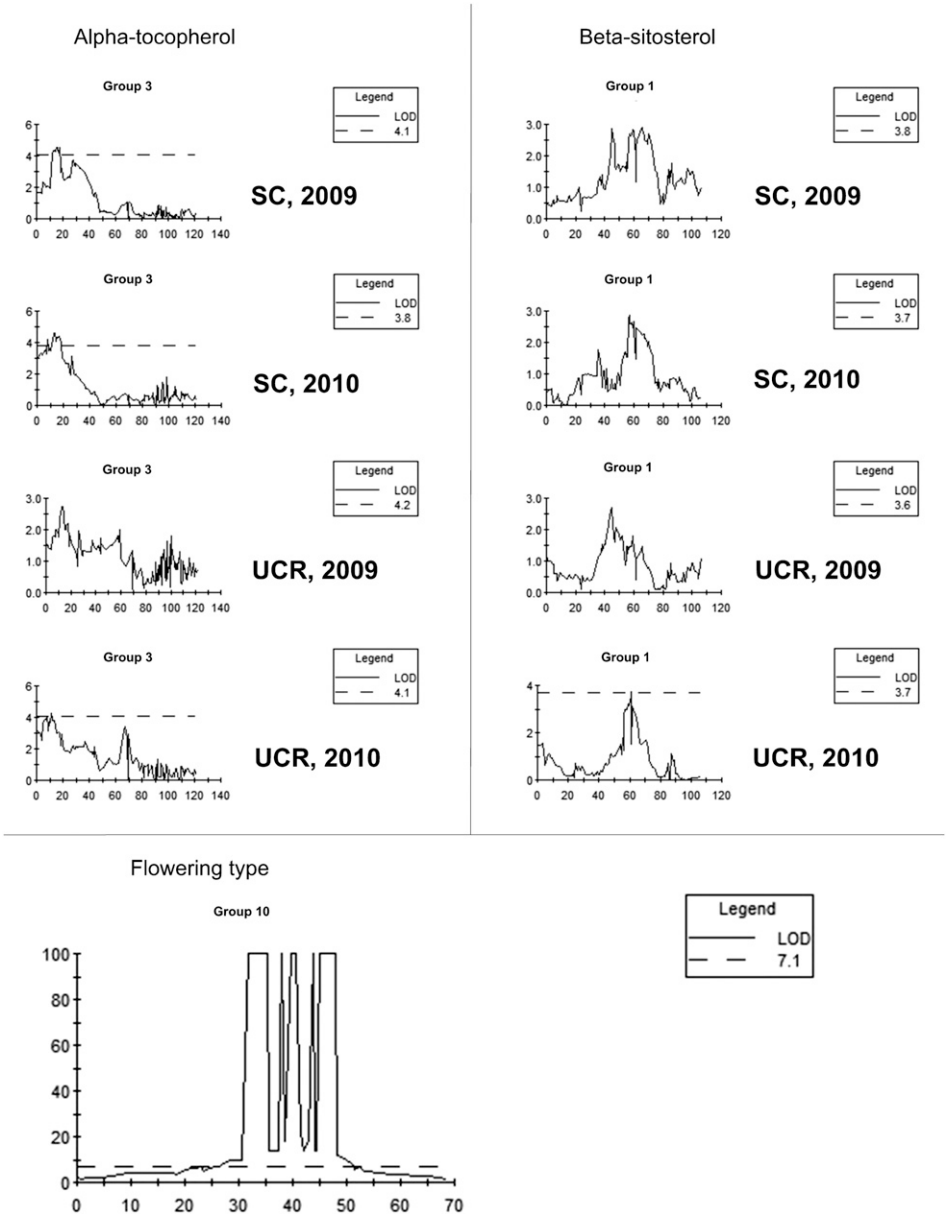


Fig. 2. Plots charting the log-of-odds (LOD) values of markers significantly associated with avocado fruit α-tocopherol contents on linkage group (LG) 3, β-sitosterol contents on LG1, and flowering type on LG10. For β-sitosterol and α-tocopherol, separate LOD plots are shown for each of 2 years and two locations studied [South Coast Research & Extension Center in Irvine, CA (SC) and Agricultural Operations of the University of California at Riverside (UCR)]. *X*-axes show map positions (cM).

revealed few significant QTLs under KW analysis (and none under IM) suggests that marker-assisted selection (MAS) for these growth-related traits is not worthwhile.

Nutritional traits. Appreciable genetic determination of the fruit nutrient phenotypes was shown by Calderón-Vázquez et al. (2013), who determined broad-sense heritability for α-tocopherol, β-sitosterol, and carotenoids to be 0.76, 0.61, and 0.47, respectively. Considerably higher values than those of the tree measurements, these values are consistent with the fact that nutritional traits are the outcome of specific biochemical pathways. Additionally, correlations among the three nutritional traits were low, the highest arising between α-tocopherol and β-sitosterol at R = 32% (Calderón-Vázquez et al., 2013). Low correlation also may be due to the discrete biochemical pathways underlying the biosynthesis of these nutrients and will facilitate independent breeding. Significant genotype effects were found for all three nutritional traits (Calderón-Vázquez et al., 2013), but for the other variance components (year, location, and interaction effects), each nutrient responded differently. Combined with the current results, these findings argue that a focus on nutritional/biochemical traits can be effective, despite limited population sizes.

Among the nutrient data, few QTLs performed well across all four environments (two locations and 2 years). Significant QTLs for carotenoid and β-sitosterol contents were never shared by more than two environments (1 and 11 QTLs, respectively, were shared by 2 environments; Table 2). Of 21 QTLs for α-tocopherol that were common to at least two environments, five were present in three environments, and two were present in all four environments (Table 2). The discovery of QTL loci that tracked nutrient content across multiple environments is encouraging and presumably reflects genes with stable expression under different environmental conditions.

For β-sitosterol, the QTL achieving significance at Riverside in 2010 did not stand out in the other year/location combinations, calling into question whether this QTL will be amenable to MAS. It is worth noting, however, that this sole significant marker on LG1 was located adjacent (within 0.49 cM) to an EST-derived FL-SSR marker (SHRSPa102; Supplemental Table 3) that had a very low LOD value in most IM datasets, suggesting SHRSPa102 may not have been correctly placed on the CA-map (Van Ooijen, 2006). The position is visible as an abrupt deep incision on the LOD graph (Fig. 2). It is conceivable that the proximity of an incorrectly placed marker affected the LOD value within the interval surrounding the significant QTL.

Population size considerations. As noted earlier in the section on QTL analysis, one aspect of this study—the small population size—clearly limited the power to generate a robust linkage map and to detect QTLs in avocado. Small population size exerts its primary effect by reducing the number of recombination events, leading to identical segregation of many markers, which results in their elimination as identicals in JoinMap (Van Ooijen, 2006) and a loss of marker information.

A paucity of recombination events also results in relatively large chromosomal segments. This result, in turn, will tend to reduce the accuracy of QTL markers identified by the mapping algorithms, because the markers may be at some distance from the functional gene. Scarce recombination events may also make mapping and QTL analysis more sensitive to the stochastic nature of allelic segregation, potentially leading to the underestimation of marker distances. In outbreeding full-sib families (CP population type in JoinMap; Van Ooijen, 2006), the mapping algorithm estimates the consensus map by averaging the positions of anchor markers segregating in both parents. However, because "hk" genotypes cannot be used (in heterozygotes sharing the same two alleles, it is impossible to tell from which parent respective alleles originated), the number of informative recombination events is thus further reduced from an already small segregation pool. Segregation type will also affect QTL estimation via the IM algorithm where flanking markers are used in the calculation of LOD values for markers with uninformative segregation. While any population size will contain a proportion of markers with uninformative segregation, small populations are likely to be more heavily impacted. Because the CA-map and QTL analyses were based on the same segregating population, errors in the calculation of QTL probabilities due to a mismatch in these two components can be ruled out (Van Ooijen, 2009).

Segregation distortion (SD), a phenomenon describing loci whose alleles do not segregate according to Mendelian expectations, affects recombination between marker loci (Wang et al., 2005) and often is accused of leading to the detection of false linkage. We chose to exclude strongly SD-affected markers before generating the linkage map, though they represented <3% of the total number of markers. This exclusion may have inadvertently removed potential QTLs, because distorted regions are as—or more—likely to contain QTLs as SD-free regions (Wang et al., 2005; Xu, 2008). In particular, SD markers are thought to be linked to loci for viability selection (Vogl and Xu, 2000), including those causing inbreeding depression, a phenomenon common to outbreeding species such as avocado. While we cannot be sure that QTLs may have been missed, the loss of power arising from ignoring distorted markers is negligible in dense maps (Xu, 2008).

Candidate gene analysis. It is disappointing that the SNPs we developed from candidate genes did not show more significant association with the nutrient phenotypes whose production the causative genes are assumed to control. One reason may be that the shortage of recombination events in our mapping population failed to detect signal. However, other factors may also be responsible. Tabor et al. (2002) argued that the candidate gene approach relies on a priori hypotheses about the role of candidate genes that may not be supported by a sufficient body of knowledge. Moreover, assumptions of gene function are generally based on studies in model organisms or major crops; yet the information may not be pertinent in avocado, an early-diverging angiosperm lineage. Further factors may be modulating effects exerted by genes outside the candidate gene pathways. Studies in *Arabidopsis thaliana* (Gilliland et al., 2006) and maize (*Zea mays*; Wang et al., 2018) identified QTLs controlling seed tocopherol content that were not part of known vitamin E pathways. In our study, CG-SNPs developed to the gene encoding the enzyme homogentisate phytyl transferase (HPT1), the first committed gene in the tocopherol *VTE2* biosynthetic pathway, were located in close proximity to markers significantly associated with α-tocopherol content and were identified as significant under KW at both locations in 2010 but at neither location in 2009. Insufficient map resolution or uninformative segregation in the flanking markers may be responsible for the failure of IM to declare significance for the HPT1 CG-SNPs.

The only other CG-SNPs showing significant association with a phenotype (flowering type) was DXPS1, a SNP developed to a candidate gene from the vitamin B complex, that controls synthesis of a thiamine-dependent enzyme involved in cell metabolism.

Vitamin E, which consists of α-tocopherol and several other tocopherol isomers, has been targeted by breeders pursuing crop biofortification in barley (*Hordeum vulgare*), maize, rapeseed (*Brassica napus*), rice (*Oryza sativa*), soybean (*Glycine max*), and tomato (*Solanum lycopersicum*) (reviewed in Fritsche et al. (2017). Peraza-Magallanes et al. (2017) found considerable variation for α-tocopherol content in avocado germplasm from Sinaloa, Mexico. Aside from the nutritional benefits arising from elevated vitamin E levels in crops, α-tocopherol has also been associated with enhanced tolerance of salinity and drought stress in rice and tobacco (*Nicotiana tabacum*) (Munné-Bosch, 2007; Ouyang et al., 2011).

Experimental populations. Avocado is a large tree that requires significant space, water, and labor resources. It takes 5 to 8 years to become productive (Lahav and Lavi, 2009), and its breeding system is very difficult to experimentally manipulate (Degani et al., 2003; Lammerts, 1942). Such cost and time considerations make it difficult and expensive to create and maintain large experimental populations and, in turn, favor working with small preexisting populations. In this regard, the UC populations used here have several strengths: 1) replication of progeny genotypes on a single clonal rootstock provides an estimate of within-genotype error variances; 2) replication in two locations provides a measure of location effects; and 3) multiple-year measurements provide a measure of temporal variance. These design features help identify important sources of environmental variance and point to important management considerations.

The current data were generated for a 'Gwen' × 'Fuerte' progeny array, and findings may not be fully transferrable to other cultivars and germplasm. However, 'Gwen'—a grandchild of 'Hass'—is central to the existing UC Riverside Breeding Program, making the QTL data relevant for MAS in the future. A crucial question to be confronted is whether QTL studies on a difficult tree crop justify the cost of land, time, and labor resources. More advanced technologies such as transformation and clustered, regularly interspaced short palindromic repeats (CRISPR)-CAS9 are appealing; but basic information about potential target genes is deficient, so for the time being MAS seems like the most practical alternative to relatively inefficient phenotypic selection. We believe that our results will encourage expanded QTL studies to guide the breeding of future cultivars in California and elsewhere, and that our findings will bring into focus the role of fruit nutritional traits with the long-term goal of breeding high-value/nutritionally enhanced cultivars achieving a market premium.

Literature Cited

Alcaraz, M.L. and J.I. Hormaza. 2009. Selection of potential pollinizers for 'Hass' avocado based on flowering time and male–female overlapping. Scientia Hort. 121:267–271.

Ashworth, V.E.T.M., M.C. Kobayashi, M. de la Cruz, and M.T. Clegg. 2004. Microsatellite markers in avocado (*Persea americana* Mill.). Developing dinucleotide and trinucleotide markers. Scientia Hort. 101:255–267.

Bergh, B.O. and E. Lahav. 1996. Avocados, p. 113–166. In: J. Janick and J.N. Moore (eds.). Fruit breeding, vol. I: Tree and tropical fruits. Wiley, New York, NY.

Borrone, J.W., R.J. Schnell, H.A. Violi, and R.C. Ploetz. 2007. Seventy microsatellite markers from *Persea americana* Miller (avocado) expressed sequence tags. Mol. Ecol. Notes 7:439–444.

Calderón-Vázquez, C., M.L. Durbin, V.E.T.M. Ashworth, L. Tommasini, K.K.T. Meyer, and M.T. Clegg. 2013. Quantitative genetic analysis of three important nutritive traits in the fruit of avocado. J. Amer. Soc. Hort. Sci. 138:283–289.

Chen, H., V.E.T.M. Ashworth, S. Xu, and M.T. Clegg. 2007. Quantitative genetic analysis of growth rate in avocado. J. Amer. Soc. Hort. Sci. 132:691–696.

California Irrigation Management Information System. 2003. CIMIS: California Irrigation Management Information System. 17 June 2019. <https://cimis.water.ca.gov/Resources.aspx>.

D'Ambrosio, S.M. 2007. Phytonutrients: A more natural approach toward cancer prevention. Semin. Cancer Biol. 17:345–346.

Degani, C., E. Lahav, R. El-Batsri, and S. Gazit. 2003. Caging single avocado trees with a beehive does not guarantee exclusive formation of selfed progeny. HortScience 38:1433–1434.

Ding, H., C. Han, D. Guo, Y.W. Chin, Y. Ding, A.D. Kinghorn, and S.M. D'Ambrosio. 2009. Selective induction of apoptosis of human oral cancer cell lines by avocado extracts via a ROS-mediated mechanism. Nutr. Cancer 61:348–356.

Ewing, B. and P. Green. 1998. Base-calling of automated sequencer traces using phred. II. Error probabilities. Genome Res. 8:186–194.

Floral Genome Project. 2005. floralgenome.org. 17 June 2019. <http://www.floralgenome.org/>.

Fritsche, S., Z. Wang, and C. Jung. 2017. Recent advances in our understanding of tocopherol biosynthesis in plants: An overview of key genes, functions, and breeding of vitamin E improved crops. Antioxidants 6:99, doi: 10.3390/antiox6040099.

Gilliland, L.U., M. Magallanes-Lundback, C. Hemming, A. Supplee, M. Korneef, L. Bentsink, and D. DellaPenna. 2006. Genetic basis for natural variation in seed vitamin E levels in *Arabidopsis thaliana*. Proc. Natl. Acad. Sci. USA 103:18834–18841.

Gordon, D.C., C. Abajian, and P. Green. 1998. Consed: A graphical tool for sequence finishing. Genome Res. 8:195–202.

Hackett, C.A. and L.B. Broadfoot. 2003. Effects of genotyping errors, missing values and segregation distortion in molecular marker data on the construction of linkage maps. Heredity 90:33–38.

Jansen, R.C. 1993. Interval mapping of multiple quantitative trait loci. Genetics 135:205–211.

Jeong, W.S. and P.A. Lachance. 2001. Phytosterols and fatty acids in fig (*Ficus carica*, var. Mission) fruit and tree components. J. Food Sci. 66:278–281.

Kruglyak, L. and E.S. Lander. 1995. Nonparametric approach for mapping quantitative trait loci. Genetics 139:1421–1428.

Kruskal, W.H. and W.A. Wallis. 1952. Use of ranks in one-criterion variance analysis. J. Amer. Stat. Assn. 47:583–621.

Kuhn, D.N., D.S.I.I.I. Livingstone, J.H. Richards, P. Manosalva, N. Van den Berg, and A. Chambers. 2019. Application of genomic tools to avocado (*Persea americana*) breeding: SNP discovery for genotyping and germplasm characterization. Scientia Hort. 246:1–11.

Lahav, E. and U. Lavi. 2009. Avocado genetics and breeding, p. 247–285. In: S.M. Jain and P.M. Priyadarshan (eds.). Breeding plantation tree crops: Tropical species. Springer-Verlag, New York, NY.

Lammerts, W.E. 1942. Progress report on avocado breeding. California Avocado Soc. Yrbk. 27:36–41.

Lander, E.S. and D. Botstein. 1989. Mapping Mendelian factors underlying quantitative traits using RFLP linkage maps. Genetics 121:185–199.

Lavi, U., E. Lahav, C. Degani, and S. Gazit. 1993. Genetics of skin colour, flowering group, and anise scent in avocado. J. Hered. 84:82–84.

Lopez-Ledesma, R., A.C. Frati-Munari, B.C. Hernandez-Dominguez, S. Cervantes-Montalvo, M.H. Hernandez-Luna, C. Juarez, and S. Moran-Lira. 1996. Monounsaturated fatty acid (avocado) rich diet for mild hypercholesterolemia. Arch. Med. Res. 27:519–523.

Luterotti, S., D. Bicanic, and R. Pozgaj. 2006. New simple spectrophotometric assay of total carotenes in margarines. Anal. Chim. Acta 573–574:466–473.

Mäeorg, E., P. Lääniste, J. Jöudu, and U. Mäeorg. 2007. Some important aspects of sterol analysis of vegetable oils. Proc. Estonian Acad. Sci. Chem. 56:59–66.

Munné-Bosch, S., E.W. Weiler, L. Alegre, M. Müller, P. Düchting, and J. Falk. 2007. α-Tocopherol may influence cellular signaling by modulating jasmonic acid levels in plants. Planta 225:681–691.

National Center for Biotechnology Information. 2005. NCBI: National Center for Biotechnology Information. 17 June 2019. <http://www.ncbi.nlm.nih.gov>.

Nickerson, D.A., V.O. Tobe, and S.L. Taylor. 1997. PolyPhred: Automating the detection and genotyping of single nucleotide substitutions using fluorescence-based resequencing. Nucleic Acids Res. 25:2745–2751.

Ouyang, S., S. He, P. Liu, W. Zhang, J. Zhang, and S. Chen. 2011. The role of tocopherol cyclase in salt stress tolerance of rice (*Oryza sativa*). Sci. China Life Sci. 54:181–188.

Peraza-Magallanes, A., M.A. Pereyra-Camacho, E. Sandoval-Castro, S. Medina-Godoy, M. Valdez-Morales, M.T. Clegg, and C.L. Calderón-Vázquez. 2017. Exploring genetic variation, oil and alpha-tocopherol content in avocado (*Persea americana*) from northwestern Mexico. Genet. Resources Crop Evol. 64:443–449, doi: 10.1007/s10722-016-0478-9.

R Core Team. 2019. R: A language and environment for statistical computing. 5 Apr. 2019. <http://www.R-project.org>.

Rendón-Anaya, M., E. Ibarra-Laclette, A. Méndez Bravo, T. Lan, C. Zheng, L. Carretero-Paulet, C.A. Perez-Torres, A. Chacón-López, G. Hernandez-Guzmán, T.H. Chang, K.M. Farr, W.B. Barbazuk, S. Chamala, M. Mutwil, D. Shivhare, D. Alvarez-Ponce, N. Mitter, A. Hayward, S. Fletcher, J. Rozas, A. Sánchez Gracia, D. Kuhn, A.F. Barrientos-Priego, J. Salojärvi, P. Librado, D. Sankoff, A. Herrera-Estrella, V.A. Albert, and L. Herrera-Estrella. 2019. The avocado genome informs deep angiosperm phylogeny, highlights introgressive hybridization, and reveals pathogen-influenced gene space adaptation. Proc. Natl. Acad. Sci. USA, doi: 10.1073/pnas.1822129116.

Ryan, E.K., K. Galvin, T.P. O'Connor, A.R. Maguire, and N.M. O'Brien. 2007. Phytosterol, squalene, tocopherol content and fatty acid profile of selected seeds, grains, and legumes. Plant Foods Hum. Nutr. 62:85–91.

Sedgley, M. 1985. Some effects of daylength and flower manipulation on the floral cycle of two cultivars of avocado (*Persea americana* Mill., Lauraceae), a species showing protogynous dichogamy. J. Expt. Bot. 36:823–832.

Sedgley, M. and C.M. Annells. 1981. Flowering and fruit-set response to temperature in the avocado cultivar 'Hass'. Scientia Hort. 14:27–33.

Sharon, D., P.B. Cregan, S. Mhameed, M. Kusharska, J. Hillel, E. Lahav, and U. Lavi. 1997. An integrated genetic linkage map of avocado. Theor. Appl. Genet. 95:911–921.

Tabor, H.K., N.J. Risch, and R.M. Myers. 2002. Candidate-gene approaches for studying complex genetic traits: Practical considerations. Nat. Rev. Genet. 3:391–397, doi: 10.1038/nrg796.

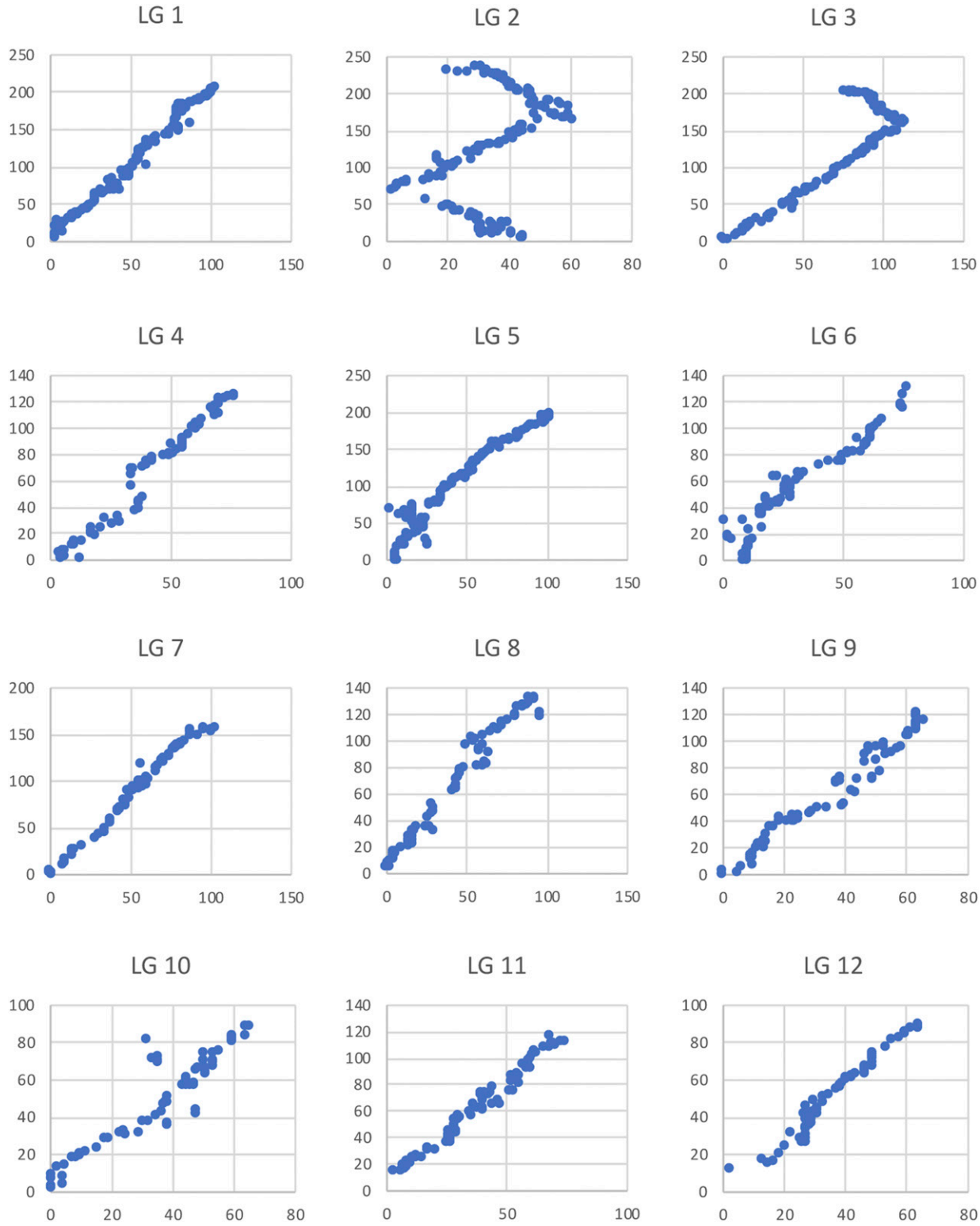
The Arabidopsis Information Resource. 2005. TAIR: The Arabidopsis Information Resource. 17 June 2019. <https://www.arabidopsis.org/>.

U.S. Climate Data. 2018. U.S. Climate Data. 17 June 2019. <https://www.usclimatedata.com/climate/>.

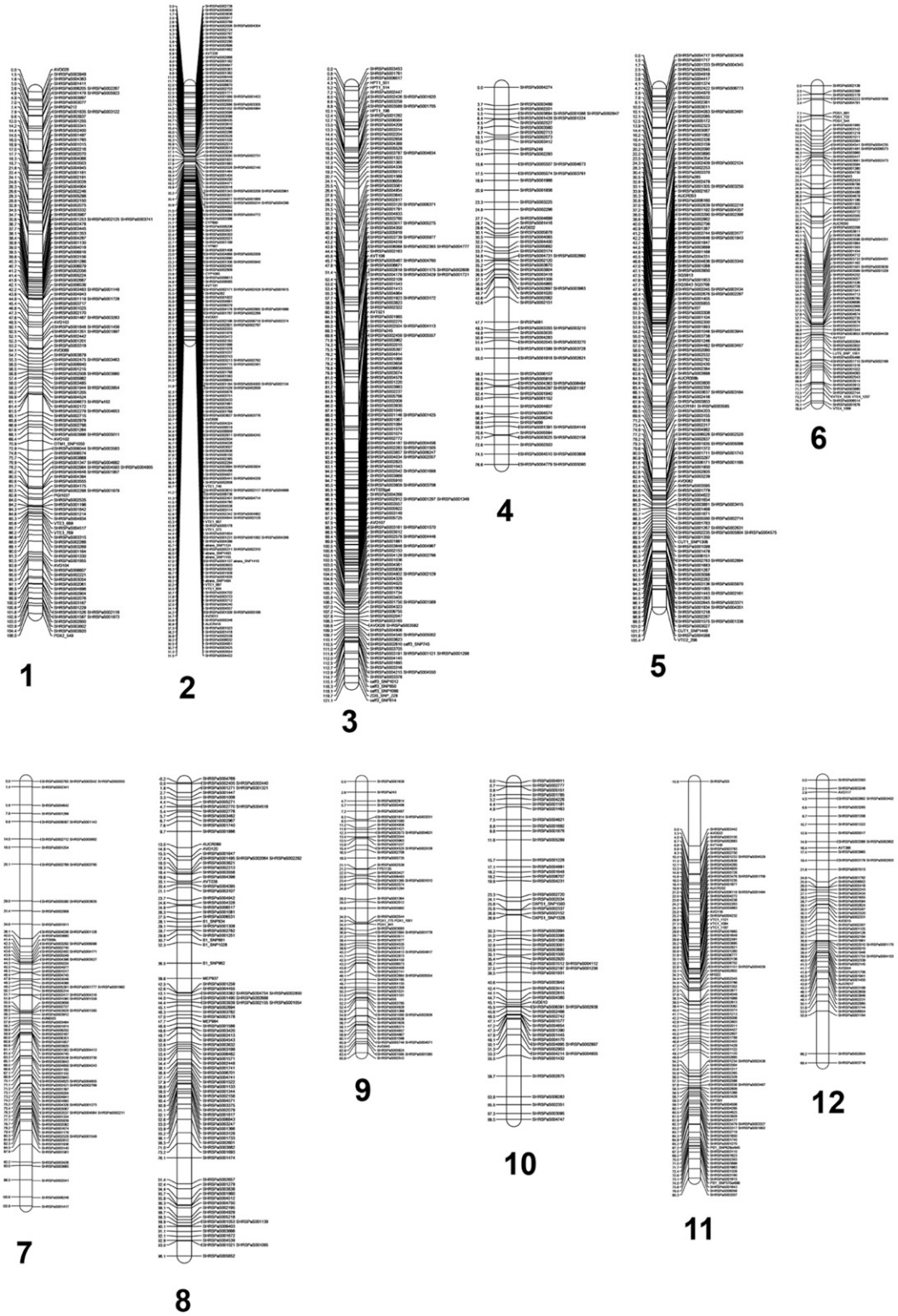
U.S. Department of Agriculture. 2018. Noncitrus fruits and nuts 2017 summary, June 2018. 17 June 2019. <http://usda.mannlib.cornell.edu/usda/current/NoncFruiNu/NoncFruiNu-06-26-2018.pdf/>.

Van Nocker, S. and S.E. Gardiner. 2014. Breeding better cultivars, faster: Applications of new technologies for the rapid deployment of superior horticultural tree crops. Hort. Res. 1:14022, doi: 10.1038/hortres.2014.22.

Van Ooijen, J.W. 2004. MapQTL® 5, Software for the mapping of quantitative trait loci in experimental populations. Kyazma, Wageningen, The Netherlands.
Van Ooijen, J.W. 2006. JoinMap® 4, Software for the calculation of genetic linkage maps in experimental populations. Kyazma, Wageningen, The Netherlands.
Van Ooijen, J.W. 2009. MapQTL® 6, Software for the mapping of quantitative trait loci in experimental populations of diploid species. Kyazma, Wageningen, The Netherlands.
Vogl, C. and S. Xu. 2000. Multipoint mapping of viability and segregation distorting loci using molecular markers. Genetics 155:1439–1447.
Voorrips, R.E. 2002. MapChart: Software for the graphical presentation of linkage maps and QTLs. J. Hered. 93:77–78.
Wang, C., C. Zhu, H. Zhai, and J. Wan. 2005. Mapping segregation distortion loci and quantitative trait loci for spikelet sterility in rice (*Oryza sativa* L.). Genet. Res. 86:97–106.
Wang, H., S. Xu, Y. Fan, N. Liu, W. Zhan, H. Liu, Y. Xiao, K. Li, Q. Pan, W. Li, M. Deng, J. Liu, M. Jin, X. Yang, J. Li, Q. Li, and J. Yan. 2018. Beyond pathways: Genetic dissection of tocopherol content in maize kernels by combining linkage and association analyses. Plant Biotechnol. J. 16:1464–1475.
Xu, S. 2008. Quantitative trait locus mapping can benefit from segregation distortion. Genetics 180:2201–2208.



Supplemental Fig. 1. Dot plots showing map positions [cM] of all single nucleotide polymorphism (SNP) markers shared between the avocado 'Gwen' × 'Fuerte' California (CA)-map (*x* axis) (this study) and the integrated consensus linkage map of a 'Simmonds' × 'Tonnage' and 'Hass' × 'Bacon' reciprocal cross [Florida (FL)-map] (*y* axis) (Rendón-Anaya et al., 2019). All shared markers located to the same avocado linkage group, but marker arrangements differed in some cases.



Supplemental Fig. 2. Avocado linkage map generated using JoinMap version 4 (Van Ooijen, 2006) and displayed with MapChart (Voorrips, 2002).

Supplemental Table 1. Parameters used for single nucleotide polymorphism (SNP) discovery from candidate genes in avocado. Details are presented in the order (1) abbreviation used on the linkage map, (2) full name of enzyme encoded by the candidate gene, (3) functionally characterized gene accession found in the public databases of the National Center for Biotechnology Information (NCBI) (with the organismal source of the sequence, where given) showing the highest similarity, (4) similarity score, (5) probability of being the same gene (E-value), (6) number of SNPs detected in the gene, (7) amplifying primer (forward), (8) amplifying primer (reverse), (9) sequencing primer, annealing temperatures listed in same order as the three primers, if different.

Carotenoids

B1: Beta-carotene hydroxylase 1; At4G25700.1, 78.8[2], 9e-18[2], 1, GAA CGA TGT TTT TGC GAT CA (B1-F147), AAC AGC CCG TAT GGC ACT C (B1-R443), CGT ATG GCA CTC CAT TGA A (B1-nest509F), 64, 65, 62

LUT5: Carotene beta-ring hydroxylase, cytochrome P450-type monooxygenase; AT1G31800.1, 71.6[2], 1e-15[2], 1, ACG GTG GTA GCT CTC GTG AT (LUT-F58), TTT TTC TCT GGT TGG ATT GGA (LUT5-R473), ACG GTG GTA GCT CTC GTG AT (LUT-F58), 64, 63, 64

PSY: Phytoene synthase (PSY), geranylgeranyl-diphosphate geranylgeranyltransferase, At5G17230.1, 158[2], 1e-41[2], 2, GCT GCA TTG GCA TTA GGA AT (PSY-F22), TTG CAA TTC CTA ATG CCA (PSY-R-GAA), GGG GAT TTT ATT AGA AAA TGA (PSY-nest658R), 64, 60, 56

ZDS: Zeta-carotene desaturase (ZDS), [*Citrus sinensis* mRNA for zeta-carotene desaturase]; emb|AJ319762.1, 89.7[3], 5e-14[3], 1, TCC TCC AGA ACC TGA GCA CT (ZDS-F372), GGT TGT TGT AGC AGC CAA A (ZDS-R-GGT), CAC ATG CAG TCC CAT TTC A (ZDS-R-CAC), 64, 61, 63

Darkening-related

PPO: Polyphenol oxidase (PPO); gi|311337316|gb|HQ380894.1| [*Nelumbo nucifera* polyphenol oxidase mRNA], 470, 1.00E-128, 1, ACC AGC TGC TTG TTC TCA TC 5093, CCC TTC CAT CGT TTC TAC CT 5094, CCC TTC CAT CGT TTC TAC CT (5094), 54

Fatty acid pathway

CUT1: Acyltransferase, Cuticular 1 (CUT 1); AT1G68530.1, 289[2], 2e-81[2], 2, CAT GGT GAT AGC TGG TGA CG, (CUT1-F27), TCT GGG ACA GAT AGG GGA TG (CUT1-R554), CATGGTGATAGCTGGTGACG (CUT1-F27), 64

Flavonoid, anthocyanin & phenylpropanoid pathways

Caff3: Caffeoyl-CoA O-methyltransferase (caff3); Os09g30360|12009.t02714| [unspliced-genomic caffeoyl-CoA O-methyltransferase 1, putative, expressed], 91.5[2], 8e-22[2], 5, TGC GGA CAA GGA CAA CTA CA (caff3-F50), CCA TGA TGC CAT CTC TAG CA (caff3-R483), CCA AAT GGT CAA AGA AAC AG (caff3-nest1284R), 64, 64, 60

OTM1: Flavonol 3′-O-methyltransferase 1 (OTM1); gb|GU324973.1| [*Eucalyptus camaldulensis* caffeic O-methyltransferase1 (COMT1) gene], 66.2[3], 8e-07[3], 7, GCA GTT CTT AAG GAA TTT CGC (OTM1-F103), GGT CGA CCT ACA TAT TGC G (OTM1-R568), GAT CAC CTT TCC ATT AGC CG (OTM1-nest70F), 62, 61, 63

PAL2: Phenylalanine ammonia-lyase 2 (PAL2); At3G53260.1, 702[2], 0.0[2], 2, CAG GAA TGC CAC ACT CTC AA (PAL2-F17), AGC AAA TGG GAA TAG GAG CA (PAL2-R1065), CAG GAA TGC CAC ACT CTC AA (PAL2-F17), 63–64

Isoprenoid & sitosterol

CYP: cycloeucalenol cycloisomerase; gi|225456279|ref|XM_002283523.1| [predicted: *Vitis vinifera* cycloeucalenol cycloisomerase-like (LOC100262783), mRNA], 659, 0, 5, GCT TCA TAC ACC TTT CCG TCA 6163, CAT GTA GCC TCA GCA ATC CA 6162, TAG GCA TTA CGG AGT TGC AG 2130, 53

FPS: farnesyl diphosphate synthase; gi|212960745|gb|FJ415102.1| *Chimonanthus praecox* farnesyl pyrophosphate synthase (FPPS) mRNA, complete cds, 690, 0, 1, TTG GTT GGT TGT GAA AGC TC 634, TTG CCC AAG AAA GAC TTC AG 737, TTG GTT GGT TGT GAA AGC TC 634, 53

MCR: 24-dehydrocholesterol reductase; gi|359473656|ref|XM_002271810.2| [predicted: *Vitis vinifera* delta(24)-sterol reductase-like (LOC100258158), mRNA], 592, 1.00E-165, 3, GGA AAG GTA TGC TTC CAA GG 20, TGT GAA GTT CAT ATA ACG AAT AGT CA 7963, TTG GCC TAG TAT CTG CAT GTT 3878, 53

SQS: squalene synthase (SQS1); gi|359475094|ref|XM_002266114.2| [predicted: *Vitis vinifera* squalene synthase-like (LOC100265798), mRNA], 682, 0, 4, TGA AAG TCA GTG CAT GTT TCT 6164, CGC GAC TTT GGT ATC TCA T 128, GCT TGA CCC CTT TTT TTG GA 8295, 55

Vitamin B complex

atrans, Vitamin B9 (folic acid), Aminotransferase class IV family (atrans), Aminotransferase class IV family (atrans); AT5G57850.1 | Symbols: | aminotransferase class IV family protein, 66.2[2], 5e-14[2], 6, CAG ATC CTG CAG CCA TGA TA (atrans-F-12), ACC TGT GGA GGC TTC ATT GG (atrans-R-457), TGA CAC TGC AGC TAT TAT (atrans-R457-ic-TGA), 64, 66, 51

BCAT3, Vitamin B5 (pantothenic acid), Branched-chain aminotransferase 3 (BCAT3), Branched-chain aminotransferase 3 (BCAT3); gb|EU194916.1| *Nicotiana benthamiana* branched-chain aminotransferase (BCAT) mRNA, 181[3], 1e-41[3], 1, CGA GGT AAA ACA TCC TAG ATC (BCAT3-F6), ACC CTT TAT TGC TGG AGT CG (BCAT3-R-ACC), GAA CCA GGA AAG CAG CAG (BCAT3-nest513F), 57, 63, 61

DXPS1, Vitamin B1 (thiamine), 1-deoxy-*D*-xylulose-5-phosphate synthase (DXPS1), 1-deoxy-*D*-xylulose-5-phosphate synthase (DXPS1); At3G21500.1 | Symbols: DXPS1 | DXPS1; 1-deoxy-D-xylulose-5-phosphate synthase, 239[2], 6e-66[2], 5, CGA GGT AAA ACA TCC TAG ATC (DXPS1-F34), AAG CAG CAG CCA AGC AGC TT (DXPS1-R-AAG), AAA TGC ATC ATA CTT TAG GAA (DXPS1-F34-R839), 57, 69, 55

PDX1, Vitamin B6, Pyridoxin biosynthesis 1 (PDX1); gi|356549199|ref|XM_003542937.1| PREDICTED: *Glycine max* pyridoxal biosynthesis protein PDX1-like (LOC100816306), mRNA, 589, 1.00E-164, 4, CAC ACC CAA GCT GCA TCA 787, AAA TCA AGC AGG CCG TCA C 789, CAC ACC CAA GCT GCA TCA 787, 59

Continued next page

Supplemental Table 1. Continued.

PDX2, Vitamin B6, Pyridoxin biosynthesis 2 (PDX2); gi|359478338|ref|XM_002285059.2| PREDICTED: *Vitis vinifera* pyridoxal biosynthesis protein PDX2-like (LOC100267348), mRNA, 100, 2.00E-17, 1, AAA CAG GGA AAC CTG TGT GG 779, GCC TGG TGG AAC AGC ATA AT 784, AAA CAG GGA AAC CTG TGT GG 779, 54

Vitamin C

MEP: GDP-mannose-3′,5′-epimerase, gi|359487867|ref|XM_002279341.2| PREDICTED: *Vitis vinifera* GDP-mannose-3′,5′-epimerase (LOC100233034), mRNA, 437, 3.00E-119, 2, TGC TTG CAT ATA CCC AGA GTT 8889, AAG GAT TGT GTT GGC AGA CC 3058, AAG GAT TGT GTT GGC AGA CC 3058, 55

PGI: phosphoglucose isomerase, gi|225458304|ref|XM_002282738.1| PREDICTED: *Vitis vinifera* glucose-6-phosphate isomerase (LOC100252335), mRNA, 515, 1.00E-142, 4, TGA TAC TTG GAA AAT ACA TGA AAA CA 3881, TAA AGC CCT CAA CTG GTT CC 870, TGA TAC TTG GAA AAT ACA TGA AAA CA 3881, 54

VTC1: GDP-mannose pyrophosphorylase (*VITAMIN C DEFECTIVE 1*), gi|224038261|gb|FJ643600.1| *Actinidia latifolia* GDP-D-mannose pyrophosphorylase (GMP) mRNA, complete cds, 614, 4.00E-172, 3, GAA ACC GAG CCT CTA GGA AC 738, AGA AGC CCG GTA AGA CCA T 740, AGA AGC CCG GTA AGA CCA T 740, 56

VTC2: GDP-L galactose phosphorylase (*VITAMIN C DEFECTIVE 2*), gi|319739580|gb|HQ224948.1| *Citrus unshiu* putative GDP-L-galactose-pyrophosphatase mRNA, complete cds, 246, 2.00E-61, 3, AAA ATC AAG CAT TCG CAG AG 340, CAG GCT CTT GGA GAG GTG AG 5859, AAA ATC AAG CAT TCG CAG AG 340, 55

Vitamin E

HPT1: Homogentisate phytyltransferase (*VTE2*), gi|219842165|dbj|AB376091.1| *Hevea brasiliensis* hpt mRNA for homogentisate phytyl transferase, complete cds, 347, 7.00E-92, 3, AGG CCA TTG ATA TTC GCA AC 9827, GAA ACC AAT CCC ATC ACC AC 9825, AGG CCA TTG ATA TTC GCA AC 9827, 55

PDS1: 4-hydroxyphenylpyruvate dioxygenase (*PHYTOENE DESATURASE 1*), gi|359485346|ref|XM_002283239.2| PREDICTED: *Vitis vinifera* 4-hydroxyphenylpyruvate dioxygenase-like (LOC100248785), mRNA, 558, 3.00E-155, 3, GCT GGA AAT GTG CTG ACT GA 991, TCC CAT GTC TTT TCC ATT GAC 7960, GCT GGA AAT GTG CTG ACT GA 991, 53

VTE1: Tocopherol cyclase (*VITAMIN E DEFECTIVE 1, VTE1*), gi|255550999|ref|XM_002516502.1| *Ricinus communis* Tocopherol cyclase, chloroplast precursor, putative, mRNA, 91.5, 2.00E-14, 5, GGG CAG TGC AAG AAT ATA ACT G 6564, CTC CAA GAT GGA AGT CGT GT 901, GGG CAG TGC AAG AAT ATA ACT G 6564, 53

VTE3: MPBQ/MSBQ methyltransferase (*VTE3*), gi|219842171|dbj|AB376094.1| *Hevea brasiliensis* mggbqmt mRNA for 2-methyl-6-geranylgeranylbenzoquinone methyltranferase, complete cds, 814, 0, 2, TGG CTT CTT CAA TGC TCA AT 350, GCA TAA TCA GTT GGG AAT GG 5758, TGG CTT CTT CAA TGC TCA AT 350, 54

VTE4: Gamma-tocopherol methyltransferase (*VTE4*), gi|219842175|dbj|AB376096.1| *Hevea brasiliensis* gamma-tmt mRNA for gamma-tocopherol methyltransferase, complete cds, 381, 2.00E-102, 5, GAA CAC CAA GCC GGA AGA TA 3026, GAG AGC ACA TGC CTG ACA AA 996, GAA CAC CAA GCC GGA AGA TA 3026, 55

Supplemental Table 2. Information on simple sequence repeat (SSR) markers of avocado, featuring marker name, source, fragment sizes in cultivars Gwen and Fuerte, distorted segregation (if applicable), forward primer, 5′ to 3′, reverse primer, 3′ to 5′, nucleotide repeat unit, annealing temperature [°C], and GenBank accession number.

AUCR008b, new, 268/278, 268/268, CTT CCG TAT CTC ATC AAA TA, AAA TCA GAC TCA AAT CAG TG, $(CT)_{22}$, 56, KC768707
AUCR017, new, 363/370, 363/376, AAA AAG GAG TTC CAC AGT ATG A, TTC AAG TCA GAA ACC CAC TAT T, $(TC)_9(AC)_9$, 58, KC768708
AUCR050, new, 323/329, 329/329, GCA GAC CTG GGT TGT ATT GA, TTC GGA GCC TAT TAT TAC GAT G, (TC)18, 60, KC768709
AUCR053, new, 245/257, 245/265, AGG TTT ACA GAA GAA CCC AGA C, GAG CCC CTA CCC AAA TCT TT, (CT)6..(TC)11, 61, KC768710
AUCR089, new, 221/223, 202/221, GGC TCA TCT TCA ACT TAT, ACT CTT GTT CTT TCA GTG T, (GA)9..(GA)14, 56, KC768711
AUCR181, new, 246/246, 237/246, TTC TAT CCA GTG AGG TAA CA, CCA ATC TAT CGC CAT AAT, (GA)16, 52, KC768712
AUCR202, new, 222/222, 222/258, TGC TTA TCT TTC AAA ACC TCT G, GGC TTT ATT CTT CCC CCT AT, (GA)15, 57, KC768713
AVD010, new, 269/292, 265/265, TCT TGG AAG GTT TGG GTT TG, ATT CGG GCA GAT ACT TTC AT, (TG)5(TG)8(GA)10, 61, KC768714
AVD026, new, 173/183, 173/206, AGA TAA TGA AGG TTC CAG AT, GGG AGG ATA GTA TGT AGA TTT, (AG)9, 55, KC768715
AVD028, new, 170/184, 184/184, GGG ATA TGC AAC AGA AAT ACG A, ATG GCA CGA CAA GGA AGT TC, (AG)18, 65, KC768716
AVD032, new, 179/185, 179/185, GTT TCA CCC CTT TTA ACA AGA C, AAT AGC ATA CTT GGT CTG GAG G, (GAA)2(GA)19, 63, KC768717
AVD036, new, 119/119, 125/125, CTT CTC CTC TTG TTC ACC CA, TAT CGG CTG TGT CTG TAT CG, (CA)3(GA)15…(CT)8..AA…(GA)12, 62, KC768718
AVD044, new, 311/313, 302/313, CTG TTG GAT GGT GTG GAT GAC, CCA GAC GTA ATG TGA GGC TCT C, (CT)15, 66, KC768719
AVD045, new, 285/285, 279/288, CCT ATG GTT TGG TGA GTT CC, TTA CAA TAC CCC TCT CGT CTG, (TTC)10(TTG)6 (GA)9, 62, KC768720
AVD050, new, 186/193, 183/186, ***, CAG AAA ATC CCT AAC CCT AC, CTC TCA GAC TCG TGA CTC ATC, (GA)26, 59, KC768721
AVD065, new, 133/135, 133/135, ***, CCT TAA ACC CTC TCC CTC ATC TC, CGT GGG ATG GAT CGA AAA TG, (TC)7, 67, KC768722
AVD082, new, 113/128, 113/120, GAC CTA CTT GGA TGA GTC CT, TTG TTG TAT TGA TCT TTC CTT, (AT)5 (GT)14, 57, KC768723
AVD089, new, 256/267, 256/269, TCA TTG TGT TCT TCG TGT GGA, TAA AAG GGG TTG GTC TCA CC, (GT)13 (GA)20, 64, KC768724
AVD103, new, 181/197, 197/197, CTC CGT TCT CAT TTA TCC TC, GGT TGT CAA AAG GCT CTT AT, (CT)20, 58, KC768725
AVD104, new, 190/221, 190/221, **, TGA ACG AAA TGG AAA CAT AT, ATT TTG AAC TTT ATT GGG CT, (CG)4(TG)15(AG)22, 58, KC768726
AVD107, new, 183/191, 183/186, GCA CAC ATC AGT CGT AAA TG, TGC TAC AGG GAG AAC TTG AA, (TG)15 (AG)8, 61, KC768727
AVD116, new, 209/217, 193/217, ACA AAT GTT ATG TTT CAC CAG A, CTG TCC AAG TGT GCT AAA TG, (GA)5.C.(AG)23 , 59, KC768728
AVD117, new, 231/231, 239/241, CGA AAG ATA GCA GGT GAG TG, GCA GTA AAG GTA GTG AAG AAT C, (GA)22, 60, KC768729
AVD120, new, 192/206, 196/206, TTC ACT ATT TTT CTT GTG GAG, AAC CAG ATG TTT CTA CAG AGA, (AG)14, 57, KC768730
AVO109, new, 152/154, 143/154, AAC TGC CTT TTC TTC TCT ATT TCA G, GGT GGG GAA CTG GGT TAG T, (TC)22, 59, KC768731
AVT001be, new, 351/365, 346/365, GGG GTA GGC AGA GGA AAT TGA A (001b.F), CCA GTC CGC ATT CAA AAG TGT T (001e.R), (TGA)8, 67, KC768732
AVT034, new, 226/228, 220/228, **, ATC GTT GTC ATC ATC GTC ATC C, CAT AGT AGG CAC TGA TGG TGT C, (TCA)5, 62, KC768733
AVT114, new, 333/345, 345/345, ***, GTT GGG ATA ATG ATT CCT GTG ATA, AGG GAA GAT GGA CCG TGA GAC C, (GAT)6(ATG)4, 63, KC768734
AUCR418, 2004, 359/378, 359/378, AGA TGG CTT TCT CCT TCT GA, TTT GAC ACA CAA TCC AAC TAT G, (GT)12(GA)13, 56, KC795695
AVD001, 2004, 223/238, 223/238, GTT TCC AAG CGA CTC ACG AG, GAT TCC ATG CTG AAT TGC CG, (CT)12, 66, KC795696
AVD003ii, 2004, 181/181, 184/200, TCC CTT CAG TCT AAG ATT AGC C, GAC CAA CAC TAT TTG CCC CAC, (TC)19, 62, KC795697
AVD006, 2004, 315/337, 315/298, GGG AGA GAT GTA TTG AGC A, ACT TGG TCG TAG ATT GTA AAT, (TC)9(AC)19, 56, KC795698
AVD013, 2004, 216/222, 220/243, TTG CCA GTG GAA CTT CAA AA, ACC CAA CCA AAG ATT TCA AT, (AG)7..(GA)3..(TCT)4, 62, KC795699
AVD015, 2004, 260/262, 260/260, *** , GAC CCC TAC CCT AAC TCT CA, CTT CTA AAC ATT CCC TAC AAA G, (GT)26, 60, KC795700
AVD022, 2004, 226/228, 221/249, *, CCA CTT GGA TTC TTG TTG GA, ATT TGG GTT CGG CTT AGG AA, (TC)13, 65, KC795701
AVO102, 2004, 159/198, 153/169, TTC GCC TTA TCA GCG TTA G, TCT TGG AAA GCC CTA CTC C, (GA)12, 58, KC795702
AVT005b, 2004, 184/188, 184/188, TTA GCA GCA GAT AGA GGG AGA G, GGA CCT GCC TTG TGG ATT AG, (CAT)5, 62, KC795703
AVT020gat, 2004, 158/162, 158/168, CTA CAT AGA TCG AAA TAA GG, ATC TGG CTA TGA AAT GTT GG, (GAT)9, 54, KC795704
AVT021, 2004, 126/136, 126/132, *, ACT CTC GCC TCT GCG TTG AT, GAC TCA ACA TGG TTA GAA CAA GGC, (ATC)8, 65, KC795705
AVT038, 2004, 184/200, 184/184, GAT TAA AGA TGA CCC TGA AG, GAT TTG GCT CAA GAT AGA TC, (TCA)8, 56, KC795706
AVT106, 2004, 342/342, 342/336, CCA ATC AAA AGG CAA ACG AAG AAC, GCA AAG GAG GCG GTT TCG AGA T, (TCA)6, 68, KC795707
AVT158, 2004, 313/313, [313/313] ACG AAG TTA CGG GCT TAT TTC ACA, TTC TTC CCC TTC TCT CAC ATA ATC, (GAT)7, 62, KC795715

Continued next page

Supplemental Table 2. Continued.

AVT191, 2004, 215/218, 215/218, TCC ACA ACT TCT ACA GGG TCG T, GGA AGA TAA CGC ACC TTG AGT TC, (ATG)7(TGG)4, 69, KC795708
AVT226, 2004, 298/304, 294/298, GGC TGA CTT TTA TAG TCG ATG T, TCC GAT TGA CAG TGG ATT GTT, (TCA)6..(CTT)4, 60, KC795709
AVT386, 2004, 229/229, 219/229, ACA ACC CAA ACA TAA ATG CT, AAT AGA AGT GAC ATC CGA CC, (TGA)8, 60, KC795710
AVT436, 2004, 149/152, 139/149, ***, ACT AAA ATG AGG GGA GAC TAG, GAG TGT AGT GAG GAG TTT GG, (ATC)9, 56, KC795711
AVT448, 2004, 193/193, 183/193, ACG GTG TTT GGA AGA AGA TG, GCA CTT CAA TCA ATG CTT AC, (GAT)8, 60, KC795712
AVT517, 2004, 229/229, 219/229, AAT CCT TCC ACT CAG AAA CT, TAC ACA AAC GAC AAG AAT GG, (GAT)6, 59, KC795713
AVMIX03, 2009, 145/174, 145/174, GAT ATT CCT GTT GTC ACT GC, AAT GTT CCC CAT GAA AGT CTC C, (TG)16, (AG)20, 56
SHRSPa043, 2009, 160/180, 164/180, TCA CTG CTC TCT TCT TGC CC, ATC TAT TGC CCT CTT GTA CTC ACT, (TC)2GCA(TC)14(TG)2N6(CAAA)2, 56
SHRSPa044, 2009, 174/181, 175/175, GCC AAC GAG GGT CAG ATC AA, CGC AAA CCA ACC GCA CA, (CTT)3(TTTTAT)4, 56
SHRSPa055, 2009, 108/123, 117/137, TCT CTT CAT CAA CTC GAC TGC, AAC GGT ATC CAA ACG CTA AT, CC(TTCT)2(TTA)2CAA(CT)16TT(CT)2, 56
SHRSPa073, 2009, 123/125, 125/125, CTG CTT TTC CCA CTG CTC, CCA GAA CAA ACT GAA CAA CAA, (AG)7AA(AG)2, 56
SHRSPa081, 2009, 218/218, 218/220, GGG CTT CAA TTC AAT CCA ATC C, TCT TCA GCA CGC CAC GAG TCT, (C)2(GA)7, 56
SHRSPa099, 2009, 79/79, 79/94, TCA TCC CAA TTC CCA CCT TC, AGC GGC GGA TTT TAG CG, (AGA)9A(AG)2, 56
SHRSPa102, 2009, 95/113, 113/119, GGC ACA AAC CCT ACA AAT ACC A, TCT TCT TGA GTC GCA GCA GC, A(GAA)6AG, 56
SHRSPa107, 2009, 151/165, 151/177, CGC AGT CTT CAA TGA TAC CA, CCC CCC TTC ACT TCC AA, (AT)4N4(AC)3TA(AC)2(CT)2(TG)2(AGA)2AA(TG)2TAT(TC)8, 56
SHRSPa197, 2009, 164/178, 164/164, CTC TCT TCT CGA GTC CGC TG, GGA ATT CCG CAC AGT AGC AT, (CT)10CAC(CTT)3CTG(TC)2(CTT)2, 56
SHRSPa203, 2009, 111/117, 109/111, ATG GTT ACA AGA ATT GGC CG, ATC AGT GCA AAA GGA CCC TG, (TA)2(CATA)3(TA)4, 56
SHRSPa212, 2009, 304/310, 304/304, ATT CCT TCT GCT GTC CCA AA, TGT GGC ATT AAA GAC GAC GA, (TC)5N30(CAG)2N10(GA)2(AGAGAA)3AGA(AGC)2, 56
SHRSPa243, 2009, 260/264, 260/264, ACA GAT GAC GGT TTT CCT GC, CTC TCA GCA TCG AGC CTT TT, (ATGATTT)2CAAC(AG)8, 56
SHRSPa245, 2009, 149/151, 149/150, CCA TGA CGG AGG TTT CTT GT, GGC AAT GGC GAT TCA GTA AT, (GT)7(T)4A(AT)3(T)5(AG)3, 56
SHRSPa249, 2009, 272/276, 270/274, CCA GAA GCT GGC AAT CTA GC, CCA AAC GGG TCC TAA TGG TA, (TA)3TT(TA)9, 56
SHRSPa262, 2009, 192/195, 192/192, GGG GAA TCC ACG GCA T, TGG AGG GGA TTC TTC TCC TT, (CTT)3(CTC)4CTGCT(TCC)3, 56
SHRSPa274, 2009, 132/139, 139/139, GTG AGT CTG TAA CGC GCA GA, GCT ACA AGA TGC AGC ACC AA, (TC)21TTT(TC)2, 56
SHRSPa285, 2009, 255/264, 255/256, ACC GTT CGT TTG GAA ATC AG, GCC AAC AGT ACA TTC CCC AT, (AT)2(AGG)7(AAG)6, 56

Supplemental Table 3. Position of genetic markers on the twelve avocado linkage groups. Quantitative trait loci (QTLs) are highlighted in bold if inferred by Interval Mapping and underlined if inferred by Kruskal-Wallis analysis. Phenotypic traits are abbreviated to A (alpha-tocopherol), B (beta-sitosterol), C (carotenoids), CP (canopy diameter), H (tree height), T (trunk diameter), F (flowering type).

group 1	
AVD028	0
SHRSPaS003949	1.496
SHRSPaS004383	1.782
SHRSPaS001411	2.955
SHRSPaS006205	3.596
SHRSPaS002267	3.596
SHRSPaS001479	4.75 C
SHRSPaS005923	4.817 C
SHRSPaS003997	4.879
SHRSPaS003077	7.016
SHRSPa212	7.442
SHRSPaS001835	7.905
SHRSPaS003122	7.905
SHRSPaS003937	9.59
SHRSPaS001255	11.981
SHRSPaS003341	14.167
SHRSPaS002400	14.425
SHRSPaS001497	14.46
SHRSPaS001760	15.963
SHRSPaS001015	16.878
SHRSPaS002216	16.981
SHRSPaS002070	17.657
SHRSPaS004066	18.294
SHRSPaS003503	19.677
SHRSPaS004945	21.771
SHRSPaS001181	22.436
SHRSPaS002191	24.148
SHRSPaS003028	24.637
SHRSPaS004904	26.288
SHRSPaS002246	26.591
SHRSPaS005298	28.294
SHRSPaS002150	28.862
SHRSPaS002075	32.832
SHRSPaS003332	34.45
SHRSPaS003987	34.69
SHRSPaS001253	35.563
SHRSPaS002125	35.592
SHRSPaS003741	35.592
SHRSPaS002478	36.73
SHRSPaS003445	37.667
SHRSPaS001353	38.098
SHRSPaS004287	38.391
SHRSPaS001130	38.614
SHRSPaS004019	39.033
SHRSPaS006916	39.476
SHRSPaS003156	39.839
SHRSPaS001286	40.345
SHRSPaS006979	40.706
SHRSPaS002056	41.216
SHRSPaS005224	41.435
SHRSPaS002667	41.923

Continued next page

Supplemental Table 3. Continued.

SHRSPaS006536	42.059
SHRSPaS003483	42.2
SHRSPaS001148	42.2
SHRSPaS004943	43.766 B
SHRSPaS001119	44.851
SHRSPaS001728	44.851
SHRSPaS003717	45.412
SHRSPaS001025	46.847
SHRSPaS002170	47.26
SHRSPaS001467	47.768 B
SHRSPaS003283	47.782 B
AVD103	49.48
SHRSPaS001848	50.115 B
SHRSPaS001456	50.115 B
SHRSPaS001351	50.483
SHRSPaS001997	50.483
SHRSPaS002442	52.105
SHRSPaS001201	52.325 B
SHRSPaS003319	53.225 B
AVD089	54.075
SHRSPaS003879	54.734
SHRSPaS002475	55.294
SHRSPaS003463	55.312 B
SHRSPaS006940	56
SHRSPaS001215	56.546
SHRSPaS002508	56.831 B
SHRSPaS003980	56.831 B
SHRSPaS005982	57.411
SHRSPaS003485	58.034
SHRSPaS001944	58.332 B
SHRSPaS003954	58.332 B
SHRSPaS001205	59.238 B
SHRSPaS004524	59.854
SHRSPaS006673	**61.087 B**
SHRSPa102	61.136
SHRSPaS002172	61.394 B
SHRSPaS002279	61.464 B
SHRSPaS004653	61.526
SHRSPaS002715	65.07
SHRSPaS002979	65.784 T
SHRSPaS002798	66.892
SHRSPaS001264	67.562 B
SHRSPaS003996	68.067
SHRSPaS005011	68.067
AVO102	69.392
OTM1_SNP1050	70.885
SHRSPaS006044	72.927
SHRSPaS003583	72.927
SHRSPaS006574	74.783
SHRSPaS003868	75.717
SHRSPaS001347	76.856
SHRSPaS004682	76.896
SHRSPaS002984	78.216
SHRSPaS004593	78.249
SHRSPaS004805	78.249
SHRSPaS004648	80.241
SHRSPaS001907	80.241
SHRSPaS004394	80.528
SHRSPaS003555	80.595

Continued next page

Supplemental Table 3. Continued.

SHRSPaS003632	11.658
SHRSPaS006670	12.004
SHRSPaS002703	12.4
SHRSPaS001771	12.549
SHRSPaS001999	12.869
SHRSPaS001453	12.909
SHRSPaS004553	13.206
SHRSPaS002686	13.738
SHRSPaS003305	13.743
SHRSPaS001552	13.994
SHRSPaS004994	14.025
SHRSPaS003599	14.239
SHRSPaS003086	14.474
SHRSPaS006435	14.68
SHRSPaS003810	15.109
SHRSPaS003496	15.362
SHRSPaS002286	16.009
SHRSPaS003528	16.178
SHRSPaS001530	16.293
SHRSPaS002014	16.946
SHRSPaS003513	16.959
SHRSPaS003206	17.12
SHRSPaS003090	17.361
SHRSPaS002731	17.361
SHRSPaS001831	17.825
SHRSPaS001883	17.895
SHRSPaS002026	18.202
SHRSPaS002140	18.202
SHRSPaS001464	18.265
SHRSPaS001404	18.436
SHRSPaS004250	19.154
SHRSPaS004471	19.467
SHRSPaS002018	19.777
SHRSPaS001343	20.195
SHRSPaS003209	20.195
SHRSPaS002961	20.242
SHRSPaS005301	20.242
SHRSPaS004677	20.43
SHRSPaS001669	20.444
SHRSPaS004053	20.788
SHRSPaS005014	20.788
SHRSPaS004298	20.8
SHRSPaS004502	20.845
SHRSPaS004944	21.024
SHRSPaS004099	21.264
SHRSPaS004772	21.264
SHRSPaS003366	21.641
CYP890	21.732
SHRSPaS006206	21.773
SHRSPaS003501	22.025
SHRSPaS004303	22.36
SHRSPaS002021	22.534
SHRSPaS001199	22.712
CYP967	22.764
SHRSPaS001408	22.862
SHRSPaS004868	22.99
SHRSPaS002009	23.043
SHRSPaS002890	23.065
SHRSPaS001306	23.151

Continued next page

Supplemental Table 3. Continued.

SHRSPaS004175	81.696
SHRSPaS002298	82.477
SHRSPaS001879	82.477
PGI1037	82.837
SHRSPaS002535	84.028 C
SHRSPaS001196	84.155
SHRSPaS001842	84.331
SHRSPaS001214	84.751
SHRSPaS004934	85.315
VTE3_689	85.621
SHRSPaS004517	85.652
VTE3_769	86.183
SHRSPaS003315	86.869
SHRSPaS002266	88.035
SHRSPaS003269	89.143 CP, T
SHRSPaS001164	89.97
SHRSPaS001330	91.25
SHRSPaS001955	93.466
AVD104	93.897
SHRSPaS006607	94.461
SHRSPaS002221	94.967
SHRSPaS003054	95.261 T
SHRSPaS002061	97.05
SHRSPaS004896	98.516
SHRSPaS002904	98.832
SHRSPaS002076	99.926
SHRSPaS003187	99.953
SHRSPaS001229	100.777
SHRSPaS001526	101.82
SHRSPaS002118	101.82
SHRSPaS001587	102.876
SHRSPaS001873	102.887
SHRSPaS002800	103.034
SHRSPaS003802	103.911
SHRSPaS003920	104.432
PDX2_549	106.045
group 2	
SHRSPaS002738	0
SHRSPaS004650	1.641
SHRSPaS003836	1.688
SHRSPaS005917	2.044
SHRSPaS003789	2.593
SHRSPaS002006	2.943
SHRSPaS004304	2.943
SHRSPaS002724	4.251
SHRSPaS002767	5.282
SHRSPaS004786	5.743
SHRSPaS002290	5.809
SHRSPaS002698	6.055
SHRSPaS001662	6.638
AVT226	6.893
SHRSPaS002866	7.376
SHRSPaS001182	7.953
SHRSPaS004847	8.917
SHRSPaS005361	9.159
SHRSPaS001382	9.816
SHRSPaS006449	11.046

Continued next page

Supplemental Table 3. Continued.

SHRSPaS005940	23.23
SHRSPaS002450	23.331
SHRSPaS002909	23.713
CYP1085	23.849
SHRSPaS006613	24.445
SHRSPaS006065	24.585
AVT191	24.716
SHRSPaS002171	25.029
SHRSPaS002428	25.029
SHRSPaS001615	25.03
SHRSPa262	25.487
SHRSPaS001822	25.571
SHRSPaS004881	25.85
SHRSPaS006379	25.999
SHRSPaS004176	26.256
SHRSPaS002685	26.314
SHRSPaS001686	26.339
SHRSPaS001787	26.467
SHRSPaS002269	26.504
AVD001	26.596
SHRSPaS002196	26.671
SHRSPaS006718	26.698
SHRSPaS002374	26.723
SHRSPaS002801	27.087
SHRSPaS002787	27.087
SHRSPaS002203	27.509
SHRSPaS001976	27.606
SHRSPaS003472	28.419
SHRSPaS002183	28.704
SHRSPaS001998	28.909
SHRSPaS001078	29.182
SHRSPaS001037	29.276
SHRSPaS003743	29.493
SHRSPaS003213	30.268
SHRSPaS002762	30.349
SHRSPaS004715	30.521
SHRSPaS002561	30.521
SHRSPaS005503	30.929
SHRSPaS001768	30.995
SHRSPaS001593	31.305
SHRSPaS006845	31.542
SHRSPaS001184	31.853
SHRSPaS004000	31.894
SHRSPaS002134	31.894
SHRSPaS001029	31.913
SHRSPaS002659	31.945
SHRSPaS005876	32.289
SHRSPaS003751	32.412
SHRSPaS003433	32.822
SHRSPaS001661	32.908
SHRSPaS003294	33.231
SHRSPaS001769	33.478
SHRSPaS003627	33.583
SHRSPaS003776	33.601
AVD006	33.666
SHRSPaS004324	34.073
SHRSPaS006019	34.319
SHRSPaS006959	34.35
SHRSPaS002611	34.624

Continued next page

Supplemental Table 3. Continued.

SHRSPaS004245	34.624
SHRSPaS002934	34.757
SHRSPaS004026	35.673
SHRSPaS003007	36.306
SHRSPaS003936	36.414
SHRSPaS006150	37.555
SHRSPaS002365	37.688
SHRSPaS002294	38.139
SHRSPaS003894	38.263
SHRSPaS003934	38.263
SHRSPaS004498	38.641
SHRSPaS004931	38.934
SHRSPaS005441	39.106
SHRSPaS004229	39.106
SHRSPaS002858	39.765 A
VTE1_746	40.708
SHRSPaS003610	41.156
SHRSPaS002117	41.16
SHRSPaS004899	41.16
SHRSPaS006736	41.207
SHRSPaS002401	41.263
SHRSPaS004714	41.32
SHRSPaS004780	41.505
SHRSPaS004538	41.987
SHRSPaS003114	42.671
SHRSPaS002342	42.766
SHRSPaS004962	42.846
SHRSPaS004844	42.916
SHRSPaS002128	42.929
VTE1_957	43.284
SHRSPaS005178	43.763
VTE1_573	44.23
SHRSPaS001854	44.449
SHRSPaS001231	44.799
SHRSPaS001082	44.799
SHRSPaS004306	44.839
SHRSPaS004386	45.052
atrans_SNP1124	45.685
SHRSPaS005311	45.828
SHRSPaS002310	45.828
atrans_SNP1493	45.955
atrans_SNP1155	46.47
SHRSPaS001137	46.962
atrans_SNP1410	47.013
SHRSPaS003933	47.457
SHRSPaS004302	48.301
SHRSPaS001939	48.704
SHRSPaS001635	48.947 A
atrans_SNP1484	49.205 T
VTE1_687	50.245
VTE1_604	50.473
SHRSPaS004702	50.683 A
SHRSPaS003723	51.783
SHRSPaS003712	52.034
SHRSPaS004240	52.485
SHRSPaS004557	54.085
SHRSPaS001509	54.156 A
SHRSPaS005198	54.219
AVD013	54.651

Continued next page

Supplemental Table 3. Continued.

SHRSPaS005346	55.582
AUCR418	56.929
SHRSPaS001523	57.267
SHRSPaS001418	58.203
SHRSPaS002539	58.75
SHRSPaS006032	59.165
SHRSPaS004951	60.469
SHRSPaS003425	60.742
SHRSPaS003554	61.27
SHRSPaS004422	61.483
group 3	
SHRSPaS003453	0 A
SHRSPaS001761	0.82
SHRSPaS006017	2.938
HPT1_551	4.297 A
HPT1_514	5.196 A
SHRSPaS002447	7.242 A
SHRSPaS002426	**7.968 A**
SHRSPaS001620	**7.968 A**
SHRSPaS003259	8.562 A
SHRSPaS003589	8.847 A
SHRSPaS001705	8.847 A
HPT1_196	10.078 A
SHRSPaS001282	**12.359 A**
SHRSPaS006564	**12.736 A**
SHRSPaS004209	**12.998 A**
SHRSPaS003314	**13.349 A**
SHRSPaS002204	**14.43 A**
SHRSPaS002658	**14.63 A**
SHRSPaS004388	**15.363 A**
SHRSPaS005529	**15.648 A**
SHRSPaS003787	**16.304 A**
SHRSPaS004634	**16.304 A**
SHRSPaS001323	**16.785 A**
SHRSPaS001365	**17.332 A**
SHRSPaS004338	**18.601 A**
SHRSPaS005013	19.334
SHRSPaS001566	20.682 A
SHRSPaS006054	24.144 B
SHRSPaS003561	25.5 A
SHRSPaS004954	26.428
SHRSPaS003645	27.638 A
SHRSPaS002817	28.082
SHRSPaS003120	29.223
SHRSPaS006371	29.223
SHRSPaS001781	31.467
SHRSPaS004933	33.176
SHRSPaS003760	35.949
SHRSPaS003017	37.112
SHRSPaS005275	37.112
SHRSPaS004350	38.714
SHRSPaS005919	40.402
SHRSPaS003739	42.778
SHRSPaS005977	42.778
SHRSPaS004018	43.234
SHRSPaS006088	43.779
SHRSPaS002393	43.793

Continued next page

Supplemental Table 3. Continued.

SHRSPaS004777	43.793
SHRSPaS002163	44.44
AVT106	45.573
SHRSPaS005467	45.724
SHRSPaS004760	45.724
SHRSPaS006671	47.806
SHRSPaS002618	51.357
SHRSPaS001175	51.357
SHRSPaS002606	51.384
SHRSPaS004178	51.384
SHRSPaS003429	51.438
SHRSPaS001721	51.438
SHRSPaS002109	52.417
SHRSPaS001543	53.001
SHRSPaS001413	53.351
SHRSPaS004864	55.314
SHRSPaS001923	57.692
SHRSPaS003172	57.692
SHRSPaS003823	58.283
SHRSPaS002322	58.956
AVT021	60.065
SHRSPaS001985	64.309
SHRSPaS002275	66.882
SHRSPaS002504	68.988
SHRSPaS004113	68.988
SHRSPa245	69.281
SHRSPaS002459	69.755
SHRSPaS005557	69.755
SHRSPaS003962	71.614
SHRSPaS002015	74.346
SHRSPaS005397	75.484
SHRSPaS004914	76.205
SHRSPaS001060	77.405
SHRSPaS003658	78.24
SHRSPaS006658	78.799
SHRSPaS003074	79.865
SHRSPaS004578	80.978
SHRSPaS001220	81.536
SHRSPaS003983	81.681
SHRSPaS002237	83.475
SHRSPaS005766	84.518
SHRSPaS002008	84.829
SHRSPaS003930	85.979
SHRSPaS001045	87.354
SHRSPaS001146	87.997
SHRSPaS001425	87.997
SHRSPaS001067	88.099
SHRSPaS001084	89.34
SHRSPaS001579	90.134
SHRSPaS001074	90.363
SHRSPaS002772	91.171
SHRSPaS004187	91.398
SHRSPaS004456	91.398
SHRSPaS002283	91.553
SHRSPaS001505	91.639
SHRSPaS003857	91.76
SHRSPaS006247	91.76
SHRSPaS004034	92.393
SHRSPaS002057	92.434

Continued next page

Supplemental Table 3. Continued.

SHRSPaS002825	92.984
SHRSPaS001043	93.063
SHRSPaS002042	94.008
SHRSPaS001688	94.008
SHRSPaS003869	94.203 C
SHRSPaS005910	94.666
SHRSPaS003959	94.996
SHRSPaS003708	94.996
AVT020gat	95.543
SHRSPaS004268	95.871
SHRSPaS002912	96.08
SHRSPaS001297	96.08
SHRSPaS001349	96.114
SHRSPaS003557	96.609
SHRSPaS005922	96.844
SHRSPaS003149	97.148
SHRSPaS005725	97.155
AVD107	97.867
SHRSPaS003161	98.297 B
SHRSPaS001570	98.297 B
SHRSPaS003012	98.538 C
SHRSPaS002578	99.379
SHRSPaS004446	99.379
SHRSPaS001881	99.906
SHRSPaS003848	100.455
SHRSPaS004967	100.455
SHRSPaS002153	100.782
SHRSPaS004129	102.052
SHRSPaS002786	102.14
SHRSPaS001036	102.494
SHRSPaS004561	102.995
SHRSPaS005938	103.371
SHRSPaS004802	103.959
SHRSPaS002129	104.034
SHRSPaS004329	104.575
SHRSPaS004025	104.764
SHRSPaS001908	105.067
SHRSPaS001734	105.659
SHRSPaS003405	105.849
SHRSPaS001750	106.226
SHRSPaS001569	106.226
SHRSPaS004323	106.98
SHRSPaS006755	107.221
SHRSPaS002047	107.833
SHRSPaS003165	108.257
AVD026	108.567
SHRSPaS003582	108.602
SHRSPaS004906	109.305
SHRSPaS004540	109.725
SHRSPaS005002	109.725
SHRSPaS003623	110.087
SHRSPaS002610	110.49
caff3_SNP745	110.505
SHRSPaS003705	111.025
SHRSPaS003191	111.782
SHRSPaS001121	111.782
SHRSPaS001298	111.813
SHRSPaS004145	111.991
SHRSPaS001695	112.477

Continued next page

Supplemental Table 3. Continued.

SHRSPaS003316	112.658
SHRSPaS004215	112.867
SHRSPaS004550	112.905
SHRSPaS003378	114.667
caff3_SNP1012	115.113
caff3_SNP850	116.291
caff3_SNP1099	118.125
ZDS_SNP_228	119.741
caff3_SNP814	121.125
group 4	
SHRSPaS004274	0
SHRSPaS003489	3.71
SHRSPaS002201	4.519
SHRSPaS003694	5.476
SHRSPaS001086	5.505
SHRSPaS002947	5.505
SHRSPaS001428	6.431
SHRSPaS001224	6.431
SHRSPaS002527	6.487
SHRSPaS003560	7.928
SHRSPaS002713	9.719
SHRSPaS002073	10.118
SHRSPaS003412	10.492
SHRSPa249	12.654
SHRSPaS002293	13.388
SHRSPaS005507	15.622
SHRSPaS004673	15.622
SHRSPaS005574	17.487
SHRSPaS003761	17.487
SHRSPaS001966	18.916
SHRSPaS001856	20.868
SHRSPaS003225	23.349
SHRSPaS002296	24.762
SHRSPaS004699	27.68
SHRSPaS001416	28.68
AVD032	29.556
SHRSPaS005878	30.148
SHRSPaS004065	30.5
SHRSPaS004400	32.508
SHRSPaS005892	33.172
SHRSPaS003174	33.727
SHRSPaS004731	34.796
SHRSPaS002860	34.796
SHRSPaS002120	35.133
SHRSPaS003670	35.165
SHRSPaS003904	35.947
SHRSPaS003418	36.926
SHRSPaS001309	37.139
SHRSPaS004865	38.006
SHRSPaS002697	38.573
SHRSPaS003963	38.573
SHRSPaS001020	38.656
SHRSPaS002062	40.595
SHRSPaS002151	42.569
SHRSPa081	47.675 A
SHRSPaS003355	49.264
SHRSPaS003210	49.264

Continued next page

Supplemental Table 3. Continued.

SHRSPaS003035	49.799
SHRSPaS004283	50.889 A
SHRSPaS002045	51.427
SHRSPaS003270	51.427
SHRSPaS001599	53.104
SHRSPaS003728	53.104
SHRSPaS001918	55.033
SHRSPaS002821	55.033
SHRSPaS006157	58.152
SHRSPaS005918	59.503
SHRSPaS004363	60.623
SHRSPaS006484	60.623
SHRSPaS004297	60.846
SHRSPaS001187	60.846
SHRSPaS001940	62.417
SHRSPaS001152	63.042
SHRSPaS004807	64.759
SHRSPaS004574	66.427 A
SHRSPaS006340	66.904
SHRSPa099	67.989 A
SHRSPaS001391	68.806 A
SHRSPaS004149	68.806 A
SHRSPaS005584	70.569
SHRSPaS003025	70.718 A
SHRSPaS002156	70.718 A
SHRSPaS002503	72.624
SHRSPaS004510	74.513
SHRSPaS003806	74.513
SHRSPaS004779	76.59
SHRSPaS005080	76.59
group 5	
SHRSPaS004717	0
SHRSPaS003438	0
SHRSPaS001717	1.497
SHRSPaS001333	1.729
SHRSPaS004345	1.729
SHRSPaS002845	2.542
SHRSPaS004918	3.044
SHRSPaS004417	3.837
SHRSPaS001374	4.084
SHRSPaS002422	4.696
SHRSPaS006773	4.696
SHRSPaS004970	5.929
SHRSPaS005532	7.941
SHRSPaS002381	8.074
SHRSPaS003011	10.028
SHRSPaS004083	10.079
SHRSPaS003491	10.079
SHRSPaS002085	12.132
SHRSPaS005172	12.461
SHRSPaS002323	13.873
SHRSPaS003067	14.41
SHRSPaS001062	16.227
SHRSPaS002326	18.388
SHRSPaS003159	19.027
SHRSPaS002090	20.155
SHRSPaS003890	22.174

Continued next page

Supplemental Table 3. Continued.

SHRSPaS004354	23.46
SHRSPaS002409	24.309
SHRSPaS002124	24.309
SHRSPaS002253	28.261
SHRSPaS003370	30.437
SHRSPa285	30.495
SHRSPaS002479	32.822
SHRSPaS001305	33.132
SHRSPaS003250	33.132
SHRSPaS002167	33.944
AUCR053	35.318
SHRSPaS006160	35.832
SHRSPaS002639	36.965
SHRSPaS002219	36.965
SHRSPaS001192	37.198
SHRSPaS004357	37.198
SHRSPaS003290	37.962
SHRSPaS002399	37.962
SHRSPaS002862	38.557
SHRSPaS002756	39.973
SHRSPaS001387	40.935
SHRSPaS003744	41.2
SHRSPaS003177	41.2
SHRSPaS004646	42.222
SHRSPaS001843	42.222
SHRSPaS001847	43.704
SHRSPaS003699	44.482
SHRSPaS001168	44.892
SHRSPaS004331	45.536
SHRSPaS004636	46.567
SHRSPaS003340	46.567
SHRSPaS001068	46.994
SHRSPaS003950	47.079
SQS913	47.547
SHRSPaS001953	47.574
SQS843	47.689
SQS769	47.689
SHRSPaS003345	47.886
SHRSPaS003134	47.886
SHRSPaS002676	48.351
SHRSPaS002297	48.351
SHRSPaS001405	49.074
SHRSPaS005955	49.712
SHRSPa107	50.306
SHRSPaS003308	51.546
SHRSPaS001104	51.922
SHRSPaS002300	52.798
SHRSPaS001993	53.855
SHRSPaS001046	54.152
SHRSPaS003944	54.152
SHRSPaS003738	55.035
SHRSPaS001246	55.99
SHRSPaS004482	57.458
SHRSPaS003457	57.458
SHRSPaS002060	58
SHRSPaS002532	58.814
SHRSPaS002792	59.919
SHRSPaS002430	60.217
SHRSPaS002384	62.505

Continued next page

Supplemental Table 3. Continued.

SHRSPaS003998	63.551
AUCR008b	64.489
SHRSPaS003800	64.817
SHRSPaS002350	65.429
SHRSPaS003637	66.141
SHRSPaS003184	66.141
SHRSPaS002416	66.886
SHRSPaS003803	67.856
AUCR181	68.798 B
SHRSPaS003585	68.814
SHRSPaS004203	69.545
SHRSPaS003155	69.6
SHRSPaS001818	71.195
SHRSPaS002317	73.386
SHRSPaS004982	74.913
SHRSPaS006026	77.238
SHRSPaS002520	77.238
SHRSPaS002837	79.158
SHRSPaS001935	79.307
SHRSPaS005098	79.307
SHRSPaS001372	79.552 B
SHRSPaS001711	79.961
SHRSPaS001743	79.995
SHRSPaS003297	80.872
SHRSPaS006171	81.644
SHRSPaS001195	81.644
SHRSPaS001950	81.685
SHRSPaS002905	82.637
SHRSPaS003239	82.796
AVD082	83.12
SHRSPaS003595	83.44
SHRSPaS001779	83.561
SHRSPaS004622	84.326
SHRSPaS001654	84.624
SHRSPaS003881	85.174
SHRSPaS003415	85.174
SHRSPaS001468	85.277
SHRSPaS001671	85.662
SHRSPaS005580	86.313
SHRSPaS002714	86.313
SHRSPaS001783	86.831
SHRSPaS001267	87.253
SHRSPaS002631	87.314
SHRSPaS002235	87.937
SHRSPaS005804	87.937
SHRSPaS004575	87.942
SHRSPaS001350	88.51
CUT1_SNP1306	89.121
SHRSPaS001099	89.578
SHRSPaS001478	90.057
SHRSPaS006151	90.292
SHRSPaS002783	90.798
SHRSPaS002894	90.839
SHRSPaS001683	91.68
SHRSPaS001287	91.805
SHRSPaS003098	92.094
SHRSPaS002282	94.01
SHRSPaS003136	94.101
SHRSPaS005970	94.101

Continued next page

Supplemental Table 3. Continued.

SHRSPaS001065	94.201
SHRSPaS001443	94.479
SHRSPaS002161	94.479
SHRSPaS001283	95.518
SHRSPaS002645	96.052
SHRSPaS003371	96.052
SHRSPaS001934	97.576
SHRSPaS004351	97.599
SHRSPaS001218	98.013
SHRSPaS002287	98.911
SHRSPaS001575	99.526
SHRSPaS001336	99.526
SHRSPaS003027	100.976
CUT1_SNP1449	101.69
SHRSPaS004588	101.755
VTC2_296	105.432
group 6	
SHRSPaS002138	0
SHRSPaS002308	2.036
SHRSPaS002179	2.057
SHRSPaS002223	3.124
SHRSPaS001656	3.124
SHRSPaS004781	3.413 C
PDS1_881	7.053
PDS1_722	7.269
PDS1_544	7.967
SHRSPaS001995	10.87
SHRSPaS003142	12.145
SHRSPaS001219	12.955
SHRSPaS001011	14.029
SHRSPaS002564	14.586
SHRSPaS004541	15.257
SHRSPaS004235	15.332
SHRSPaS001491	16.133
SHRSPaS006573	16.133
SHRSPaS003960	16.273
SHRSPaS005447	16.671
SHRSPaS003681	17.077
SHRSPaS002473	17.077
SHRSPaS003594	17.2
SHRSPaS001380	18.04
SHRSPaS004730	19.216
SHRSPa043	21.618
SHRSPaS002424	23.714
SHRSPaS006788	24.824
SHRSPaS001335	24.868
SHRSPaS004488	26.295
SHRSPaS004679	26.831
SHRSPaS001186	26.944
SHRSPaS001355	28.248
SHRSPaS003837	31.527
SHRSPaS003772	31.717
SHRSPaS002505	32.661
SHRSPaS005027	33.196
AUCR050	34.272 C
SHRSPaS002209	36.754
SHRSPaS003811	40.129 F

Continued next page

Supplemental Table 3. Continued.

SHRSPaS001538	43.101 C
SHRSPaS003598	44
SHRSPaS004251	44
SHRSPaS001664	44.722
SHRSPaS001503	45.129
SHRSPaS001454	46.13 C
SHRSPaS004712	46.891
SHRSPaS003733	47.914
SHRSPaS004401	47.914
SHRSPaS001162	48.38 C
SHRSPaS001501	49.827
SHRSPaS003639	49.827
SHRSPaS003569	50.771
SHRSPaS001329	50.771
SHRSPaS004252	51.504
SHRSPaS003057	52.282
SHRSPaS001536	53.217 C
SHRSPaS002728	53.586
SHRSPaS001541	54.131
SHRSPaS004713	54.717 C
SHRSPaS006785	55.63
SHRSPaS006696	56.019
SHRSPaS002669	57.187
SHRSPaS002346	57.548 C
SHRSPaS004674	57.642
SHRSPaS002735	57.657
SHRSPaS005679	58.06
SHRSPaS002031	58.214
SHRSPaS001544	58.819
SHRSPaS003653	59.557
SHRSPaS004439	59.557
AVT517	60.034
SHRSPaS003264	60.159
SHRSPaS002852	60.758 C
SHRSPaS004639	61.419
LUT5_SNP_1351	63.284
SHRSPaS005466	64.024
SHRSPaS001710	66.054
SHRSPaS002169	66.054
SHRSPaS001516	66.303
SHRSPaS001022	67.002
SHRSPaS004093	67.613
SHRSPaS002543	68.008
SHRSPaS003514	68.611
SHRSPaS003812	71.592
SHRSPaS003990	71.716
SHRSPaS002744	71.959
VTE4_1035	73.171
VTE4_1257	73.181
SHRSPaS006514	74.199
SHRSPaS001676	76.112
VTE4_1068	76.567
group 7	
SHRSPaS002765	0
SHRSPaS003542	0
SHRSPaS002055	0
SHRSPaS002341	1.43

Continued next page

Supplemental Table 3. Continued.

SHRSPaS004642	5.777
SHRSPaS001288	7.818
SHRSPaS006087	9.835
SHRSPaS001143	9.835
SHRSPaS002712	13.951
SHRSPaS005692	13.951
SHRSPaS001254	15.95
SHRSPaS002789	20.106
SHRSPaS003795	20.106
SHRSPaS005590	28.967
SHRSPaS003635	28.967
SHRSPaS002908	31.364
SHRSPaS001911	34.608
SHRSPaS004036	38.092
SHRSPaS001128	38.092
SHRSPaS003660	40.049
AVT005b	41.438
SHRSPaS003292	42.302
SHRSPaS006098	42.302
SHRSPaS002740	42.95
SHRSPaS002493	43.577
SHRSPaS004171	43.577
SHRSPaS005049	43.877
SHRSPaS004396	44.014
SHRSPaS003527	44.014
SHRSPaS005034	44.338 CP
SHRSPaS004977	45.476
SHRSPaS001017	46.308
SHRSPaS004745	46.374
SHRSPaS003046	47.916
SHRSPaS004086	48.296
SHRSPaS005391	49.181
SHRSPaS001777	49.234
SHRSPaS001982	49.234
SHRSPaS005314	50.066
SHRSPaS002417	51.661
SHRSPaS004316	51.661
SHRSPaS001080	51.792
SHRSPaS001559	51.829
SHRSPaS003656	55.462
SHRSPaS002727	55.753
SHRSPaS003828	55.993
SHRSPaS001585	55.993
SHRSPaS003912	56.342
AVMIX03	57.273
SHRSPaS003464	57.902 A
SHRSPaS001974	58.197
SHRSPaS006202	58.641
SHRSPaS003167	58.916
SHRSPaS006351	59.97
SHRSPaS001957	60.769
SHRSPaS003820	60.924
SHRSPaS001583	61.076
SHRSPaS004413	61.076
SHRSPaS004740	61.383
SHRSPaS003538	63.158
SHRSPaS003730	63.158
SHRSPaS003843	65.118
SHRSPaS004859	66.458

Continued next page

Supplemental Table 3. Continued.

SHRSPaS004243	66.458
SHRSPaS001165	66.64
SHRSPaS001155	67.112
SHRSPaS003943	68.947
SHRSPaS004825	70.072
SHRSPaS004855	70.072
SHRSPaS002421	71.113
SHRSPaS002768	71.113
SHRSPaS001397	71.324
SHRSPaS005004	73.063
SHRSPaS004941	73.206
SHRSPaS001685	74.199
SHRSPaS004326	75.207
SHRSPaS001273	75.207
SHRSPaS003087	75.407
SHRSPaS003537	76.283
SHRSPaS004064	76.283
SHRSPaS002211	76.323
SHRSPaS001334	77.288
SHRSPaS005939	77.71
SHRSPaS002082	78.718
SHRSPaS001674	79.237
SHRSPaS001178	79.383
SHRSPaS002529	80.322
SHRSPaS001549	80.322
SHRSPaS002812	81.914
SHRSPaS001936	82.25
SHRSPaS003140	84.516
SHRSPaS001561	87.923
SHRSPaS003426	92.232
SHRSPaS003665	93.013
SHRSPaS002041	96.47
SHRSPaS006248	100.563
SHRSPaS001417	102.78
group 8	
SHRSPaS004769	-0.213
SHRSPaS002405	0
SHRSPaS002440	0
SHRSPaS001271	1.8
SHRSPaS001321	1.8
SHRSPaS001447	2.706
SHRSPaS001008	3.328
SHRSPaS005271	4.385
SHRSPaS002770	4.741
SHRSPaS004518	4.741
SHRSPaS002776	5.367
SHRSPaS003462	5.678
SHRSPaS002967	6.711
SHRSPaS001740	7.579
SHRSPaS001886	9.702
AUCR089	12.983
AVD120	14.763
SHRSPaS001647	15.543
SHRSPaS001495	17.419
SHRSPaS002064	17.432
SHRSPaS002292	17.436
SHRSPaS003821	17.958

Continued next page

Supplemental Table 3. Continued.

SHRSPaS002313	18.26
SHRSPaS003558	18.412
SHRSPaS004398	19.77
AVT038	20.061
SHRSPaS004095	20.379
SHRSPaS003107	21.122
SHRSPaS004942	23.729
SHRSPaS004328	24.552
SHRSPaS006517	24.818
SHRSPaS001081	26.287
SHRSPaS006531	27.54
B1_SNP834	28.094
SHRSPaS001308	29.08
SHRSPaS002782	29.727
SHRSPaS001251	29.771
B1_SNP881	30.736
B1_SNP1028	32.272
B1_SNP962	36.536
MEP937	39.587
SHRSPaS001259	42.546
SHRSPaS004455	42.557
SHRSPaS003382	43.082
SHRSPaS004754	43.098
SHRSPaS002850	43.098
SHRSPaS001490	43.958
SHRSPaS002688	43.958
SHRSPaS003939	44.416
SHRSPaS002155	44.416
SHRSPaS001054	44.428
SHRSPaS002694	45.138
SHRSPaS003782	46.3
SHRSPaS002178	46.998
MEP984	47.706
SHRSPaS001586	48.833
SHRSPaS003420	49.552
SHRSPaS002413	49.683
SHRSPaS004543	50.838
SHRSPaS003832	52.642
SHRSPaS003199	53.02
SHRSPaS006482	53.441
SHRSPaS001571	53.859
SHRSPaS002448	54.435
SHRSPaS001741	56.094
SHRSPaS006701	56.834
SHRSPaS004741	57.098
SHRSPaS001522	57.935
SHRSPaS001133	58.62
SHRSPaS001344	59.001
SHRSPaS002158	59.554
SHRSPaS004571	60.417
SHRSPaS003375	60.885
SHRSPaS002079	61.085
SHRSPaS001817	62.094
SHRSPaS006843	62.606
SHRSPaS003247	63.012
SHRSPaS001366	63.921
SHRSPaS003128	65.152
SHRSPaS001733	66.105
SHRSPaS002601	68.303

Continued next page

Supplemental Table 3. Continued.

SHRSPaS003882	71.02
SHRSPaS001693	73.188
SHRSPaS001474	76.122
SHRSPaS002657	81.443
SHRSPaS001279	82.43
SHRSPaS003838	84.438
SHRSPaS001860	85.722
SHRSPaS004512	85.761
SHRSPaS004750	86.3 A
SHRSPaS002195	88.125 A
SHRSPaS004929	88.655 A
SHRSPaS005218	89.329
SHRSPaS001053	89.871
SHRSPaS001139	89.871
SHRSPaS006403	90.057
SHRSPaS003666	91.135
SHRSPaS001672	92.098
SHRSPaS004539	92.928
SHRSPaS001021	92.986
SHRSPaS001095	92.986
SHRSPaS005652	96.073
group 9	
SHRSPaS001638	0
SHRSPa243	2.563
SHRSPaS002814	4.658
SHRSPaS005406	5.705
SHRSPaS003487	7.177
SHRSPaS001914	9.174
SHRSPaS003251	9.174
SHRSPaS001580	9.501
SHRSPaS004956	11.214
SHRSPaS001421	11.636
SHRSPaS003573	12.287
SHRSPaS004831	12.287
SHRSPaS003344	13.353
SHRSPaS005963	13.487
SHRSPaS001237	13.826
SHRSPaS004520	15.419
SHRSPaS002439	15.419
SHRSPaS002709	16.501
SHRSPaS005735	18.52
SHRSPaS002538	21.062
FPS1135	21.199
SHRSPaS003427	22.533
SHRSPaS006483	22.753
SHRSPaS001395	23.351
SHRSPaS001013	23.351
SHRSPaS002574	24.633
SHRSPaS001284	24.888
SHRSPaS001364	28.495
SHRSPaS002012	28.996
SHRSPaS005992	30.586
SHRSPaS002544	33.984
PDX1_775	34.29
PDX1_1001	34.316
PDX1_941	34.412
SHRSPaS003093	36.045

Continued next page

Supplemental Table 3. Continued.

SHRSPaS001684	36.902
SHRSPaS001778	36.902
SHRSPaS003511	37.341
SHRSPaS001077	38.351
SHRSPaS004535	38.957
SHRSPaS001472	39.564
SHRSPaS004613	40.161
SHRSPaS004817	40.166
SHRSPaS002973	41.749
SHRSPaS004150	42.521
SHRSPaS006073	43.23
SHRSPaS004409	43.821
SHRSPaS002741	43.975
SHRSPaS002884	46.137
SHRSPaS005554	46.137
SHRSPaS004195	47.827
SHRSPaS004155	48.717
SHRSPaS001359	49.813
SHRSPaS001531	50.341
SHRSPaS001101	51.049
SHRSPa055	51.331
SHRSPaS003785	52.199
SHRSPaS004926	52.367
SHRSPaS001369	52.927
SHRSPaS001090	54.8
SHRSPaS002926	54.8
SHRSPaS003526	56.59
SHRSPaS001628	56.735
SHRSPaS006374	58.118
SHRSPaS004657	58.653
SHRSPaS004867	58.916
SHRSPaS001598	60.118
SHRSPaS005746	60.78
SHRSPaS004071	60.78
AVD045	62.226
SHRSPaS005924	62.88
SHRSPaS001595	63.385
SHRSPaS001385	63.385
SHRSPaS002542	65.632
group 10	
SHRSPaS004911	0
SHRSPaS002777	0.664
SHRSPaS005151	0.773
SHRSPaS001785	2.409
SHRSPaS004226	3.195
SHRSPaS001191	4.397
SHRSPaS001463	4.891
SHRSPaS004821	7.541
SHRSPaS001692	**8.803 F**
SHRSPaS001876	**9.796 F**
SHRSPaS005289	**11.626 F**
SHRSPaS001228	**15.671 F**
SHRSPaS004991	**17.08 F**
SHRSPaS001648	**18.179 F**
SHRSPaS006707	**19.193 F**
SHRSPaS004231	**19.909 F**
SHRSPaS002720	**23.273 F**

Continued next page

Supplemental Table 3. Continued.

SHRSPaS002034	**24.112 F**
DXPS1_SNP1593	**25.756 F**
SHRSPaS002337	**25.91 F**
SHRSPaS002152	**26.808 F**
DXPS1_SNP1328	26.876
SHRSPaS002994	**30.261 F**
SHRSPaS003395	30.957
SHRSPaS001393	**31.674 F**
SHRSPaS003001	**32.854 F**
SHRSPaS003892	**33.914 F**
SHRSPaS001500	**35.058 F**
SHRSPaS002920	**35.434 F**
SHRSPaS001512	**36.688 F**
SHRSPaS004112	**36.71 F**
SHRSPaS002197	**37.499 F**
SHRSPaS001256	**37.532 F**
SHRSPaS001931	**38.485 F**
SHRSPaS003940	**40.615 F**
SHRSPaS003414	**42.421 F**
SHRSPaS002815	**44.139 F**
SHRSPaS004380	**44.68 F**
AVD010	**45.094 F**
SHRSPaS006391	**45.452 F**
SHRSPaS002938	**45.511 F**
SHRSPaS002466	**45.617 F**
SHRSPaS002742	**46.511 F**
SHRSPaS001577	**47.115 F**
SHRSPaS004654	**47.196 F**
SHRSPaS001390	**47.349 F**
SHRSPaS001445	**47.949 F**
SHRSPaS004170	**48.06 F**
SHRSPaS004995	**50.098 F**
SHRSPaS002997	**50.098 F**
SHRSPaS002903	**51.317 F**
SHRSPaS004214	**53.308 F**
SHRSPaS004955	**53.308 F**
SHRSPaS001432	**55.544 F**
SHRSPaS002875	**59.658 F**
SHRSPaS006283	63.9
SHRSPaS002351	65.464
SHRSPaS003095	67.268
SHRSPaS004747	68.473
group 11	
SHRSPa203	-15.593
SHRSPaS003442	0
AVD022	3.311
SHRSPaS003135	4.039
SHRSPaS002683	6.661
AVT448	6.884
SHRSPaS003783	8.863
SHRSPaS002750	9.273
SHRSPaS001233	10.35
SHRSPaS004529	10.421
SHRSPaS002839	11.257
SHRSPaS004285	12.698
SHRSPaS004920	13.306
SHRSPaS005726	14.805

Continued next page

Supplemental Table 3. Continued.

SHRSPaS003476	15.75
SHRSPaS001709	15.75
SHRSPaS001235	16.485
SHRSPaS001977	18.371
AUCR202	19.875
SHRSPaS006118	20.982
SHRSPaS001494	21.015
SHRSPaS004272	21.992 CP
SHRSPaS004238	23.552
SHRSPaS002263	24.169
SHRSPaS004983	24.275
AVD116	25.043
SHRSPaS004232	25.151 CP
VTC1_1121	26.8
VTC1_1084	27.267
VTC1_1187	28.072
SHRSPaS001665	29.627
SHRSPaS001649	29.65
SHRSPaS002491	29.789
SHRSPaS003895	30.222
SHRSPaS002621	30.634
SHRSPaS001260	30.855
SHRSPaS006777	31.904
SHRSPaS003138	32.112
SHRSPaS006702	32.209
SHRSPaS001151	32.761
SHRSPaS004039	32.761
SHRSPaS002602	33.055 A
M1022	34.256
SHRSPaS002545	34.413 A
SHRSPaS003786	34.81
SHRSPaS001352	34.984 A
SHRSPaS003977	37.506
SHRSPaS004049	37.609
SHRSPaS001989	38.343
SHRSPaS002813	38.474
SHRSPaS003082	39.352
SHRSPaS003374	40.396 A
SHRSPaS001213	41.746
SHRSPaS005008	42.21
SHRSPaS002803	42.863
SHRSPaS002011	43.178 A
SHRSPaS004427	44.109 A
SHRSPaS002807	45.033
SHRSPaS001789	46.037
SHRSPaS002403	46.57
SHRSPaS001429	47.204
SHRSPaS001122	47.655
SHRSPaS001120	49.289
SHRSPaS002895	49.913
SHRSPaS001234	54.212
SHRSPaS002438	54.212
SHRSPaS003304	54.86
SHRSPaS001317	55.615
SHRSPaS002265	55.849
SHRSPaS002328	56.457
SHRSPaS002588	57.347
SHRSPaS002038	57.903
SHRSPaS003497	57.913

Continued next page

Supplemental Table 3. Continued.

SHRSPaS002609	58.345
SHRSPaS001388	58.538
SHRSPaS003428	58.719
AVT001	59.309
SHRSPaS004508	59.726
SHRSPaS004295	60.143
SHRSPaS004625	60.53
SHRSPaS003928	61.52
SHRSPaS004177	61.856
SHRSPaS003479	62.278
SHRSPaS003327	62.278
SHRSPaS003317	63.21
SHRSPaS001802	63.21
SHRSPaS002719	63.668
SHRSPaS001650	64.337
SHRSPaS001745	64.852
SHRSPaS001270	65.225 A
PSY_SNP629or945	67.225
SHRSPaS003110	67.335
SHRSPaS001623	69.225
SHRSPaS002303	70.506
SHRSPaS003888	71.047
SHRSPaS001863	71.71
SHRSPaS001328	72.389
SHRSPaS003180	72.64
SHRSPaS001815	73.147
PSY_SNP370or686	73.956
SHRSPaS001643	75.612
SHRSPaS006056	78.049
SHRSPaS003207	80.349

group 12

SHRSPaS003393	0
SHRSPaS003248	2.081
AVD117	2.89
SHRSPaS002662	4.505
SHRSPaS003402	4.505
SHRSPaS003265	6.588
SHRSPaS001356	8.656 B
SHRSPaS001322	10.728 B
SHRSPaS005017	12.781 B
SHRSPaS003368	14.855 B
SHRSPaS002902	14.855 B
AVT386	16.374 B
SHRSPaS003965	17.445
SHRSPaS003179	19.447
SHRSPaS002003	19.447
SHRSPaS001513	21.643 H
SHRSPaS001792	24.593
SHRSPaS006852	25.916
SHRSPaS005416	25.966
SHRSPaS002243	26.645
SHRSPaS003434	27.133
SHRSPaS001655	27.961
SHRSPaS004584	28.702
SHRSPaS002624	29.09
SHRSPaS005587	29.971
SHRSPaS003320	30.136

Continued next page

Supplemental Table 3. Continued.

SHRSPaS002331	30.94
AVD015	32.143
SHRSPaS002307	33.669
SHRSPaS001125	35.166
SHRSPaS004126	36.183
SHRSPaS002194	37.07
SHRSPaS001861	38.751
SHRSPaS002010	38.896
SHRSPaS001170	38.941
SHRSPaS005010	38.956
SHRSPaS001946	39.443
SHRSPaS001754	39.858
SHRSPaS004103	39.924
SHRSPaS002339	40.529
SHRSPaS002145	41.25
AVD044	41.729
SHRSPaS001706	41.848
SHRSPaS001941	42.528
SHRSPaS001455	42.954
AUCR017	43.91
SHRSPaS003189	45.218
SHRSPaS003659	46.144
SHRSPaS003946	46.473
SHRSPaS002231	48.098
SHRSPaS002995	50.081
SHRSPaS001744	51.89
SHRSPaS006854	53.504
SHRSPaS001194	55.852 A
SHRSPaS002854	66.236
SHRSPaS003716	68.354 T